Ecology, 86(6), 2005, pp. 1463–1471

POPULATION SYNCHRONY INDUCED BY RESOURCE FLUCTUATIONS AND DISPERSAL IN AN AQUATIC MICROCOSM

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Abstract. Two of the principal explanations for regional population synchrony, large-scale environmental variability and dispersal, have received considerable theoretical attention. Although time series analysis has helped to validate the relative importance of these two explanations, very little of this theory has been confirmed by experiment. Here, we demonstrate the dual synchronizing effect of dispersal and temporal environmental variation. We used an experimental model system based on the rotifer *Brachionus calyciflorus* and its algal prey *Chlorella vulgaris*. We constructed temporal prey fluctuations with two periodic components that matched the generation time and life span of the rotifer. By varying the amplitude of these two periods we created prey variability with ''white'' (both periods had equal power) and ''red'' (the longest period had greatest power) spectra. In the absence of dispersal only the red fluctuations induced synchrony in the population dynamics of the rotifer. Dispersal had a strong and rapid synchronizing effect. The combination of red (but not white) fluctuations and dispersal resulted in the highest levels of synchrony. These results confirm the predictions of recent theory, but they also suggest that the temporal structure of environmental variability determines its capacity to synchronize population dynamics over large spatial scales.

Key words: dispersal; environmental variability; microcosm; Moran effect; predator–prey dynamics; synchrony.

INTRODUCTION

Synchronous fluctuations in the densities of regionally dispersed populations is a well-documented phenomenon for a range of species (Pollard 1991, Post 2003), and has been observed from regional to continental scales (Sutcliffe et al. 1996, Post and Forchhammer 2002). Because the risk of metapopulation extinction increases with increasing synchrony (Petchey et al. 1997, Engen et al. 2002) establishing the cause of synchronous population fluctuations is a fundamental problem with clear consequences for the long term conservation of fragmented populations (Earn et al. 2001).

There exist three principle explanations for population synchrony. The first, commonly known as the Moran effect (Mackenzie 1952, Moran 1953), suggests that if two regional populations have the same intrinsic (density-dependent) structure, they will be correlated under the influence of common environmental variation. Such variation may include high levels of spatially correlated fluctuations in the physical environment, such as temperature and rainfall (Koenig 2002), as well as food or some other resource. The second envisages an important role for inter-population dispersal, whereby the movement of individuals acts to reduce the heterogeneity of local population fluctuations. Finally, spatially extended interspecific interactions, like predation, may induce synchrony by imposing a common source of mortality across a region (Myers 1998, Ims and Andreassen 2000). Here, we consider the synchronizing effect of dispersal, and the Moran effect in the form of resource variation.

Extensive time series analysis has associated the Moran effect with large-scale climatic phenomena, such as the North Atlantic Oscillation (NAO) or the El Niño-Southern Oscillation (Post and Forchhammer 2002, Stenseth et al. 2002, Straile 2002). Theory predicts that the level of synchrony induced by such climatic phenomena depends upon the underlying demography. Under conditions of linear density dependence the correlation between regional populations will be equal to the correlation of the shared local density independent variability. This does not precisely hold for nonlinear density dependence and, under such conditions, the correlating effect of the environment may be weaker or even vanish (Royama 1992, Bjørnstad 2000, Blasius and Stone 2000, Greenman and Benton 2001). For oscillating systems, synchrony can be caused by environmental forcing (Bjørnstad 2000, Greenman and Benton 2001). However, rapid desynchronization by environmental variability has been reported under more complex dynamics (Bjørnstad et al. 1999). These results suggest that nonlinear density de-

Manuscript received 8 September 2004; revised 19 October 2004; accepted 21 October 2004. Corresponding Editor: J. Huisman.

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pendence precludes synchronization, although the Moran effect may still induce a weak form of synchrony, phase synchrony, even for systems exhibiting chaotic dynamics (Cazelles and Boudjema 2001).

The limited spatial extent of most dispersal events is thought to constrain its synchronizing effect to small spatial scales (Ruxton 1996, Kendall et al. 2000, but see Schwartz et al. 2002). However, reaction-diffusion theory suggests that the capacity of local dispersal to induce large-scale synchrony will depend upon the strength of local density dependence (Hassell et al. 1991, Bjørnstad et al. 2002). To date, models assuming weaker density dependence generally conclude that dispersal may be of lesser importance than the Moran effect (Haydon and Steen 1997, Lande et al. 1999, Ripa 2000).

