Ecology, 85(1), 2004, pp. 150–157

RESONANCE INFLATES CARRYING CAPACITY IN PROTIST POPULATIONS WITH PERIODIC RESOURCE PULSES

MARY C. ORLAND[1] AND SHARON P. LAWLER

Department of Entomology, University of California, Davis, 1 Shields Avenue, Davis, California 95616 USA

Abstract. Resonance is an interaction between extrinsic environmental variability and intrinsic population processes that can raise population mean density or amplify environmental fluctuations in systems with periodic environmental fluctuations. This study empirically demonstrates significant effects on population dynamics from resonance and describes the conditions under which they occur. In a laboratory microcosm experiment with the ciliate protist *Colpidium striatum*, resources were periodically alternated between high and low concentrations at different frequencies. Resonance raised the mean population density of rapidly fluctuating treatments by 21% compared to a constant control run at the average nutrient concentration, and eventually approximated the mean density of the highest nutrient control. The resonant resource perturbations occurred on a time scale intermediate to the reproduction and starvation rates of the organisms. It is likely that metabolic nonlinearities in these reproductive and starvation responses interacted with the periodic resources fluctuations of intermediate frequency to produce the population boost through the cumulative storage of resources in the cells of the protists. The populations also showed a frequency threshold effect in the translation of environmental variability into population variability. The patterns of population abundance and variability observed in this experiment indicate that resonance between intrinsic and extrinsic processes may be an important factor to consider in population dynamics.

Key words: environmental variability; microcosms; periodic disturbance; population dynamics; protists; pulsing; resonance; scale.

INTRODUCTION

Ecologists have long debated the relative importance of density dependence and environmental variability to population dynamics (Nicholson and Bailey 1935, Andrewartha and Birch 1954). It is generally agreed that variability in the environment will decrease population abundance and/or increase population variability in single-species systems (May et al. 1974, Henson and Cushing 1997). This is based upon the classic perspective of environmental factors moving a population away from equilibrium, and density dependence bringing the population back toward equilibrium. However, recent work has shown that the phenomenon of resonance can result in higher population abundance in variable environments than a population could achieve in a constant environment (Costantino et al. 1998, Henson 2000). Resonance is a term in physics and engineering for an interaction between two periodic signals that results in amplification or dampening (attenuation) of those signals (Henson 2000), and it will only occur when the two signals operate on specific time scales relative to each other. Resonance in ecology is characterized by a synergistic interaction between intrinsic population processes and periodic extrinsic environmental variability. The very few studies explicitly investigating resonance in ecology fall into two categories, those investigating the resonance in cycling predator–prey systems (Ghosh 1983, King and Schaffer 1999), and those investigating resonance between a consumer and a periodic exogenous fluctuation of resources or environmental conditions (Costantino et al. 1998, Blarer and Doebeli 1999). This study investigates the latter type of resonance.

Research to date has shown there are two different ways in which resonance can arise in populations experiencing periodic environmental disturbances (Costantino et al. 1998, Blarer and Doebeli 1999). An interaction between an extrinsic fluctuation and an independent periodic intrinsic population cycle can result in resonance (Henson and Cushing 1997, Henson 2000). This form of resonance was demonstrated in a microcosm experiment with flour beetles (Jillson 1980, Costantino et al. 1998). The beetle populations experienced an intrinsic population cycle that was the result of stage-dependent cannibalism (Jillson 1980). When the amount of flour available to the beetles was changed periodically, population abundance in the treatment with the most rapid fluctuations increased over a constant control. Subsequent modeling efforts attributed this resonant effect to the increases in flour occurring on approximately the same time scale as the metamorphosis of the most cannibalistic stage of the beetles, thereby by reducing cannibalism rates and increasing population density (Costantino et al. 1998). Theoretical

Manuscript received 20 June 2002; revised 10 February 2003; accepted 14 May 2003.Corresponding Editor: M. A. Lewis.
[1] E-mail: mcorland@ucdavis.edu

work has also asserted that population increases from resonance can occur when there is an interaction between a periodic environmental perturbation and a nonlinear diapause response to that perturbation in a stage-structured population (Blarer and Doebeli 1999). It was shown that if there exists a nonlinear response in the fraction of organisms going into diapause in the face of periodic environmental changes, it is possible for the environmental fluctuations to be amplified via resonance. In addition, mean population density declined relative to a constant environment when a stochastic component was added to the periodic environmental fluctuations in this model. The form of resonance described by this model is different from that described in the flour beetle microcosm because it was not dependent upon an independent intrinsic population cycle, and instead resulted from an interaction between a periodic environmental fluctuation and nonlinear organismal responses to those fluctuations. While some natural populations exhibit intrinsic cycles (e.g., Hamrin and Persson 1986), most do not. This form of resonance thereby has the potential to be more universally applicable.

