OIKOS 102: 663–671, 2003

Environmental noise and population dynamics of the ciliated protozoa *Tetrahymena thermophila* in aquatic microcosms

Jouni Laakso, Katja Löytynoja and Veijo Kaitala

Laakso, J., Löytynoja, K. and Kaitala, V. 2003. Environmental noise and population dynamics of the ciliated protozoa *Tetrahymena thermophila* in aquatic microcosms. – Oikos 102: 663–671.

Population theory predicts that the reddened environmental noise, especially in combination with high population growth rate, reddens population dynamics, increases population variability and strengthens environment–population correlation. We tested these predictions with axenic populations of ciliated protozoa *Tetrahymena thermophila*. Populations with low and high growth rate were cultured in a stable environment, and in environments with sublethal temperature fluctuations that had blue, white and red spectra (i.e. negatively autocorrelated, uncorrelated, or positively autocorrelated, respectively). Population size and biomass of individuals were determined at 3-h intervals for 18 days.

Dynamics of all populations were reddened, suggesting that internal mechanisms can redden the population spectra. However, population dynamics were reddest, variability highest, and environment–population correlation strongest in the red environment as predicted. Contrary to theoretical predictions and previous empirical findings, population growth rate (r_{max} being equal to 0.05 and 0.3 h^{-1}) had no effect on population dynamics.

Mean cell size and variability of cell size were affected by the presence and type of environmental noise suggesting that the physiological consequences of variability depend on colour. Environmental variability decreased mean population size and biomass and the decrease was strongest in rapidly fluctuating blue and white environments. The latter finding implies that rapid fluctuations are physiologically stressful, an effect that is not accounted for in the basic population models.

J. Laakso, K. Löytonoja and V. Kaitala, Dept of Biological and Environmental Science, Univ. of Jyväskylä, PO Box 35, FIN-40351 Jyväskylä, Finland (jotla@cc.jyu.fi).

Population fluctuations result from environmental variability (i.e. 'noise'), from the intrinsic properties of populations, and from the interaction between the two (May 1973, Steele 1985, Pimm 1991, Sugihara 1994, 1995, 1996, Leirs et al. 1997, Kaitala et al. 1997a, b, Mysterud et al. 2000, Ranta et al. 2000, Benton et al. 2001, Kaitala and Ranta 2001, Laakso et al. 2001). The qualitative properties of environmental noise that may determine the impact on populations include noise distribution and noise spectrum. The spectra of environmental noise and population time series are often described as spectral colours in analogy to the wavelength of light (Halley 1996). Blue variations are negatively autocorrelated with more power (i.e. variability) in the high frequencies of the spectra, white variations are uncorrelated with even power, and red variations are positively autocorrelated with high power in low frequencies. Note that these terms should be considered as relative to the length of times series. In nature, both environmental and population time series are commonly reddened, i.e. dominated by slow fluctuations, and have increasing variability through time (Steele 1985, Lawton 1988, Pimm and Redfearn 1988, Halley 1996, Miramontes and Rohani 1998, Inchausti and Halley 2001).

Basic population models predict that the population size 'tracks' environmental fluctuations best when the environmental changes are slow (reddened), and when

Accepted 10 March 2003

ISSN 0030-1299

population growth rate is high. Consequently, the colour of the population dynamics resembles that of the environment, population variability is high, and correlation between environment and population abundance is strong (May 1973, Roughgarden 1975, Steele 1985, Lawton 1988, Pimm and Redfearn 1988, Pimm 1991, Sugihara 1995, Kaitala et al. 1997a, b). In stable environments, high growth rate populations without overcompensating density dependence should be less variable than low growth rate populations because a population with high growth rate is thought to be more tightly regulated around its equilibrium than a low growth rate population (May 1973, but see Luckinbill and Fenton 1978, Petchey 2000 for contrasting experimental evidence).

The mechanisms underlying population responses to environmental variation are usually treated in a very simplified way in the basic population models discussed above. For example, environmental noise is assumed to transfer linearly to population processes. Assuming non-linear responses of population growth rate or carrying capacity to the environment can make the relationship between population size and the environment weaker or non-linear, and distort the noise spectrum perceived by the individuals, possibly affecting the spectrum of population dynamics (Laakso et al. 2001, 2003). Moreover, the spectrum of environmental fluctuations may determine the physiological consequences of environmental variation (Elliott 1974, Luckinbill and Fenton 1978). The type of environmental changes (e.g. frequency spectrum) can also determine how stressful and energetically costly the environment is, and cause shifts in the allocation of resources between growth, reproduction and survival (Townsend and Calow 1981), with possible population level consequences.

