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REGULATION AND ENVIRONMENTAL VARIABILITY IN EXPERIMENTAL POPULATIONS OF PROTOZOA[1]

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Abstract. Regulation of population size is described for 2 protozoan species in environments that become progressively more variable in time. The ciliate, *Colpidium campylum*, rapidly adjusts population levels to fixed equilibria set by bacterial food supply. As the equilibrium is varied more frequently, tracking populations of this species destabilize and eventually become extinct. A much larger species, *Paramecium primaurelia*, regulates slowly to fixed equilibria but assumes more even densities in variable environments. Effects of changing environments are determined here by the frequency and not the magnitude of changing equilibria.

Key words: bacteria; Colpidium*; density-dependence; equilibrium; fluctuation; perturbation;* Paramecium*; population; protozoa; stability; variability.*

INTRODUCTION

One fundamental area of theory that has often been the subject of diverse and conflicting viewpoints among ecologists, concerns how natural populations are controlled. In relation to this, a variety of possible circumstances are recognized: At one extreme, populations are usually density-controlled and at or near their equilibrium while at the opposite extreme, populations are limited in such a way that they rarely approach levels at which density-controls act. Most populations are thought to exist under somewhat intermediate circumstances, sometimes being under density-control near their equilibrium and at other times not. We assume here only that there are some populations which, for at least some period of time, are at or near their maxima and also that the factors that determine equilibrium density may not necessarily remain constant. This study is concerned with the consequences to a species of its particular ability to reach and hold that equilibrium as it varies in time.

Related theoretical areas have often dealt with the dynamic behavior of model populations in fluctuating environments (Fretwell 1972, Levins 1969, Lewontin 1969, Nisbit and Gurney 1976, May 1974, 1975, May and Oster 1976). However, few studies have considered population regulation in terms of adaptive strategy. Southwood et al. (1974) weigh this problem by examining some effects of varying and nonvarying environments on the ability to regulate. This study suggests that gradually changing environments in which population controls are heavily equilibrium dependent, favor slowly regulating populations that deviate little about their equilibrium. Whereas, fluctuating environments where populations are in constant pursuit of dynamic equilibria should favor rapidly regulating species that vary widely. Since many such basic aspects of regulation are as yet uninvestigated, we attempt here to supply some initial experimental evidence of the effectiveness of regulation in several species in terms of population stability, in environments that vary to a greater or lesser degree.

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METHODS

One problem in conducting experiments of this type is that in order for regulation in different species to be compared on an equivalent basis, the measurement of regulation here must be made independently of their various controlling equilibria. Nicholson (1957) and later Murdoch (1970) have suggested a method that permits this in which the densities of a subdivided population are both increased above and reduced below that of a control. Regulating populations then converge at their own rate to the density maintained by the control population. The speed with which displaced populations converge to their equilibrium density can then be compared for different species.

While the use of a field system would add relevance to these experiments, investigating questions of equilibria and the dynamic response of species to them requires species with short generation times and readily manipulable population densities. Several kinds of ciliated protozoans fit these requirements well and have long served as model systems in such studies.

Three ciliate species were selected for comparison here: *Paramecium primaurelia*, the largest in size and slowest growing, *P. tetraurelia*, intermediate in size and growth rate, and *Colpidium campylum*, the smallest and most rapidly growing. All 3 species are cultured in Cerophyl medium, prepared as in Sonneborn (1970) and innoculated with the bacteria *Enterobacter aerogenes*. Replicate populations were grown in 5 cc of bacterized Cerophyl from which 0.5 cc aliquots were removed daily. Cell densities were counted by dilution, if necessary, and the sample replaced with 0.5 cc fresh bacterized medium. Population numbers are determined in these experiments by the quantity of bacteria supplied.

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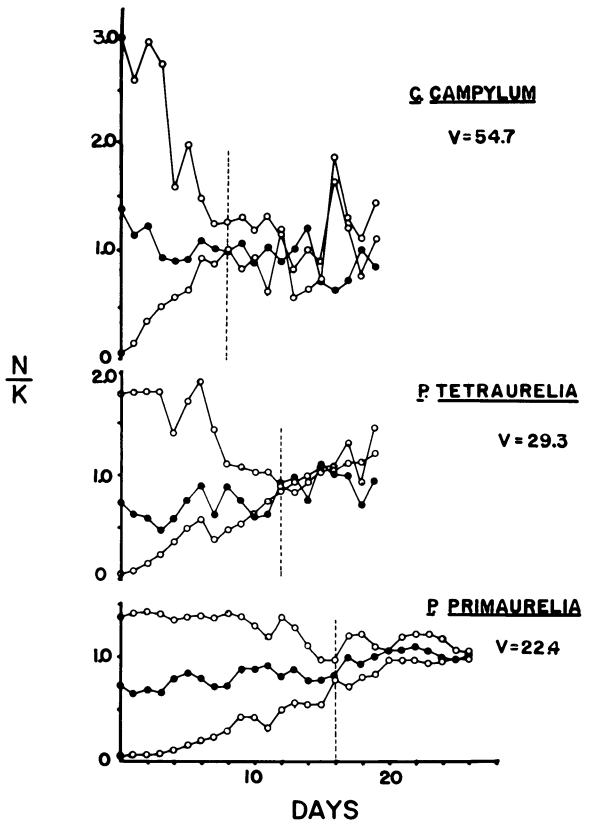

FIG. 1. Populations of 3 ciliate species regulate to equilibria after displacement. Convergence (dashed line) and coefficient of variation (V) is shown for each species.