Whenever there is periodic environmental variability in an ecological system, there is the opportunity for resonance to occur. Periodic environmental fluctuations such as seasons, circadian cycles, tides and El Nino events are widespread (Odum et al. 1995), so the possibility exists for resonance to be a common ecological phenomenon. It is conceivable that many species have their responses to periodic changes in the environment, particularly seasons, timed in such a way as to take advantage of the population boost that results from resonance. Shifts in the seasons with the advent of global warming have caused mismatches between peak food supply and breeding times (Thomas et al. 2001), so global warming could cause population declines if organisms have their responses synchronized to seasons to take advantage of resonance. There may also exist agricultural and biotechnology applications whereby harvests can be increased with less resource input by taking advantage of resonance (Matthijs et al. 1996).

Models specifically addressing periodic environmental changes generally predict lower population abundance or higher variability with increasingly frequent periodic environmental fluctuations (Nisbet and Gurney 1976, Rosenblat 1980, Henson and Cushing 1997). These results are in line with the classic single-species models on the effects of environmental variability on population dynamics, and are exemplified by the case where the basic logistic model with a periodically oscillating carrying capacity shows a decreased mean population density as compared to the steady state (Rosenblat 1980, Cushing 1986). A few more complicated versions of these single-species models allow for periodic environmental variability to increase population abundance over the carrying capacity (Henson and Cushing 1997), such as when the intrinsic growth rate is also allowed to vary periodically (Cushing 1986), or response terms relating population density to periodic environmental variables are nonlinear (Rosenblat 1980).

An experimental system for detecting resonance

An aquatic laboratory microcosm experiment with protists is a particularly appropriate method to document the impact of resonance on population abundance and variability. Microcosms allow theory pertaining to long term population dynamics to be tested with real organisms rather than mathematics (Lawler 1998). The short generation time of protist species (Finlay 1977) allows measurement of sufficiently long-term dynamics for all frequencies of perturbations. We performed an aquatic microcosm experiment with the bactivorous ciliate *Colpidium striatum* in an attempt to document resonance and the conditions under which it will occur. We chose periodic resource alternations between high and low nutrient concentrations as the form of perturbation. Alternating between high and low nutrient levels means that the average external nutrient input is approximately the same across all treatments. With this form of perturbation, the variation of external input is also the same across treatments. Our study organism, *Colpidium striatum*, is not cannibalistic, and does not have the clearly defined stage structure of flour beetles. Therefore, this organism is more similar to the organisms of unstructured, single-species population models. There is no conclusive evidence of strong periodic intrinsic cycles with single-species *Colpidium striatum* populations grown under the conditions of this or any other microcosm experiments, so we expect to find the form of resonance that involves a nonlinear organismal response to environmental fluctuations. A previous microcosm study with aquatic protists showed that population variability can either increase or decrease with the frequency of a periodic resource perturbation depending upon the species identity (Luckinbill and Fenton 1978). Our experiment is one of a small group of microcosm studies investigating the impact of the frequency of environmental change on population dynamics (e.g., Petchey 2000).

There are two distinct criteria that might reasonably be used to infer that a given population subject to environmental fluctuations is ''resonant.'' A resonant population exhibits either (1) a boost in average population density relative to that of a corresponding constant environment, or (2) an amplification of environmental fluctuations. Observation of either of these two effects within a particular frequency band of perturbation is further evidence of resonance. We used these criteria to ascertain whether resonance occurred in our experiment.

Materials and Methods

We grew populations of the bactivorous ciliate *Colpidium striatum* in cultures with a mixed bacterial flora.

Resources were perturbed between high and low concentrations in cycles of 4, 8, 12, 16, 20, and 28 d in length, with three replicates for each time interval treatment. Three sets of control populations were kept under approximately constant resource conditions at high, low, or average nutrient concentrations. The control populations were centrifuged and transferred to fresh nutrient media once every 4 d, which corresponds to the time interval between high nutrient concentration renewals in the 4-d cycle treatment. This is the equivalent control used in other microcosm experiments with similar upward and downward periodic resource manipulations (Luckinbill and Fenton 1978, Jillson 1980). The high nutrient concentration was 1.0 g of powered Protozoa Pellet (Carolina Biological Supply, Burlington, North Carolina, USA) per liter of water, while the low nutrient concentration was 0.2 g of protist pellet per liter. The water was half deionized water and half spring water, with 0.1 g/L of Herptivite herpetological vitamins (Carolina Biological Supply) added to ensure protist vigor. Adding more resources to the media translates directly into an increase in protist density (Kaunzinger and Morin 1998). We assumed that the comparatively rapid response time of the bacteria prevent them from being dynamically important from the point of view of the protists. This is the common justification for considering a single species protist microcosm as a resource–consumer system rather than a predator–prey system, and this method has yielded results consistent with consumer–resource models in the past (e.g., Vandermeer 1969, Morin 1999).