We tested predictions of basic population models in microcosms with populations of particle-feeding protozoa *Tetrahymena thermophila* disturbed by sublethal temperature fluctuations with different frequency spectra. To address the physiological consequences of environmental noise, we measured the size distribution of test organisms. Tests of ecological theory with protozoa are usually conducted in systems with several bacterial species as food organisms (Luckinbill and Fenton 1978, Petchey 2000), and the species composition and dynamics of the basal level is typically not assessed. However, like the theoretical predictions tested in this work, we aim at avoiding species interactions and having constant basal level properties. Bacterial growth rate has a strongly non-linear relationship with temperature (Neidhardt et al. 1990) and hence it is possible that it complicates the temperature relationship of the organisms feeding on bacteria because food abundance would potentially depend on temperature. Moreover, protozoan grazing commonly changes traits or composition of the bacterial community which may affect the availability and quality of food to the grazers (Nakajima and Kurihara 1994, Jürgens and Sala 2000, Langenheder and Jürgens 2001). To avoid this, we constructed a closed one-species system with an axenic ciliate *Tetrahymena thermophila* to test the effect of environmental variability, colour of the variations, and intrinsic growth rate on population dynamics. Populations of *T. thermophila* were cultured in two nutrient levels (equaling maximum growth rates 0.05 and 0.3 h^{-1}), and subjected to three varying temperatures, blue, white, and red, and stable temperature. The rationale for including blue noise in the experiment arises from the fact that not all biologically significant variations occur between generations (e.g. daily temperature fluctuations and waves in shoreline), and that blue noise can have counterintuitive consequences on the colour of population dynamics (Laakso et al. 2001, 2003). To get sufficiently long time series for spectral analysis, we sampled the populations at 3h intervals for 18 days, representing a maximum of 137 generations for *T. thermophila*.

Material and methods

Study species and microcosms

We used the aquatic ciliated protozoa *Tetrahymena thermophila* (axenic stock CCAP 1630/1U obtained from Culture Collection for Algae and Protozoa, UK). The species has a short generation time and well-known biology (Hill 1972, Elliott 1974, Fenchel 1987). *Tetrahymena* feeds on particles (e.g. bacteria, non-living particles) and macromolecules (pinocytosis). This strain reproduces asexually through fission and population growth rate is strongly affected by temperature, and composition and concentration of the nutrient medium (Elliott 1974). *Tetrahymena* cell size is typically about 30 μm but large changes in size distribution may occur under sub-optimal conditions such as food depletion, and in low and high temperatures. The culture medium (“ePP”) used in all our experiments was sterile aqueous solution of proteose peptone (Difco Bacto™ Peptone) and Sigma Liver Concentrate (Sigma–Aldrich Co.) in 10:1 ratio (w/w).

The microcosms were modified from 250 ml polycarbonate cell culture bottles (Corning). To allow gas exchange, caps of the microcosms were equipped with glass fibre filters (GF/52 Schleicher & Schuell, ∅ 23 mm). Water evaporation was reduced by placing pieces of aluminium foil with 30 ventilation holes (∅ 1 mm) under the caps. Population samples were taken at 3-h intervals through a 50-cm (∅ 1.5 mm) silicon tube. To avoid microbial contamination, 30 cm of the sampling tube was outside the microcosm at 5°C (see below) and the medium was drawn only outwards. After the sampling fresh nutrient medium was pumped from stock bottles to the microcosms through silicon tubes con-

nected to 5-ml syringes. The volume of the culture medium was maintained at 50 ml by checking it once a day with 60-ml syringes. Deviations from the 50 ml volume due to evaporation or sampling errors were corrected by adding sterile medium or removing culture medium (mean $\pm$ SD addition 0.15 ± 1.2 ml).

The temperature regulation system was modified from Cohen et al. (1998). Thirty-two microcosms were placed in a cold room (5°C) on three stands and heated from underneath with resistors attached to moulded aluminium plates. Airflow under the microcosms was used to cool down the microcosms. Temperatures were measured using sensors (LM 232) placed inside the microcosms. The measurement and power regulation system consisted of a standard PC with A/D converter, MUX and measurement card for the temperature data, and a power unit with solid-state relays for heating the microcosms. The software for temperature recording and regulation was written in C (J. Maaranen, unpubl.). The measured temperatures were saved in 30-s intervals. The desired temperatures were generated with a Matlab code at 30-min intervals with linearly extrapolated three additional points between the intervals to smooth the temperature transitions.

Determination of population size

Prior to sampling, the microcosms were agitated gently and 2×1.5 ml medium was removed, saving the latter 1.5 ml for determination of population size. After sampling, 3.0 ml of fresh ePP was injected into the bottles (turnover rate 6%/3 h). Samples were fixed with 20% acetic acid (end concentration 1%) and stored in 5°C for counting. Population sizes and biomasses were determined as follows: a well-mixed 250 µl sub-sample was injected into a glass cuvette rack (depth 2.34 mm) and six randomly placed greyscale images (total area 40.0 mm^2) of the sedimented individuals were digitised with an Olympus SZX microscope ($32\times$ magnification), connected to video camera (Panasonic WV-CL702). The images were captured with a Matrox Meteor II video capture board and Image Pro Plus™ (v.4.0) image analysis software. The individuals were identified using an image recognition program written for Image Pro (J. Laakso, unpubl.). Briefly, the software removed background brightness differences, enhanced the object boundaries, and counted objects with dimensions width > 5 µm, length > 10 µm, area 150–1500 μm^2, width/length > 0.33, and the ratio of a theoretical ellipse perimeter to the ratio of the measured object perimeter being within 0.95–1.1. The cell volume was calculated from individuals' measured width and length using an ellipsoid approximation $V = 4/3\pi a^2 b$, where a = radius of the width and b = radius of the length.

Manipulation of *Tetrahymena* growth rate with food

A preliminary experiment was conducted to find suitable ePP medium concentrations for manipulating *Tetrahymena* maximum growth rate, calculated as

$$r_{max} = (\ln(N_t) - \ln(N_{initial}))/t$$

where N_t is the population size, and t the time in hours between samplings.
r_{max} was measured at 25°C at low population density (initially 2%, and always $< 10\%$ of the carrying capacity in 0.25% ePP) on 24-well tissue culture plate after acclimating the populations to the different food levels. *Tetrahymena* growth rate was close to zero at ePP 0.05% and saturates at ePP $\sim 0.25\%$ (data not shown). Hence, ePP 0.07% ($r_{max} = 0.05\ h^{-1}$) and 0.25% ($r_{max} = 0.3\ h^{-1}$) concentrations were chosen as widely differing maximum growth rates but yet having measurable population sizes.