A neglected aspect of the Moran effect is the importance of the temporal structure (as opposed to the spatial correlation) of environmental variation. Theory suggests that the extent to which a single population is entrained by environmental variability will depend upon its periodicity (Roughgarden 1975). In particular, populations are unlikely to be greatly influenced by environmental fluctuations with dominant periods inferior to their characteristic response time ($1/r$) (May 1976). Thus, it is conceivable that the efficacy of the Moran effect may not only be related to the degree of spatial correlation of environmental fluctuations but also the degree of temporal correlation, or the periodicity, of environmental variation. For example, the NAO has dominant periodicities between five and 14 years (Appenzeller et al. 1998), which are believed to have a strong direct and indirect synchronizing influence on many large herbivore populations (Forchhammer et al. 2002, Post and Forchhammer 2002). Because the majority of theoretical studies of the Moran effect assume that populations are forced by a statistically uncorrelated environmental variation (Ranta et al. 1995, but see Ives and Klopfer 1997, Petchey et al. 1997, Heino 1998), which by definition has no characteristic periodicity, the importance of the temporal structure of environmental variation for population synchrony has remained relatively unexplored.

Little experimentation has been conducted to validate the assumptions and predictions of this theory. Myers (1990) sought to induce changes in the phase of the oscillations of the western tent caterpillar, *Malacosoma californicum pluviale*, by introducing eggs into target populations from neighbouring populations. In three out of seven introductions the population decline phase was delayed by a year suggesting that common environmental factors were not responsible for synchronous population cycles in this species. McCauley (1993) demonstrated that the predator–prey oscillations of a *Daphnia*–algae system, when initiated out of phase, did not converge to synchrony when maintained under the common light and temperature fluctuations of a greenhouse. Both of these experiments suggest a weak or non-existent role for an environmentally driven Moran effect. More recently, Benton et al. (2001) examined the synchronizing effect of fluctuating food, with different levels of spatial correlation, upon the population dynamics of the soil mite *Sancassania berlesei*. They demonstrated fluctuations in isolated population densities (i.e., not linked by dispersal) that became increasingly synchronous as the spatial correlation was increased. To date, no experiment has simultaneously examined the synchronizing effects of population dispersal and environmental fluctuations.

Here, we present the results of an experiment that examined the synchronizing effect of resource fluctuations and dispersal in an experimental model system. Our intent was to both test recent theory and to explore our hypothesis relating the synchronizing effect of environmental variability to its temporal structure. The principle empirical questions were (1) Can dispersal and resource fluctuations synchronize two asynchronously fluctuating populations? and (2) Do their combined effects represent a stronger synchronizing force than either alone?

Methods

We used monoclonal populations of the freshwater rotifer *Brachionus calyciflorus* (a cyclic parthenogen that has an average generation time of ~5 d and a life span of ~10 d at 20°C; see Plate 1) and its prey the green alga *Chlorella vulgaris*. The *B. calyciflorus–C. vulgaris* populations were maintained in 6 mL of autoclaved COMBO-Animate (Kilham et al. 1998) contained within sterile Petri dishes (9 mL) placed within a single incubator set to 20°C and a 12 h light:12 h dark photoperiod (50 $\mu mol \cdot m^{-2} \cdot s^{-1}$). At this temperature *B. calyciflorus* is known to produce sustained oscillations (Halbach 1979). Populations were started with 20 individuals (3.3 individuals/mL) of *B. calyciflorus* and 1×10^6 cells/mL of *C. vulgaris*.

Experimental design and sampling

The basic experimental unit consisted of two unconnected Petri dishes of *B. calyciflorus–C. vulgaris*, one of which was labeled S1 the other S2. Following a factorial design, four replicates of this two-dish unit were randomly assigned to two dispersal treatments and four fluctuation treatments: control, constant, red, and white (2 dispersal treatments $\times$ 4 fluctuation treatments $\times$ 8 dishes = 64 populations). In each treatment, the four S1 replicate dishes of *B. calyciflorus–C. vulgaris* populations were established on day zero and were followed 8 d later by the commencement of the populations in the set of S2 replicate dishes. In this way, the S1 and S2 populations were established out of phase. The treatments (see *Dispersal* and *resource fluctuations*) were commenced on day 14 of the experiment (day 14 for S1 and day 6 for S2) and were maintained