We held environmental conditions for all 27 populations as uniform as possible by keeping them in a circulating water bath at 23°C (±0.01°C). We performed all manipulations under sterile conditions to prevent contamination, and no eukaryote contaminants were detected during the experiment. Populations were kept in 35-mL plastic bottles with the caps loose to allow for air exchange. Changes to a population's resource levels were executed by moving the population to a new solution of bacterized nutrient media. We concentrated the protists by centrifuging the populations at 230 gravities for 5 min. We then removed the old solution from the pelletized protists, added the new nutrient solution, and put the populations into new bottles. This methodology resulted in over 90% of the protists being transferred, and over 80% of the nutrient solution being exchanged (M. Orland, *unpublished data*). Trials indicate that centrifuging at this speed and duration has no detectable effect on the behavior, survival, or reproduction of *Colpidium striatum* (M. Orland, *unpublished data*). We standardized the beginning of the cycles across all treatments by first running each population through a low nutrient phase equal to that treatment's perturbation interval, and commencing the statistical analysis at the beginning of the first high-nutrient phase.

We performed a population density count every second day for 40 d. After thorough mixing, a 3-mL sample of solution was removed from each bottle, and replaced with fresh nutrient media. We used a computer-based image analysis system (NIH IMAGE; available online)[2] to measure the population density in a 1-mL subsample of each replicate. We measured the generation time of *Colpidium striatum* to be 5.0 h under the temperature and average nutrient conditions of this study in a side experiment (as per methods in Holyoak and Lawler 1996), so this experiment ran for ~200 generations.

Return time

We ran a separate experiment to measure the return time of the populations using the same basic techniques and environmental conditions described above. We define return time to be the time it takes for replicate populations with different initial densities but the same nutrient supply to converge to the same density, as in Luckinbill and Fenton (1978). Three initial densities of *Colpidium* spanned the range of densities encountered in the experiment above, each with three replicates. The *Colpidium* were first concentrated to the different initial starting densities using the centrifuge method, and then transferred to new bottles with bacterized media at the average nutrient concentration. We sampled the populations every day, plotted the abundance as a function of time, and chose the time at which the densities converged as the return time. The only nutrient renewal was the replacement of the medium removed from the bottles for sampling. An approximation of the starvation rate of *Colpidium striatum* can also be derived from the high-density replicates in the return time experiment.

Statistical techniques

We plotted and analyzed the time series to determine the effect on population dynamics of the relative timescale of environmental resource fluctuations. We summarized the effect on abundance by computing the mean population density (number of protists/ml of media) for each treatment. In order to make this metric comparable across treatments, we based our calculations on complete upward and downward nutrient cycles. We began the mean density calculation at the first data point in the upward nutrient manipulations, and continued it through the data point at the last complete low nutrient phase. One of the side effects of this method is that there is a difference between treatments in the number of data points for the mean abundance calculations. This is an unavoidable consequence of having perturbation frequencies of different lengths that are not exactly divisible into one another, but it is inherently taken into account in the calculations of the variability and standard errors. We performed an AN-