Temperature responses of *Tetrahymena* under stable conditions

To determine the suitable temperature range for the main experiment, we measured *Tetrahymena* maximum growth rate (r_{max}) and carrying capacities (K) in stable temperatures in a 3- and 7-day experiment using the temperature regulator system (Fig. 2a and b). *Tetrahymena* were cultured in 12 temperatures (10–40°C) in 0.25% ePP medium. For determining r_{max} the populations were sampled at 3–6 h intervals for 6-24 h without adding new resources (the longest interval and time at suboptimal temperatures and shortest times at optimal temperatures). The densities when estimating r_{max} were initially 2% of K at 25°C (1 ml inoculum of late-log phase culture to 49 ml fresh ePP) and $< 10\%$ of K at the end of the r_{max} measurement, representing a situation where depletion of food resources are not growth limiting. The r_{max} estimate applies only for times between samplings, and is lower if 6%/3h sampling mortality is accounted for. Carrying capacity was possible to estimate only from the longer 7-day experiment, where mean population sizes between samples taken at 159–165 h were taken as K (ePP turnover 6%/3 h). Note that the K estimates at low temperatures can slightly be underestimated due to slow population growth and limited duration of the experiment. However, the K at ~ 10°C must necessarily be close to zero because the measured r_{max} is zero at ~ 10°C, and the medium turnover, not included in r_{max} estimate, imposes an additional mortality of 6%/3 h to the population.

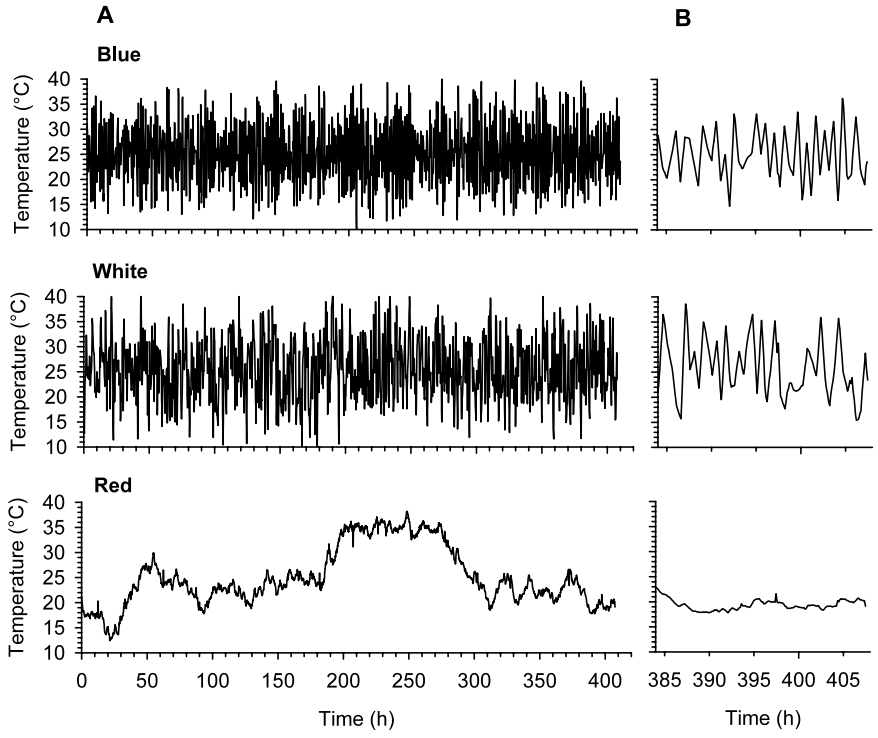

Fig. 1. Example time series of measured temperature fluctuations from blue, white and red environments. Left column (A) shows the whole time series and right column (B) the last 24 h, which equals to approximately ten generations for *Tetrahymena* assuming that the population has a growth rate of 0.3 h^{-1}.

Main experiment

Slowly and rapidly growing *Tetrahymena* populations were cultured in four different temperature regimes: stable 25°C, rapidly fluctuating (blue), uncorrelated fluctuations (white), and slowly fluctuating (red, $n = 4$ for each treatment). The temperature series (816 steps at 30 min intervals, independent series for each replicate) were produced by summing 408 ($T_{max}/2$) sine waves with uniform random phase, and amplitude following power law $A = 1/f^{\gamma}$ where γ was -1, 0, and 1 for blue, white, and red treatments, respectively. Thus, minimum wavelength was 1 h (dominated in the blue series) and maximum 18 days (dominated in the red series). The white series contained equal power at all frequencies. The minimum, maximum and mean of the desired temperature series were 10°C, 40°C and 25°C, respectively. The realised temperatures followed closely the desired temperatures (mean 25.1 ± 0.16°C, SD 5.47 ± 0.29 across all replicates; examples of the temperature fluctuations are shown in Fig. 1). The colour of temperature fluctuations (exponent γ estimated from frequencies $< 0.77\ h^{-1}$ using 7.5 min moving average) is expressed as mean $\pm$ SD, were -0.63 ± 0.047, 0.14 ± 0.034, and 1.0 ± 0.065 for blue, white and red treatments, respectively. Realised dominant frequencies were 1.4 ± 0.2, 10 ± 6, and 408 h for blue, white and red temperatures, respectively. Thus, the realised spectra differed from the desired spectra but nevertheless were of widely differing colours.