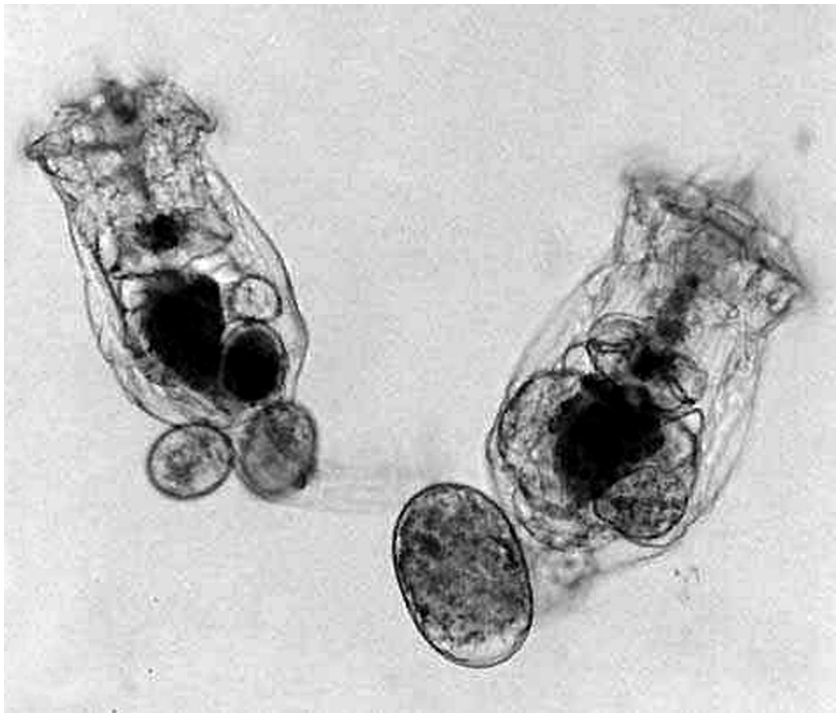

PLATE. 1. Two female *Brachionus calyciflorus* individuals carrying two male eggs (left) and one amictic egg (right). Photo credit: Blandine Descamps-Julien.

for 64 d (~13 rotifer generations). The experiment ended on day 78.

Over the 78 days, the total number of *B. calyciflorus* individuals in the S1 and S2 dishes was estimated every 48 h by stereomicroscope. Population densities occasionally reached levels that were too high (120–200 individuals/mL) to be sensibly counted in their entirety. At these times, the Petri dish was swirled, two samples of approximately 1 mL of medium (the exact volume was estimated by weight with the use of a microbalance) were removed, and the total number of individuals within each sample counted. Following enumeration, all individuals within the dish were transferred to sterile Petri dishes (by pipette in as little of the original medium as possible) and placed in 6 mL of renewed medium containing a cell density of *C. vulgaris* defined by the fluctuation treatment for that day (see *Resource fluctuation*). *C. vulgaris* densities were estimated with a Malassez haemocytometer and adjusted by dilution from a single laboratory stock culture.

Dispersal

Each of the four S1 populations was randomly assigned to an S2 population for the duration of the experiment. We thereby created four coupled systems where unidirectional dispersal always occurred from the S1 to the S2 population. Every 48 h, from day 14 until the end of the experiment, and immediately after counting and renewal of the medium, we removed 10% (0.6 mL of well-mixed culture) of each S1 population. The rotifer individuals were isolated by aspiration from this sample, in as little liquid as possible, and were placed in their assigned S2 population. The remaining medium was replaced in the original S1 population. Because we removed a fixed volume of medium the number of dispersing individuals was proportional to the population size; this simple dispersal pattern has been adopted by many theoretical studies.

Resource fluctuations

We established four different resource fluctuation treatments: a control where *C. vulgaris* were allowed to freely fluctuate; a constant treatment where we fixed *C. vulgaris* at a constant concentration for the duration of the experiment, and two fluctuating *C. vulgaris* treatments in which their component frequencies differed in their relative amplitude. In each of the four treatments, *B. calyciflorus* densities were allowed to freely fluctuate.

Control treatment.—Control of *C. vulgaris* densities was ceased on day 14 and their densities allowed to freely fluctuate until the end of the experiment. To prevent the accumulation of dead rotifer individuals and any potential autotoxic effects (Kirk 1998), every eight days following density estimation we estimated the density of *C. vulgaris* in each replicate and renewed it with fresh medium at the same algal density. Because of time constraints this treatment was not conducted at the same time as the others and was initiated in the