[2] URL: ⟨http://rsb.info.nih.gov/nih-image/⟩

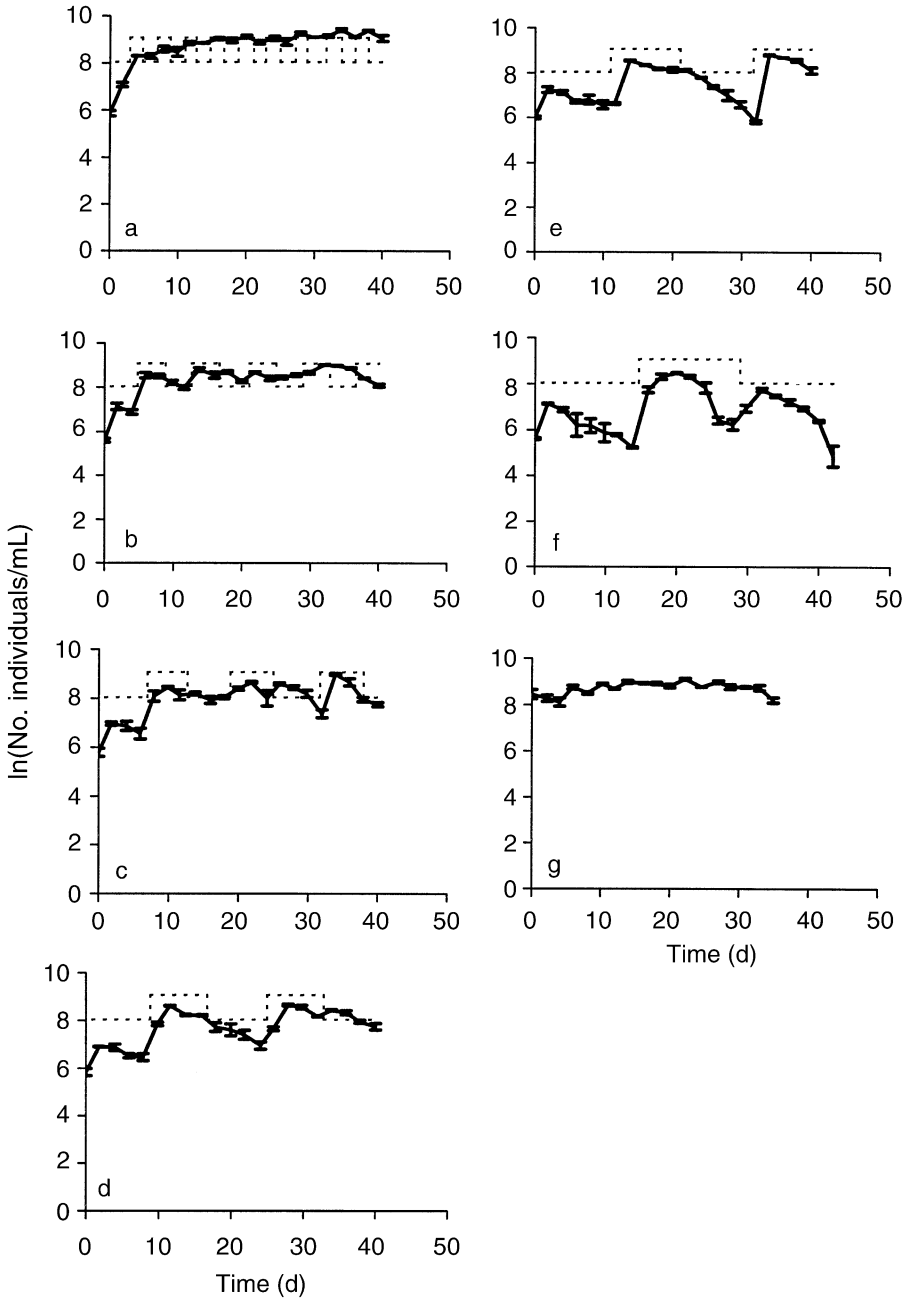

FIG. 1. Time series of the various treatments: (a–f) 4-, 8-, 12-, 16-, 20-, and 28-d perturbation cycles, respectively, and (g) average nutrient control. The dashed lines represent the nutrient conditions of the populations, and the values of those lines are set equal to the average density in the high and low nutrient controls. Error bars represent ±1 SE.

OVA with a posthoc Tukey test in SYSTAT (Systat Software, Inc., Richland, California, USA) to determine whether the mean densities were significantly different ($P = 0.05$), and a Shapiro-Wilk test in SAS (2001) to confirm that the data were sufficiently normally distributed for this technique.

We summarized the effect on population variability by computing the coefficient of variation (CV) of the time series for each treatment, where CV = standard deviation/mean. The CVs were calculated for complete upward and downward cycles. We performed an ANOVA with a posthoc Tukey test to determine whether the coefficients of variation were significantly different, and a Shapiro-Wilk test for normality. We calculated a coefficient of variation for the extrinsic resource fluctuations by considering resource signals that varied between high and low resource levels that differ by a factor of five, with an 85% exchange efficiency. We

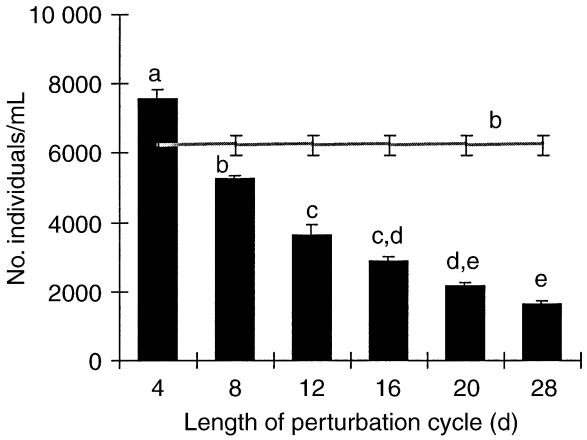

FIG. 2. Mean population densities for the various treatments. The solid line represents the density of the average nutrient control. Note that the mean population density in the 4-d cycle treatment was higher than the average nutrient control, which is suggestive of resonance. The lowercase letters indicate significance ($P < 0.05$). Error bars represent ±1 SE.

used the formula for the standard deviation in which the entire population is known because this is a calculated rather than measured value. The coefficient of variation of the extrinsic resource fluctuations is the same across all treatments, regardless of the length of time between manipulations.