Prior to the experiment, *Tetrahymena* were acclimated to the two nutrient levels (1 ml of *Tetrahymena* late-log phase stock culture living in 2% peptone and 0.2% yeast extract medium transferred to 49 ml of fresh 0.07% and 0.25% ePP medium) for two days. When setting up the microcosms, 1 ml of the acclimated *Tetrahymena* culture was added to 49 ml of sterile nutrient medium and the microcosms were transferred to stable 25°C in the temperature regulator. After 4 days, large differences in population densities between the replicates were observed. To reduce the variation, replicates within each growth rate treatment were aseptically mixed and poured back to the microcosms. After 12 h the microcosms were transferred back to the temperature regulator and the fluctuating temperature series were initiated. Populations were sampled at 3-h intervals, resulting in 137 data points, a maximum of 137 generations for *Tetrahymena*.

Three samples (time steps 64, 100 and 101) were lost during the experiment. Missing values were replaced with a mean of two nearest points. Possible contaminations were checked at the end of the experiment by plating a fluid sample on 1% ePP agar and checking for microbial growth. Two microcosms were discarded due to contamination with bacteria (high growth rate treatments in white and stable environments).

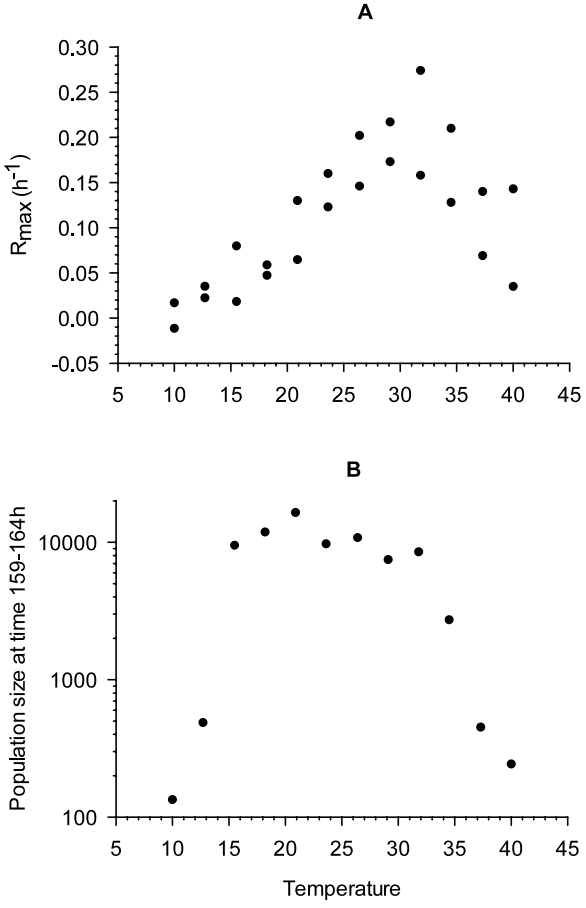

Fig. 2. (A) Temperature dependence of *Tetrahymena thermophila* maximum growth rate in fresh 0.25% ePP resource. (B) Temperature dependence of *Tetrahymena thermophila* carrying capacity measured as mean of three measurements between t = 159–165 h with 6% turnover/3 h of the 0.25% ePP resource.

Data analysis

Prior to all analyses, the first twenty data points were removed from the time series to eliminate the effect of initial transient, and population sizes and biomasses were log-transformed. However, population variability (CV rather than SD because the food treatment affects mean population size) and spectra were calculated from untransformed data. Populations cultured in stable temperature were excluded from the analyses when the theoretical predictions are about fluctuating environments only.

Environmental tracking was measured by Pearson's correlation between abundance/biomass and average temperature over the preceding 3 h. The 3-h mean was chosen because *Tetrahymena* generation time is in that scale and longer times would also strongly average out rapid temperature fluctuations in blue and white treatments. As the preliminary experiments suggested a non-linear optimum-type relationship between population size and temperature, we also tested for a significant second order (polynomial) relationship between temperature and population size.

The colour of the population dynamics were estimated as parameter γ of the power law $1/f^{\gamma}$ by first calculating Fourier spectra (Matlab v.6.0) of the population dynamics (linear trend removed) and then fitting a linear model $\ln(\text{power}) = \phi + \alpha \ln(\text{frequency})$ to the population spectrum, from where the estimate of γ was obtained as $-\alpha/2$.

The effect of environmental variation and growth rate on the population dynamics (population mean, CV, correlation coefficients and γ) were tested with ANOVA with two growth rates and three colour treatments as factors, and subsequent post-hoc multiple comparisons (Bonferroni correction).

Results

Performance in different stable temperatures

Under stable temperature conditions the *Tetrahymena* maximum growth rates (r_{max}) and carrying capacities (K) followed an optimum type response curve, K peaking at ~ 20°C and r_{max} at ~ 30°C (Fig. 2).