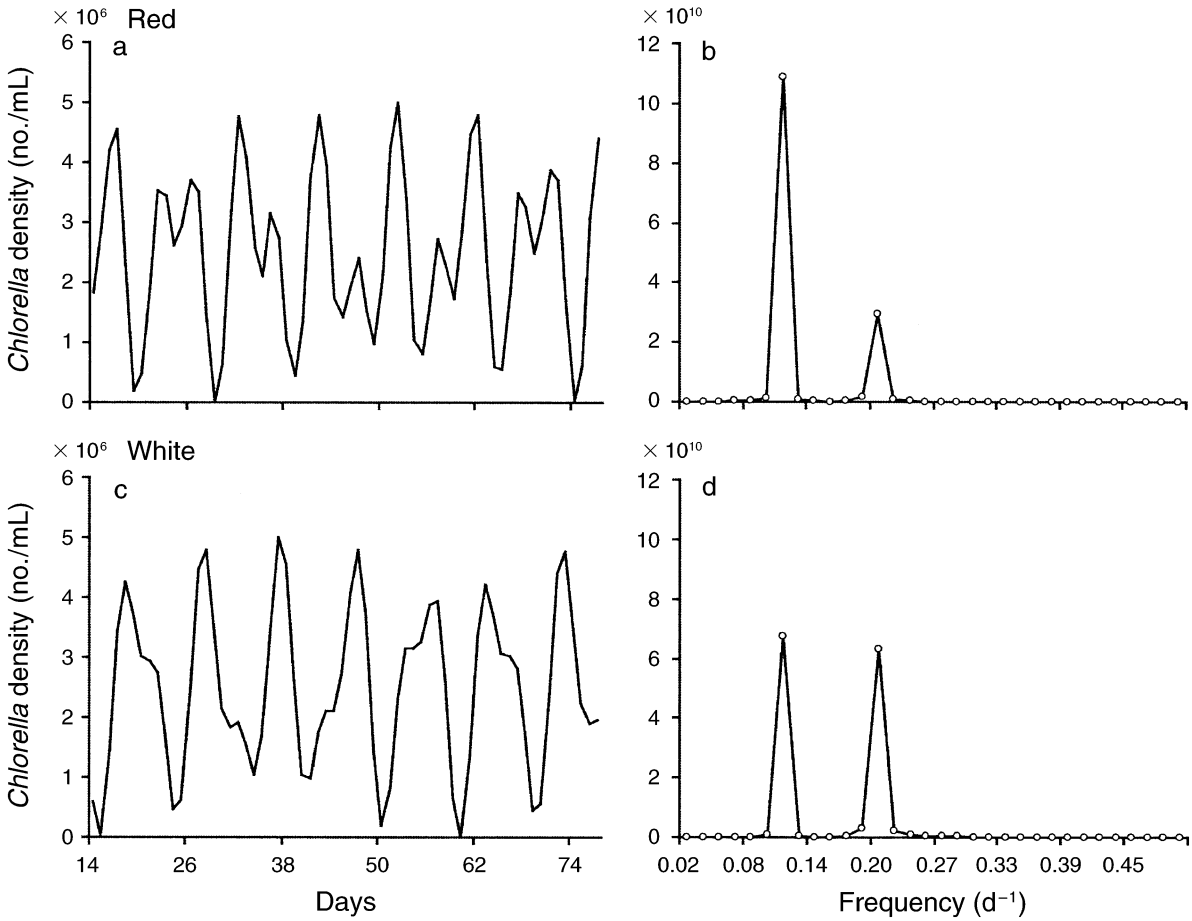

FIG. 1. Time series of the white and red treatment *Chlorella* fluctuations (a and c) used in the fluctuation treatments. Adjacent are their respective periodograms, indicating the relative power of the two component frequencies (b and d). In the white series, the two frequencies have equal power, while in the red there is greater power at the lower frequency.

same incubator two days after the end of the main experiment.

Constant treatment.—From day 14, and every 48 h following estimation of *B. calyciflorus* densities, we renewed the medium in its entirety and replaced it with fresh *C. vulgaris* at a density of 2.5×10^6 cells/mL. This concentration is equal to the mean concentration of the two fluctuating *C. vulgaris* series described below.