RESULTS

Time series of population abundances revealed fluctuations that correspond to resource manipulations (Fig. la–g). The fluctuations become larger in amplitude in treatments with longer intervals between perturbations. The fluctuations in the control appear to largely correlate with the resource renewal every 4 d, generally showing a slight increase on every second data point (Fig. 1g). The dashed lines in Fig. 1 indicate the extrinsic resource fluctuations between high and low concentrations, and they are plotted at the mean abundance for the high and low controls.

There was a strong pattern of increasing population density with more frequent resource perturbations (Fig. 2). For the treatment with a 4-d perturbation cycle, the average abundance was higher than that of the average carrying capacity by 21% ($P = 0.006$). This result is consistent with the presence of resonance. The mean abundance in the 4-d cycle treatment was still significantly lower than the average density of the high nutrient control, although in the second half of the time series it approximated the mean density of the highest nutrient control.

Population variability increased at longer frequencies of resource manipulations (Fig. 3). The 4-, 8-, and 12-d cycle treatments were not significantly different from each other or from the control in their variability, and all were less variable than the calculated extrinsic variability. The calculated extrinsic variability value was a coefficient of variation (CV) of the imposed fluctuations in the resource perturbations, and was the same across all treatments. The 16-, 20- and 28-d treatments showed increasing variability as the time between resource manipulations lengthened. The 20- and 28-d treatments were more variable than the calculated extrinsic resource variability. The variability of the 16-d treatment appears to be identical to the extrinsic variability value. Interestingly, the half-cycle of this treatment interval corresponded to the time scale of the return time, which was between 7 and 8 d (Fig. 4).

Estimates of starvation rates from the high density replicates (Fig. 4) show that when well-fed *Colpidium striatum* were placed in an environment with insufficient nutrients, the populations were ~5% lower after 2 d, 20% lower after 4 d, 40% lower after 6 d, and 80% lower after 8 d.

DISCUSSION

Abundance effects

The existence of resonance was indicated by the mean population density being 21% greater than the mean control in the treatment with the most rapid resource perturbation interval. If the carrying capacity is defined as the mean density of the control, it is apparently possible for a population to exceed the average carrying capacity of a system indefinitely under resonant conditions. The half-cycle period (2 d) of the resonant treatment frequency was intermediate to the generation time of organisms under abundant resources (5.0 h), and the length of time nearly all organisms could survive a period of insufficient resources (~3 d;

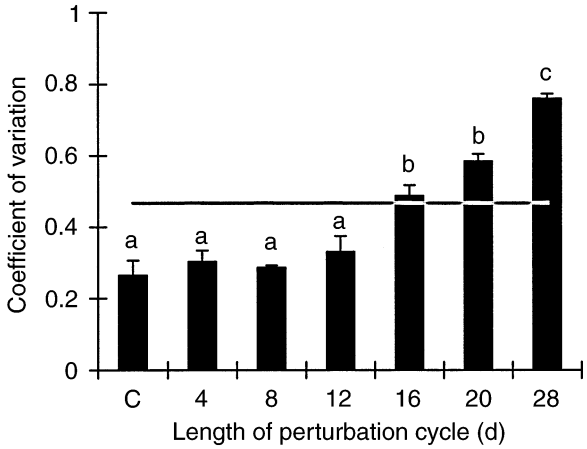

FIG. 3. Population variability for the various treatments, as measured by the coefficient of variation (CV). The solid line indicates a calculated CV of resource fluctuations resulting from experimental perturbations for all treatments. Note the threshold response as a function of perturbation scale in the translation of environmental variability to population variability. For treatments with perturbation cycles ≤12 d, the population variability was not significantly different from the control or the other treatments, whereas variability steadily increased at longer perturbation cycles.

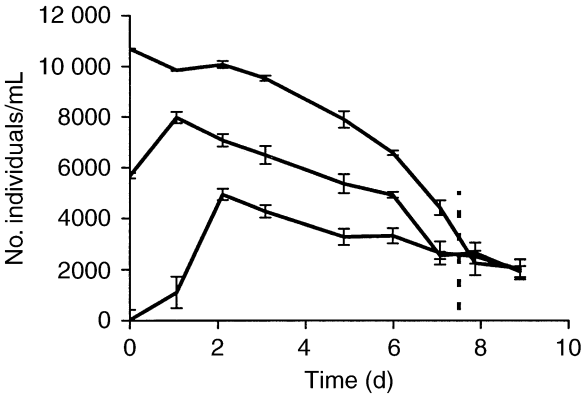

FIG. 4. The populations with different initial densities in the average nutrient concentration media converge to the same density after ~8 d, which is thereby considered to be the return time of the population. Also, the approximate starvation rate of *Colpidium striatum* can be surmised from the decline rate in the highest density replicates.