Variable environment

Cell size

High growth rate treatment increased mean cell size in all but blue environments (Fig. 3, $F_{3,22} = 43.3$, $p <$

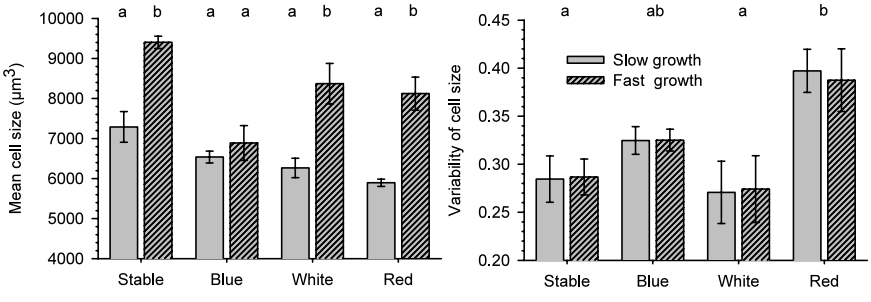

Fig. 3. Mean cell size ($\pm$ SE) and variability of cell size (CV $\pm$ SE). Letters above bars indicate significant ($p < 0.05$ with Bonferroni correction) contrasts between all treatment combinations for mean cell size and contrasts between colour treatment for variability of cell size and numbers vs biomass correlation.

0.001 for growth rate, $F_{3,22} = 3.4$ $p = 0.033$ for colour × growth rate) and cell size was largest in stable environment ($F = 10.6$, $p < 0.001$ for colour). Cell size was also temporally variable and variability was highest in red environment (Fig. 3, $F = 8.13$ $p = 0.001$ for colour).

Yield

Tetrahymena mean numbers and biomass were on average 2.3 and 2.8 times larger in high growth rate treatments (Fig. 4, $F_{1,22} = 438$, $F_{1,22} = 735$, $p < 0.001$ for numbers and biomass, respectively). Presence and type of environmental variations also affected population yield ($F_{3,22} = 11.3$ for numbers, $F_{3,22} = 24.7$ for biomass, $p < 0.001$ for both). Yield was largest in stable and red environments.

Population variability

Population variability was largest in red environment, but was not affected by growth rate (Fig. 4, environment $F_{3,22} = 11.7$, $F_{3,22} = 21.3$, $p < 0.001$, growth rate $F_{1,22} = 0.52$, $F_{1,22} = 1.91$, $p = 0.47$, $p = 0.18$, environment × growth rate $F_{3,22} = 2.98$, $F_{3,22} = 0.89$, $p = 0.56$, $p = 0.46$ for population size and biomass, respectively). Moreover, variability of population size (mean CV 0.39) was significantly higher than variability of biomass (mean CV 0.32, $F_{1,29} = 32.6$, $p < 0.001$).

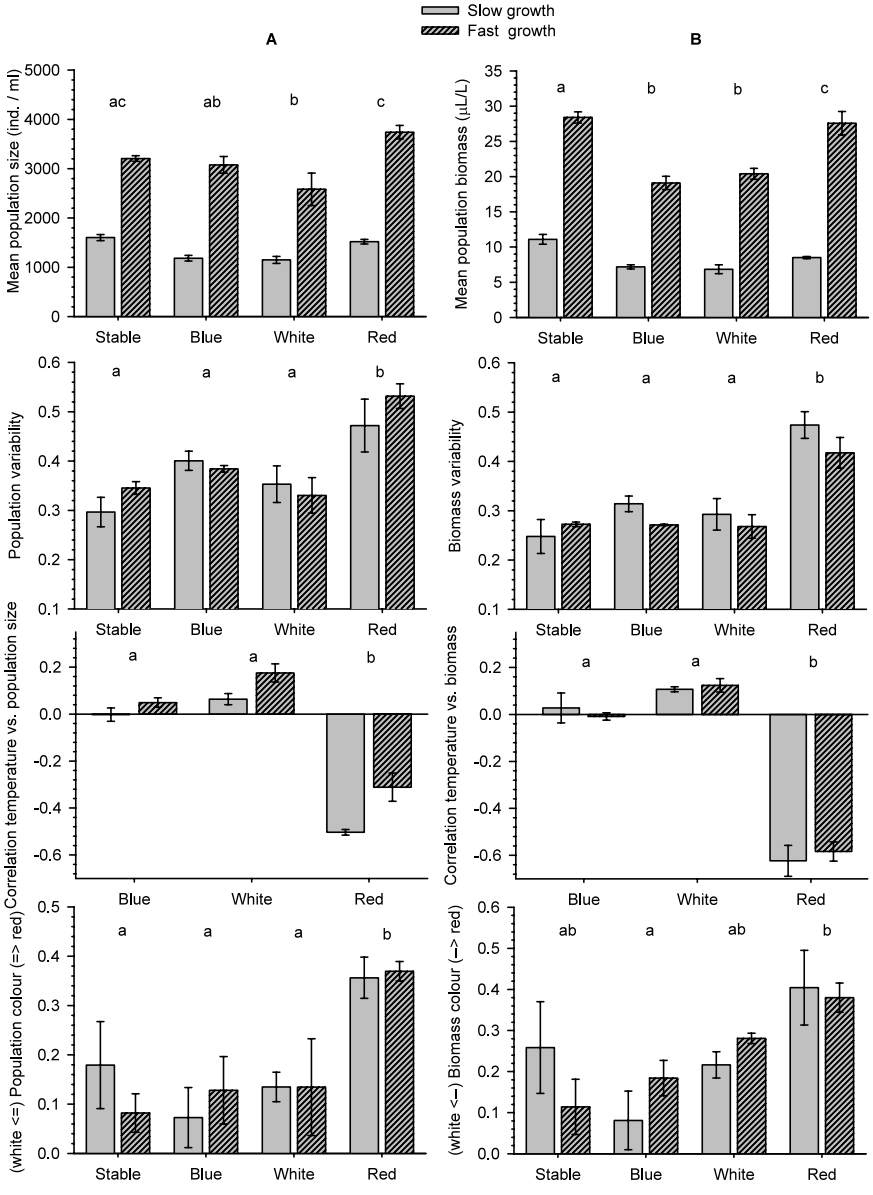

Fig. 4. Mean yield, coefficient of variation (CV ± SE), environmental tracking (population vs temperature as a 3-h mean before sampling), and colour (spectral exponent $\gamma \pm$ SE) of population size (column A) and biomass dynamics (column B). Positive spectral exponent values indicate reddened time series. Letters above bars indicate significant ($p < 0.05$ with Bonferroni correction) contrasts between colour treatments.