Fluctuation treatments.—To assess whether the frequency structure of environmental fluctuations is important for population synchrony we constructed two time series of changes in algal density that differed in the relative amplitude of their two component frequencies; a ''red'' series in which the lower frequency had the greatest amplitude and a ''white'' series in which both frequencies were of equal amplitude. To construct these series we used the following trigonometric function:

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

where n is the length of the series, f is the frequency (units of cycles per day), t is the time (units of 24 h), γ determines the relation between amplitude and frequency, and θ_f is a uniform deviate $[0, 2\pi]$ that adds random phase to each sine wave. Both series were composed of two sinusoids with frequencies of 0.2 and 0.11/d (periods of 5 and 9 d), respectively; for the red series $\gamma = 1$, for the white series $\gamma = 0$ and in both cases $n = 64$ (Fig. 1). The highest frequency (the 5-d period) was chosen because it corresponds to the generation time of *B. calyciflorus* at 20°C (Halbach 1979). Theory predicts that populations are unlikely to be greatly influenced by environmental fluctuation with a period inferior to the characteristic response time of a population ($1/r$), which for *B. calyciflorus* equates to $1/0.23 = 4.9$ d. The lower frequency (9-d period) is approximately equivalent to the lifetime of this rotifer species at 20°C and the mean *C. vulgaris* densities used here. To ensure that the ''red'' and ''white'' series differed only in the relative dominance of the two periods (their spectral density) and were otherwise identical we used the spectral mimicry method described in Cohen et al. (1998). We scaled the resulting time series so that the mean, maximum and minimum algal densities

chosen for the series were based upon survivorship and fecundity data provided by Halbach (1979). At the minimum algal density used here ($\approx 8 \times 10^3$ cells/mL) *B. calyciflorus* has a survivorship of less than 7 d and a maximum fertility of <0.05 offspring per female per hour and, at the maximum algal density (5×10^6 cells/mL), a survivorship of 9 d and a maximum fertility of 0.08 offspring per female per hour. At the mean algal density (2.5×10^6 cells/mL), *B. calyciflorus* has a survivorship of 17 d and a maximum fertility of 0.12 offspring per female per hour.

From day 14, and every 48 h following estimation of *B. calyciflorus* densities, we renewed the medium in its entirety and replaced it with fresh *C. vulgaris* at the prescribed density indicated by the series.

Data analysis

To analyze the change in synchrony over time, we arbitrarily broke up the 64-d time series of rotifer densities into two 32-d intervals. All statistical analyses were conducted on the natural logarithm of densities using SAS software (SAS Institute 1999).

Synchrony

Various measures have been proposed and used to estimate synchrony between two or more populations (Buonaccorsi et al. 2001). Here, we used the intraclass correlation coefficient, r_i (Zar 1984), as a measure of synchrony between the S1 and S2 populations in each interval (Rusak et al. 1999). This statistic is the recommended method when it is impossible to designate dependent and independent series in any given n series comparison (Zar 1984). When population fluctuations become increasingly synchronous r_i approaches 1. If populations become increasingly asynchronous, then the correlation becomes negative, -1 when $n = 2$. The intraclass correlation coefficient assumes samples are drawn from normal distributions with equal variances we thus normalized the counts by transforming them to z scores (Zar 1984). We calculated intraclass correlation coefficient for each S1 and S2 unit for each of the two experimental intervals and then examined the change in correlation over the two intervals with a univariate repeated measures ANOVA. The final model represented only significant factors and their interaction. Differences between treatments were analyzed by a post-hoc Bonferroni-adjusted t test.

Results

With the exception of the control treatments that were stopped on day 58 (due to incubator failure), all treatments were maintained for the planned duration, and no extinctions were observed in any of the series (Fig. 2).

Repeated-measures ANOVA of r_i coefficients revealed significant effects of environment ($F_{3,24} = 18.11$, $P < 0.0001$), dispersal ($F_{1,24} = 11.52$, $P < 0.0001$), and time ($F_{1,24} = 9.18$, $P < 0.0001$). The significant time × environment interaction ($F_{3,24} = 3.12$, $P < 0.01$) and time × dispersal interaction ($F_{1,24} = 5.72$, $P < 0.0004$) indicate a change in synchrony over the two intervals. As the environment × dispersal interaction was not significant ($F_{3,24} = 1.52$, $P < 0.43$), we present the results with and without dispersal separately. All statistical details for the treatment comparisons reported below may be found in Table 1 and Fig. 3.

Without dispersal.—In interval 1, the red, white, and constant treatments showed low but positive r_i values (Fig. 3a), while the control treatment had a negative r_i, however none of these values were significantly different from zero. Statistically significant changes in synchrony were observed (Table 1, Fig. 3a) for the red treatment and, to a lesser extent, the control treatment over the two intervals. There was no significant change in r_i within the constant and white treatments over the two intervals. Within interval 2, synchrony in the red treatment was significantly and substantially greater than the other treatments (red $r_i = 0.70$, white $r_i = 0.06$, constant $r_i = -0.26$, control $r_i = 0.23$); the r_i of the control treatment was not significantly different from zero ($t = 1.57$, df = 9, $P = 0.15$).