Fig. 5). It is plausible that metabolic nonlinearities in these reproductive and starvation responses could interact with periodic resources fluctuations of intermediate frequency to produce a population boost. To illustrate, suppose that when nutrients are abundant, the organisms can reproduce quickly, and dedicate a larger fraction of the energy they consume to reproduction and cell growth as compared to situations when resources are more limited. This results in a disproportionately faster storage rate of resources (energy) in the cells of the organisms during high resource pulses. It has been documented that *C. striatum* increase both cell size and total abundance under abundant nutrient conditions (Balciunas and Lawler 1995). In addition, under the resonant treatment perturbation frequency, the starvation rate of the organisms was slow enough that essentially all organisms were able to maintain themselves during the 2-d low-resource periods. This delayed starvation could have been aided by the organisms switching to a slower metabolic rate during times of resource shortage. A cessation of reproduction during the low resources times may also have potentially lessened overexploitation of resources, so that the next high-resource period was yet another period of high-energy storage. The cumulative effect of the change in the balance between reproduction and starvation rates in the resonant 4-d treatment cycle would have been the accumulation of energy within the cells of the population, which may have lead to both the observed boost in mean population density and the increasing population density through time. A parameterized bioenergetics model investigating the nonlinear reproduction and starvation responses necessary for this form of resonance to occur is a logical follow up to this experiment. It was not necessary to invoke bacterial dynamics to explain the observed resonance, although we did not measure bacteria directly so we cannot conclusively rule out the possibility that they played a role in the dynamics.

According to the criteria outlined previously, resonance is substantiated by the boost in population density occurring within a specific frequency band of environmental perturbation. In our experiment, we did not show the existence of an upper bound on this resonant frequency band (Fig. 5). A treatment that could do this would have a cycle length of <5 h, the intrinsic rate of growth of the organisms, because if the resource perturbations were more rapid than the generation time, the organisms would probably average over the extrinsic variability and resonance would not occur. However, executing resource perturbations at the frequency of once every 2.5 h or less is logistically impossible with this experimental system because it takes several hours to complete the nutrient manipulations, and several more hours to count the samples. Limitations in our experimental system thereby prevent us from being able to document the entire frequency band of resonant perturbations, but this could be addressed in future modeling efforts.

The identical result of a population exceeding the carrying capacity at rapid frequencies of resource fluctuations via resonance was found in a microcosm experiment with flour beetles (Jillson 1980, Constantino et al. 1998). Our experiment differs from the flour beetle experiment in that resonance occurred when there was no perceptible independent intrinsic cycle, and the protists are not cannibalistic or strongly stage struc-

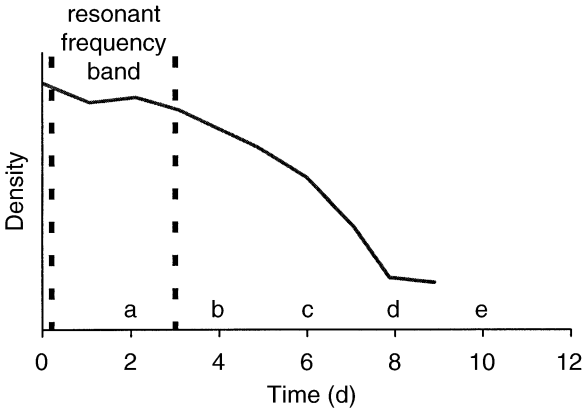

FIG. 5. Illustration of conditions for resonance. The vertical dashed line to the left indicates the generation time of *C. striatum* under abundant resource conditions (5.0 h), and the vertical dashed line to the right indicates the approximate length of time that essentially all organisms can survive a period of resource limitation. This second dashed line is approximated from the line indicating starvation times, which is identical to the high-density treatment in Fig. 4. The letters correspond to the different perturbation frequency treatments, placed at the half-cycle lengths for the 4-d (a), 8-d (b), 12-d (c), 16-d (d), and 20-d (e) treatments. Resonance is expected to occur at frequencies intermediate to the time scales of these reproduction and starvation processes. Only the 4-d cycle (a) meets this condition, and this was the one treatment that evinced resonance.