Environmental tracking

Tetrahymena numbers and biomass were poorly correlated with temperature both in blue and white environments, whereas the red environment produced significant negative correlations (numbers $F_{2,17} = 123$, biomass $F_{2,17} = 147$, $p < 0.0001$ for both, Fig. 4 and 5). Growth rate had a weak positive effect on correlation coefficient of population numbers and temperature, but no significant effect on correlation of population biomass and temperature (growth rate on numbers $F_{1,17} = 16.3$, $p = 0.001$, biomass $F_{1,17} = 0.03$, $p = 0.86$; growth × environment on numbers $F_{2,17} = 2.05$, $p = 0.16$, biomass $F_{2,17} = 0.38$, $p = 0.69$). We also found a significant second order relationship with temperature in 7 out of 8 red treatments. However, the biomass-environment relationship was largely negative and linear, and the addition of second order term had a limited contribution to the explanatory power (R squared 0.36 and 0.42 for linear and second order models, respectively).

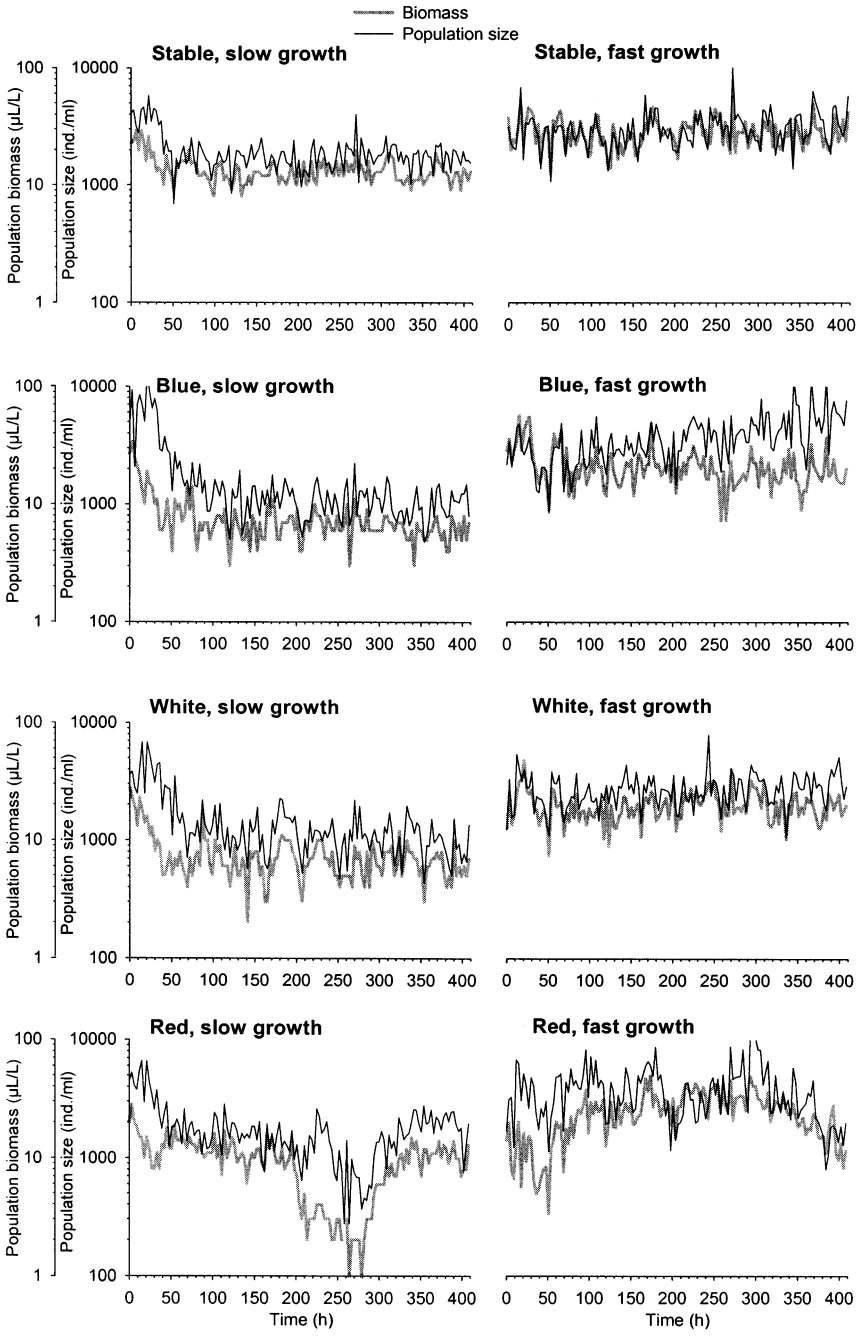

Fig. 5. Examples of population time series (black line for numbers and grey line for biomass) in stable, blue, white, and red environments (rows, respectively). Left column shows slowly growing populations and right column fast growing populations. The fluctuating temperature time series shown in Fig. 1 correspond to the population series in the left column.