With dispersal.—In the first interval, the control and constant series r_i values were negative and were not significantly different from zero (Fig. 3b). Positive values of r_i were already apparent in the white and red treatments, but there was no statistical difference between these two treatments.

There were significant differences between the first and second interval for the within-treatment comparison for all but the white treatment (Table 1, Fig. 3b). Within interval 2, r_i values were greatest under the red treatment ($r_i = 0.92$) which was significantly greater than the white ($r_i = 0.55$) but not the control ($r_i = 0.84$) or constant ($r_i = 0.77$) treatments. Values of r_i in the white treatment were significantly lower than the control, but not the constant treatment.

Discussion

An important empirical issue in ecology is the relative role environmental variability and dispersal play in effecting population synchrony. To date the large body of theory on this topic has remained virtually untested. In this experiment, both biotic environmental variability and dispersal induced population synchrony over an interval equivalent to ~13 rotifer generations. Overall dispersal had a stronger synchronizing effect (Fig. 3), although the temporal pattern of resource fluctuations was also important. Unlike some theoretical studies (Lande et al. 1999, Kendall et al. 2000, Ripa 2000) we found no statistical interaction between these two factors, and so we discuss each in turn below.

In the absence of dispersal, only the reddened resource fluctuations had a substantial synchronizing effect over the two experimental intervals. This result suggests that the Moran effect may be expected only under certain patterns of environmental variability