tured. Our results are similar to the model of Blarer and Doebeli (1999), in that they also showed resonance without an intrinsic population cycle. However, their results differed in that population densities became less abundant and more variable with resonance. Another important difference is that both of these previous models of resonance were stage structured. While *Colpidium* are not strongly stage structured organisms, it may be that physiological structure due to, for example, metabolic nonlinearities in reproduction and starvation responses, plays a role in engendering the observed resonant response. It has been demonstrated that nonlinear responses to environmental conditions as a function of cell cycle in unicellular algae can cause complex dynamics similar to those of stage-structured chemostat models (Pascual and Caswell 1997). The resonance in our experiment has some similarities to these previous studies, but the population boost in conjunction with the lack of both strong stage structure and an intrinsic cycle make it unique. Furthermore, the more general conditions under which resonance occurred in our system suggest that it has the potential to be more widespread in ecological systems, and the documentation of a boost in population density without an increase in variability suggest that resonance has the potential to increase population stability.

It might be objected that observing the highest population density in the shortest perturbation interval treatment is a spurious result because resources are inherently renewed more frequently with more frequent nutrient perturbations. However, we designed the control in such a way that this effect can be distinguished from true resonance. The length of time between resource renewals in the control (every 4 d) was set equal to the length of the shortest treatment perturbation cycle. Because the movement to a low nutrient environment on the second day is a resource decline for the 4-d cycle treatment, its resource renewal rate is once every 4 d, identical to that of the control. Therefore, the resource renewal process alone could, at most, result in a treatment density equal to the control in the shortest period treatment, whereas one exceeding it would indicate resonance. Furthermore, the peak density of the low nutrient control (3800 individuals/mL) is well below the mean density of the 4-d cycle treatment (7800 individuals/mL), indicating that simply having fresh media added mid-cycle is also insufficient to explain the increase in abundance in the resonant treatment.

Variability

There are two qualitatively different patterns of population variability among the treatments, indicating a threshold in the relationship between population variability and the frequency of perturbations. For those treatments with low resource half-cycles longer than the return time (i.e., 16-, 20-, and 28-d cycle treatments), the population dynamics become increasingly variable at longer perturbation intervals. We believe the increasing variability results from the population tracking the intrinsic resource depletion as it increases at longer perturbation frequencies. However, when the half-cycle length is shorter than the return time of 8 d (4-, 8-, and 12-d cycle treatments), the treatments are not significantly more variable than each other, or than the control. This suggests that both the extrinsic resource perturbation and the intrinsic resource depletion do not fully translate into population variability when they occur on a time scale that is rapid relative to the response time of the organisms. Once again, the mechanism behind this threshold in population variability is most likely the storage of resources within the organisms so they can withstand periods of low resource availability, further suggesting that physiological structure stemming from nonlinearities in organismal responses is key to scale dependent responses in population dynamics. Overall, this experiment suggests that environmental resource variability will only translate into population variability when the fluctuations occur on a long time scale relative to the time scale on which the organisms operate. Interestingly, the threshold appears to be crossed at the 16-d cycle treatment interval, which has a half cycle interval of 8 d, equal to the return time of the population. The variability in the 16-d cycle treatment is also identical to the calculated value for the extrinsic variability. These results are generally consistent with previous modeling efforts investigating how the relative time scales of return time and environmental variability impact population stability (May et al. 1974).

Luckinbill and Fenton (1978) achieved this same result of less variable population dynamics at faster frequencies of resource perturbation in a microcosm experiment with *Paramecium primaurelia*. They attributed this result to the ability of *Paramecium primaurelia* to survive periods of low resource availability. In the same experiment, they found the opposite result of increased population variability at the fastest frequencies of resource perturbation for *Colpidium campylum*, a species very closely related to *Colpidium striatum*. The completely opposite responses of two different protist species to the same resource fluctuations were attributed to the more rapid reproductive rate of *C. campylum* increasing the strength of its numerical response, causing the population to ''overshoot'' the carrying capacity. We speculate that the more variable dynamics in their *Colpidium* populations could perhaps have been the result of the type of resonance that amplifies environmental fluctuations.

Conclusions

This experiment documented a form of resonance that increases population abundance as compared to a constant environment control, without increasing population variability. This boost in population density was likely the result of resonant interactions between pe-

riodic environmental resource fluctuations and nonlinearities in reproductive and starvation responses, and it occurred for the treatment frequency intermediate to the time scales of these reproduction and starvation processes. The resonance found in our experiment has some similarities to previous studies, but it also has some unique features, such as a lack of strong stage structure, that provide a challenge to theorists. Furthermore, the more general conditions under which resonance occurred in our system suggest that it has the potential to be more widespread in ecological systems. Higher abundance and lower variability are traits commonly associated with more stable and persistent populations (Connell and Sousa 1983, Goodman 1987). If resonance is documented as raising mean population density without changing population variability, it may be an important consideration for assessing population persistence in some circumstances. In general, more explicit analysis of resonance and other interactions between intrinsic and extrinsic population processes may be important to understanding population dynamics in periodically variable environments.