Colour of the population dynamics

Population dynamics were reddened in all of the environments (Fig. 4). Population colour was affected by environment, but not by the growth rate (colour $F_{3,22} = 8.00$, $p = 0.001$, $F_{3,22} = 5.49$, $p = 0.006$, growth rate $F_{1,22} = 0.03$, $p = 0.87$, $F_{1,22} < 0.001$, $p = 0.99$, colour × growth rate $F_{3,22} = 0.51$, $p = 0.67$, $F_{3,22} = 1.22$, $p = 0.33$ for population size and biomass, respectively). Population size dynamics in red environment was significantly redder than in the other environments, and biomass dynamics differed significantly between red and blue environment dynamics.

Discussion

Our results on *Tetrahymena* population dynamics support the basic model predictions (May 1973, Roughgarden 1975, Kaitala et al. 1997a, b) and the experimental findings that population variability is highest and correlation between population size and environment is strongest in red environments (Luckinbill and Fenton 1978, Petchey 2000), and that the colour of population dynamics can become reddened due to internal properties of populations (Miramontes and Rohani 1998, Petchey 2000). Majority of the experiments with protozoa have other organisms present, while our experiment eliminated the possibility that species interactions (Jürgens and Sala 2000, Langenheder and Jürgens 2001), or temperature dependent bacterial growth (Neidhardt et al. 1990) may redden population dynamics. We also found new evidence that environmental variation can redden population colour. This was not observed in an experiment by Petchey (2000) who instead found that population growth rate (confounded by species identity of slow growing ciliate *Paramecium* and fast growing *Colpidium*) caused differences in population spectra.

Our experiment failed to support the theoretical predictions that rapidly growing populations follow the environmental changes more closely than slowly growing populations, which would result in higher variability and population vs environment correlation, and have a frequency spectrum that more closely follows that of the environmental variables (May 1973, Roughgarden 1975). The lack of evidence for this may be due to the fact that the food level treatment did not cause large enough differences in realised population growth rates (i.e. population response times) when resources were limiting.

The predictions of the basic stochastic population models rely on the assumption that environmental conditions have a linear (May 1973, Roughgarden 1975) or non-linear effect on population model parameters (Laakso et al. 2001, 2003). In our data we found novel evidence that environmental colour can also influence population yield (mean size and biomass) and dynamics of size distribution. That population mean yield was lowest in rapidly fluctuating blue and white treatments suggests that populations did not just average out high-frequency fluctuations with unchanging mean. It is expected that the presence of environmental variability can reduce mean population numbers and biomass yield due to the unimodal carrying capacity responses recorded in the preliminary experiments. However, also the frequency spectra of the fluctuations determined whether mean population size responded to variations. That fast blue and white fluctuations produced smallest population numbers and least biomass suggests that the populations can face physiological difficulties or trade-offs in adapting to rapid changes. Ectothermic organisms can physiologically adapt to temperature changes by producing protective molecular chaperones (HSP proteins), and altering enzyme and lipid composition of the cell (Hochanka and Somero 1984, Moseley 1994). In our case the adaptation process may have been slower than the environmental changes in blue and white environments or energetically costly (Parsons 1990, Krebs and Feder 1998). The physiological consequences of rapid environmental changes, which could be recurrent or transiently occurring events, can not obviously be predicted from experiments performed under constant conditions. These effects may have ecological relevance in small populations where the rapid changes can increase extinction risk by reducing individuals' stress tolerance and making the population more susceptible to additional sources of stochasticity (Parsons 1990). The contribution of stress induced by high-frequency changes to population dynamics could however be incorporated to simple population models by adjusting vital rates as function of the rate of environmental change.

Mean cell size and variability of cell size were affected by the presence and type of environmental variability. These findings add to the evidence that the physiological state of the ciliates differed between the environments. Sub-optimal temperature can lead to changes in *Tetrahymena* cell structure and greater variability in cell size (Elliott 1974). Transfer of individuals into sub-optimal conditions may prevent cell division while biomass growth continues. However, transfer of the large-sized cells back to optimal conditions causes several successive cell divisions. That environmental colour may cause physiological differences between the populations and partial decoupling of population dynamics from biomass dynamics suggests that simply observing population size may not give full information about the interactions between environment and population fluctuations. Moreover, it is likely that for microbes population biomass is a better indicator of resource-consumer dynamics in variable environment because biomass growth is less sensitive to the environmental change than cell division.

To summarise, our experiment demonstrates that population dynamics (variability, environment vs. population correlations, and population colour) can be under environmental control (May 1973, Roughgarden 1975), but also the internal properties of the populations may create variability and redden the colour of population dynamics (Miramontes and Rohani 1998, Petchey 2000). Growth rate however had little effects on population dynamics in contrast to other experiments with protozoa (Luckinbill and Fenton 1978, Petchey 2000). We also found evidence that presence of environmental variability and speed of the variations (environmental colour) affects physiology. As a consequence, population mean yield decreased with increasing speed of the environmental variation, which is not predicted by the basic population models. This calls for further experiments and modelling efforts to understand the mechanisms that transfer environmental effects to population level dynamics.

Acknowledgements – We thank T. Benton, A. Beckerman, T. Hiltunen, T. Ketola, P. Lundberg, G. Loe, K. Meissner, O. L. Petchey, and E. Ranta for discussions on the topic. We would also like to thank Jani Maaranen for building the temperature regulator. The study was supported by the Academy of Finland.