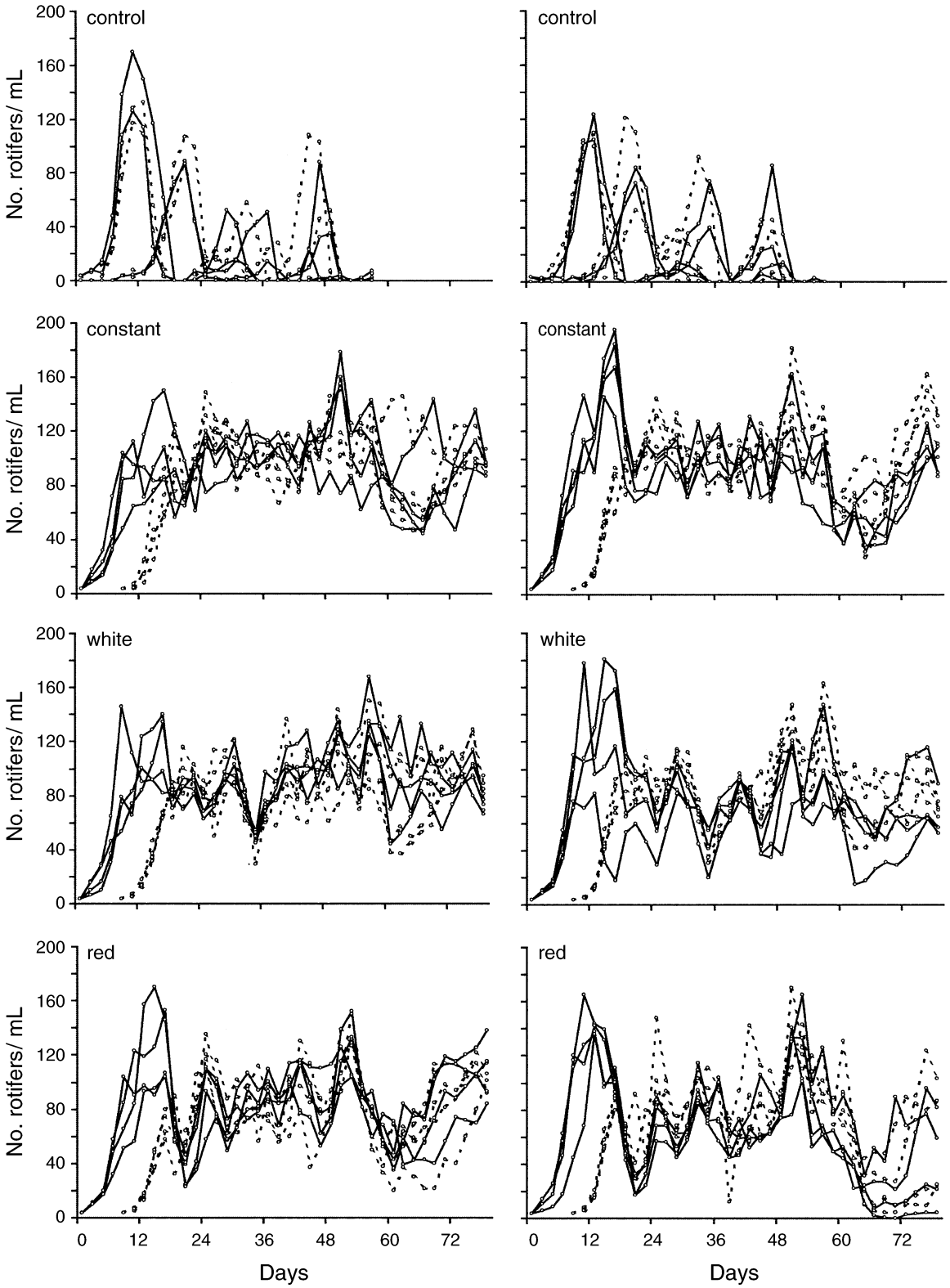

FIG. 2. Time series of rotifer population densities through the course of the experiment, shown without dispersal (left-hand panels) and with dispersal (right-hand panels). The solid lines correspond to the four replicates of the S1 series; dotted lines are four replicates of the S2 series.

TABLE 1. Statistics for the pairwise treatment comparisons (Bonferroni-corrected *t* test), conducted after repeated-measures ANOVA within and between each interval for the intraclass correlation coefficient.

	Interval 1							
	Control		Constant		White		Red	
Interval 2	*t*	*P*	*t*	*P*	*t*	*P*	*t*	*P*
Without dispersal								
Control	−2.54	0.03	2.10	0.06	2.44	0.04	2.50	0.03
Constant	−2.22	0.05	1.78	0.11	0.34	0.74	−0.40	0.70
White	−0.95	0.37	1.27	0.24	0.85	0.41	−0.06	0.95
Red	2.18	0.05	−4.40	0.002	−3.13	0.01	−2.22	0.05
With dispersal								
Control	−6.12	0.0002	−0.91	0.39	2.08	0.07	3.02	0.01
Constant	−1.64	0.14	−5.40	0.0004	2.99	0.02	−3.93	0.003
White	−3.11	0.01	−1.47	0.17	−0.93	0.38	−0.94	0.37
Red	0.41	0.69	−2.05	0.07	−3.53	0.007	−3.51	0.006

(Petchey et al. 1997, Heino 1998) even if the spatial correlation of resource fluctuation is identical (as it was here). This is a noteworthy result given that the only difference between the red and white resource fluctuations treatments was the relative amplitude of the component five and nine day periods; because both series shared the same values, although not in the same order, all other statistical characteristics were identical. Theory predicts that populations are unlikely to be greatly influenced by environmental fluctuations with a period inferior to the characteristic response time (1/*r*) of a population, which for *B. calyciflorus*, at 20°C, is 5 d. This suggests that the dominance of the nine day period in the reddened resource fluctuations was responsible for this effect, because no synchrony was observed in the white treatment where the 9-d period had the same power as the 5-d period. More specifically, it is the nine day periodicity of the minima in *C. vulgaris* densities that is the likely cause of this synchrony. Kirk (1998) demonstrated that even brief periods of starvation (or very low algal densities) can induce reduced fecundity and very rapid mortality in *B. calyciflorus* (~2 d), especially following periods of high resource levels. Inspection of Fig. 1 and Fig. 2 indicates a correspondence between the population minima and the lows in algal density. More generally, a similar synchronizing effect of resource variation, that induces mortality or reduced fecundity, has been proposed for a number of microtine rodent and ungulate populations (Bjørnstad et al. 1998, Post and Forchhammer 2002). Post and Forchammer (2002) suggest that population synchrony in northern populations of caribou (*Rangifer tarandus*) and musk ox (*Ovibos moschatus*) is highest after cold winters associated with interannual fluctuations in the NAO. This is linked causally to mortality events via restricted resource availability associated with ice-crust formation. Taken together these results support our hypothesis that the temporal structure of environmental variability may be critical in determining the efficacy of the Moran effect; a conclusion that has gone relatively unnoticed in the literature to date. Large-scale climatic phenomena, like the NAO and El Niño, are known to be dominated by certain periodicities (Appenzeller et al. 1998), and we suggest that their synchronizing effect will depend upon the coherence between these periodicities and the periodicities of the principal vital rates of a focal species.