Acknowledgments

We wish to thank Alan Hastings and Marcel Holyoak for their helpful advice and comments during the design and analysis of this experiment. This study was funded by a National Science Foundation Graduate Research Fellowship, in conjunction with a University of California, Davis Jastro-Shields grant and an Ecology Graduate Group block grant.

Literature Cited

Andrewartha, H., and L. Birch. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago, Illinois, USA.

Balciunas, D., and S. Lawler. 1995. Effects of basal resources, predation, and alternative prey in microcosm food chains. Ecology **76**:1327–1336.

Blarer, A., and M. Doebeli. 1999. Resonance effects and outbreaks in ecological time series. Ecology Letters **2**:167–177.

Connell, J., and W. Sousa. 1983. On the evidence needed to judge ecological stability. American Naturalist **121**:789–823.

Costantino, R. F., J. Cushing, B. Dennis, R. Desharnais, and S. Henson. 1998. Resonant population cycles in temporally fluctuating habitats. Bulletin of Mathematical Biology **60**: 247–273.

Cushing, J. 1986. Oscillatory population growth in periodic environments. Theoretical Population Biology **30**:289–308.

Finlay, B. 1977. The dependence of reproductive rate on cell size and temperature in freshwater ciliated protozoa. Oecologia **30**:75–81.

Ghosh, P. 1983. Resonance in predator–prey systems. Lecture Notes in Biomathematics **52**:283–289.

Goodman, D. 1987. The demography of chance extinction. Viable populations for conservation. Pages 11–35 *in* M. Soule, editor. Cambridge University Press, New York, New York, USA.

Hamrin, S., and L. Persson. 1986. Asymmetrical competition between age classes as a factor causing oscillating populations in an obligate planktivorous fish species. Oikos **47**: 223–232.

Henson, S. 2000. Multiple attractors and resonance in periodically forced models. Physica D: Nonlinear Phenomena **140**:33–49.

Henson, S., and J. Cushing. 1997. The effect of periodic habitat fluctuations on a nonlinear insect population model. Journal of Mathematical Biology **36**:201–226.

Holyoak, M., and S. Lawler. 1996. The role of dispersal in predator–prey metapopulation dynamics. Journal of Animal Ecology **65**:640–652.

Jillson, D. 1980. Insects respond to fluctuating environments. Nature **288**:699–700.

Kaunzinger, C., and P. Morin. 1998. Productivity controls food-chain properties in microbial communities. Nature **395**:495–497.

King, A., and W. Schaffer. 1999. The rainbow bridge: Hamiltonian limits and resonance in predator–prey dynamics. Journal of Mathematical Biology **39**:439–469.

Lawler, S. 1998. Ecology in a bottle. Experimental ecology: issues and perspectives. Pages 236–253 *in* W. Resetarits and J. Bernardo, editors. Oxford University Press, New York, New York, USA.

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

Matthijs, H., H. Balke, U. Van Hes, B. Kroon, L. Mur, R. Binot. 1996. Application of light emitting diodes in bioreactors: flashing light effects and energy economy in algal cultures (*Chiarella pyrenaidasa*). Biotechnology and Bioengineering **50**:98–107.

May, R., G. Conway, M. Hassell, and T. Southwood. 1974. Time delays, density dependence and single species oscillations. Journal of Animal Ecology **43**:747–770.

Morin, P. 1999. Productivity, intraguild predation, and population dynamics in experimental food webs. Ecology **80**: 752–760.

Nicholson, A., and V. Bailey. 1935. The balance of animal populations, part 1. Proceedings of the Zoological Society, London **3**:551–598.

Nisbet, R., and W. Gurney. 1976. Population dynamics in a periodically varying environment. Journal of Theoretical Biology **56**:459–475.

Odum, W., E. Odum, and H. Odum. 1995. Nature's pulsing paradigm. Estuaries **18**:547–555.

Pascual, M., and H. Caswell. 1997. From the cell cycle to population cycles in phytoplankton nutrient interactions. Ecology **78**:897–912.

Petchey, O. 2000. Environmental colour affects aspects of single-species population dynamics. Proceedings of the Royal Society of London B **267**:747–754.

Rosenblat, S. 1980. Population models in a periodically fluctuating environment. Journal of Mathematical Biology **9**: 23–36.

SAS Institute. 2001. SAS version 8.2. SAS Institute, Cary, North Carolina, USA.

Thomas, D., J. Blondel, P. Perret, M. Lambrechts, and J. Speakman. 2001. Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. Science **291**:2598–2600.

Vandermeer, J. 1969. The structure of communities: an experimental approach with protozoa. Ecology **50**:362–371.