References

Benton, T. G., Lapsley, C. T. and Beckerman, A. T. 2001. Population synchrony and environmental variation: an experimental demonstration. – Ecol. Lett. 4: 236–243.

Cohen, A. E., Gonzalez, A., Lawton, J. H. et al. 1998. A novel experimental apparatus to study the impact of white noise and 1/f noise on animal populations. – Proc. R. Soc. Lond. B 265: 11–15.

Elliott, A. M. 1974. Biology of *Tetrahymena*. – Van Nostrand Reinhold.

Fenchel, T. 1987. Ecology of protozoa: the biology of free-living phagotrophic protists. – Science Tech Publishers.

Halley, J. M. 1996. Ecology, evolution and 1/f noise. – Trends Ecol. Evol. 11: 33–38.

Hill, D. L. 1972. The biochemistry and physiology of *Tetrahymena*. – Academic Press.

Hochanka, P. W. and Somero, G. N. 1984. Biochemical adaptation. – Princeton Univ. Press.

Inchausti, P. and Halley, J. 2001. Investigating long-term ecological variability using the global population dynamics database. – Science 293: 655–657.

Jürgens, K. and Sala, M. 2000. Predation-mediated shifts in size distribution of microbial biomass and activity during detritus decomposition. – Oikos 91: 29–40.

Kaitala, V. and Ranta, E. 2001. Is the impact of environmental noise visible in the dynamics of age-structured populations. – Proc. R. Soc. Lond. B 268: 1769–1774.

Kaitala, V., Ylikarjula, J., Ranta, E. and Lundberg, P. 1997a. Population dynamics and the colour of environmental noise. – Proc. R. Soc. Lond. B 264: 943–948.

Kaitala, V., Lundberg, P., Ripa, J. and Ylikarjula, J. 1997b. Red, blue and green: dyeing population dynamics. – Ann. Zool. Fenn. 34: 217–228.

Krebs, R. A. and Feder, M. E. 1998. Experimental manipulation of the cost of thermal acclimation in *Drosophila melanogaster*. – Biol. J. Linn. Soc. 63: 593–601.

Laakso, J., Kaitala, V. and Ranta, E. 2001. How does environmental variation translate into biological processes? – Oikos 92: 119–122.

Laakso, J., Kaitala, V. and Ranta, E. 2003. Nonlinear biological responses to disturbance: consequences on population dynamics. – Ecol. Modell. 162: 247–258.

Langenheder, S. and Jürgens, K. 2001. Regulation of bacterial biomass and community structure by metazoan and protozoan predation. – Limnol. Oceanogr. 46: 121–134.

Lawton, J. H. 1988. More time means more variation. – Nature 334: 563.

Leirs, H., Stenseth, N. C., Nichols, J. D. et al. 1997. Stochastic seasonality and nonlinear density-dependent factors regulate population size in an African rodent. – Nature 389: 176–180.

Luckinbill, L. S. and Fenton, M. M. 1978. Regulation and environmental variability in experimental populations of Protozoa. – Ecology 59: 1271–1276.

May, R. M. 1973. Stability and complexity in model ecosystems. – Princeton Univ. Press.

Miramontes, O. and Rohani, P. 1998. Intrinsically generated coloured noise in laboratory insect populations. – Proc. R. Soc. Lond. B 265: 785–792.

Moseley, P. L. 1994. Mechanisms of heat adaptation: thermotolerance and acclimatization. – J. Lab. Clin. Med. 123: 48–52.

Mysterud, A., Yoccoz, N. G., Stenseth, N. C. and Langvatn, R. 2000. Relationships between sex ratio, climate and density in red deer: the importance of spatial scale. – J. Anim. Ecol. 69: 959–974.

Nakajima, T. and Kurihara, Y. 1994. Evolutionary changes of ecological traits of bacterial populations through predator-mediated competition 1. Experimental analysis. – Oikos 71: 24–34.

Neidhardt, F. C., Ingraham, J. L. and Schaechter, M. 1990. Physiology of the bacterial cell: a molecular approach. – Sinauer Associates.

Parsons, P. A. 1990. The metabolic cost of multiple environmental stresses: implications for climatic change and conservation. – Trends Ecol. Evol. 5: 315–317.

Petchey, O. L. 2000. Environmental colour affects aspects of single-species population dynamics. – Proc. R. Soc. Lond. B 267: 747–754.

Pimm, S. L. 1991. The balance of nature. – Univ. Chicago Press.

Pimm, S. L. and Redfearn, A. 1988. The variability of population densities. – Nature 334: 613–614.

Ranta, E., Lundberg, P., Kaitala, V. and Laakso, J. 2000. Visibility of the environmental noise modulating population dynamics. – Proc. R. Soc. B 267: 1851–1856.

Roughgarden, J. 1975. A simple model for population dynamics in stochastic environments. – Am. Nat. 109: 713–736.

Steele, J. H. 1985. A comparison of terrestrial and marine ecological systems. – Nature 313: 355–358.

Sugihara, G. 1994. Nonlinear forecasting for the classification of natural time series. – Philos. Trans. R. Soc. Lond. A 348: 477–495.

Sugihara, G. 1995. From out of the blue. – Nature 378: 559–560.

Sugihara, G. 1996. Red/blue chaotic power spectra. – Nature 381: 199.

Townsend, C. R. and Calow, P. 1981. Physiological ecology. An evolutionary approach to resource use. – Blackwell.