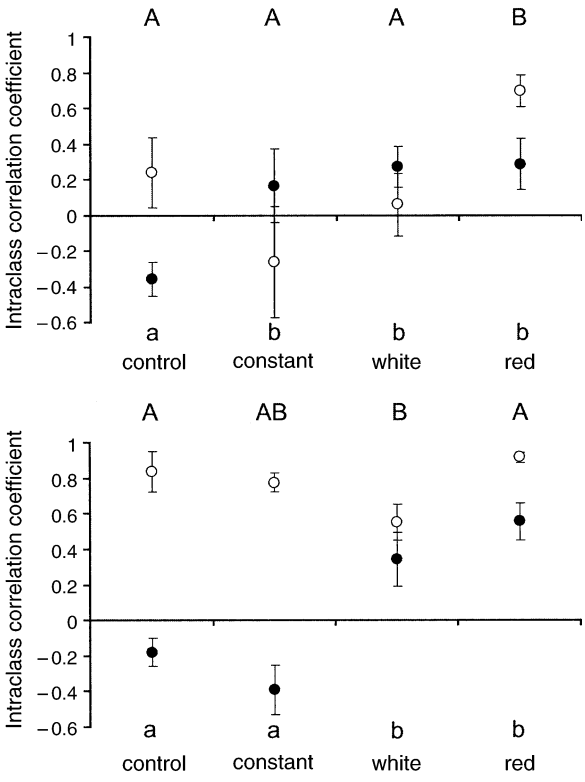

FIG. 3. Population synchrony without dispersal (top panel) and with dispersal (bottom panel). Solid circles correspond to values for interval 1, open circles to interval 2. Error bars show ±SE; different letters indicate statistically significant differences (Bonferroni-adjusted $P < 0.05$) for the first interval (lowercase) and second interval (uppercase) of the experiment.

Dispersal had a clear synchronizing effect on all treatments except the populations exposed to white *C. vulgaris* fluctuations. The strong main effect of dispersal can be seen in the large increases in synchrony in the control × dispersal treatment, in which no resource fluctuations were imposed (Fig. 3b). Here, although the first oscillation of S1 and S2 series was out of phase, by the third oscillation the two series were in close synchrony. In the absence of dispersal, the control populations did not remain negatively correlated (out of phase) and showed a weakly positive correlation. This was expected because in the absence of any synchronizing effect each replicate will diverge slowly from the others (as seen in Fig. 2) so that in the long term there should be no correlation in their fluctuations; the weak correlation we observed (Fig. 3a) was not significantly different from zero. Of particular note in the red dispersal treatment (Fig. 2), where synchrony was greatest, is the divergence in the trajectories of the coupled S1–S2 populations; an effect not apparent in the white dispersal treatment (Fig. 2). Interestingly, only the red × dispersal treatment attained a greater level of synchrony than the control series, although this difference was not statistically significant. The possibility that reddened fluctuations may enhance the synchronizing effect of dispersal, or conversely that white fluctuations may interfere with the synchronizing effect of dispersal, will be an interesting avenue for future research.

We deliberately used a simple dispersal rule that mimicked that used by recent theoretical studies. Furthermore, to aid interpretation we only coupled two populations. Recent theory (Ylikarjula et al. 2000) indicates that the synchronizing effects of dispersal may be strongly dependent upon the dispersal rule used and the number of coupled populations. Future experimental work will assess how robust our results are to changes in the number of populations and the type of dispersal rule connecting them.

Conclusion

Several conclusions stem from this work. The first is that these results confirm a synchronizing effect of both dispersal and environmental variability. In addition we found support for our hypothesis that the temporal structure of environmental variability (relative strength of the component frequencies) may be important in determine the efficacy of the Moran effect. This suggests a frequency explicit analysis of climate driven population synchrony might be useful. Establishing a link between the dominant periods of important climate phenomena (e.g., NAO, El Niño) and those of the principal life-history traits of a study organism would greatly improve our ability to predict when the Moran effect will be the most likely cause of regional synchrony. An immediate question of applied value would be to what extent is the hypothesized link between long term climate change and exacerbated short-term climate variations (Corti et al. 1999) responsible for the synchronized regional species responses to climate change currently being detected (Parmesan and Yohe 2003)? Lastly, these results highlight the utility of experimental model systems as tools for exploring the link between the causality inferred from the statistical analysis of ecological time series, that has been so preponderant in the study of synchrony phenomena, and that formalized in simple strategic models.

Acknowledgments

We thank Catherine Louis-Alexis for help with density estimation. A. Gonzalez acknowledges the financial support of the Quantitative Ecology Coordinated Action Incentive of the Ministry of Research (France). We thank Bernard Cazelles and Tim Benton for their thought provoking discussions, and Gregor Fussmann for his comments on an earlier draft.

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