These 3 species were chosen for comparison here as representatives of a number of bacteria-feeding ciliates which seem empirically to show similar patterns in the dynamics of their populations. That is, smaller, more rapidly growing species respond more quickly to changes in bacterial food level. This would, of course, be predicted from their comparatively high value of r_m. However, strong density-dependence seems to be accompanied here by wide population variability about the equilibrium with frequent and rapid overshooting followed by quick reversals in trend. Larger species with a lower r_m respond more slowly, as might be expected, but they adhere much more closely to the equilibrium density with relatively minor fluctuations about it. Thus, a sort of spectrum seems empirically evident here, ranging from species that respond rapidly and crudely to those that respond slowly and accurately.

The species *P. primaurelia*, *P. tetraurelia* and *C. campylum* of this study vary in both size and growth rate and as such should exhibit the trends in regulating to equilibria. To test this, 6 replicate populations of each of these species were grown to their saturation limit in 0.15% Cerophyl (Sonneborn, 1970) where they were allowed to adjust for 14 days.

At this time, 2 of the replicate cultures were retained untreated as controls. Densities of populations in the other 4 experimental cultures were then standardized by combining them (20 cc) in a single tube, briefly vortexing and then redispensing them (5 cc each) to their original tubes. Equalizing experimental cultures in this way reduces the variance that would result from differences in density when populations are displaced.

Experimental populations were then displaced from their equilibrium. Low speed hand-centrifugation was used to concentrate ciliate populations. Experimental cultures were briefly centrifuged until cells concentrated in a loose pellet at the bottom. This dense population was then removed using a long tip pipette from 2 of the experimental populations and added to each of the other 2. Using this method more than 95% of populations could be removed from each culture in approximately 0.25–0.5 cc, leaving only a few cells behind to initiate growth again. Cell growth rate and motility appeared unaffected by the use of this technique. Thus, for each species there were 2 untreated control populations and 4 experimental populations. Two of these had cell densities near zero and 2 were approximately twice the density of populations before displacement. Converging experimental populations were sampled daily over the following 28–30 days.

Regulation in experimental populations

Figure 1 shows the density changes in displaced populations of the 3 species. Experimental populations converge to the same approximate density as controls. Saturation density (K) is estimated here as the average density populations maintain between convergence and the termination of the experiment. The densities of displaced populations are expressed as a percentage (N/K) of this mean value, allowing comparison of different species. Thus, Fig. 1 shows that although a constant quantity of bacteria is supplied daily during these experiments the equilibrium to which populations converge after displacement may vary somewhat. More importantly, the 3 species demonstrate different rates of regulation to equilibria, with the smaller, faster growing species *C. campylum* regulating the most rapidly (7–8 days). As shown by the coefficient of variation (V), these species also demonstrate highly different amounts of variability around their equilibrium densities, with *C. campylum* the most variable and *P. primaurelia* varying least. These species, then, range in character from a speedy but variable regulator on the one hand to a slow and relatively exacting species at the other extreme.

The patterns of regulation shown serve as useful descriptions only under limited circumstances. The equilibria to which species adjust here are relatively constant and set by the predictable supply of bacteria in the system. For natural populations, however, variations in the level of such controlling factors must more often be the rule. The role that regulatory ability

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plays in maintaining constant population numbers must be viewed, therefore, in relation to changing environmental conditions. Thus, it seems reasonable to ask whether population responses to varying environments reflect the same regulatory patterns shown here under constant conditions. Do slowly regulating species lag behind and thus vary more widely, while fast regulators closely track the changing equilibrium? Or does instability enhance the tendency of strong regulators to overcompensate, causing wider oscillations?

Fluctuating experimental equilibria

For species adjusting to variable equilibria, 3 circumstances seem possible: (1) The controlling equilibrium (H) changes less frequently than the time it takes for the species to regulate to it (τ). Such populations are usually closely adjusted to their equilibrium ($\tau/H < 1.0$); (2) the time between changes in equilibrium is equal to that required for the population to regulate to them ($\tau/H = 1.0$) and; (3) controlling equilibria change before populations regulate to them ($\tau/H > 1.0$). Such populations seldom or never reach equilibrium.

Since the level of bacteria determines population numbers in these systems, the time that equilibria remain constant can be varied by simply changing the food level supplied to systems more or less frequently. The relative abilities of fast and slow regulating species at maintaining constant population sizes can then be compared in several environments ranging in character there from highly constant ($\tau/H < 1.0$) to highly variable ($\tau/H > 1.0$).

In order to thow this, different concentrations of bacterial food were prepared by modifying the standard preparation of Cerophyl. Sterile, filtered (0.45 μ), aged Cerophyl (Sonneborn, 1970) was used to dilute the fresh bacterized medium (0.15%) down to 0.075% or 0.05% strength. Bacterial concentrations were varied in experiments then, between a high level (full strength medium) and a lower level (dilute medium), for each species.

When changing from one food level to another, the protozoans were concentrated by low speed centrifugation and resuspended in the desired dilution of medium. That same concentration of medium was resupplied in daily sampling of the populations until the equilibrium was shifted again. Food levels for *P. primaurelia* then, varied between full strength (0.15%) and 0.05% (⅓ strength). For *C. campylum*, concentration varied between full strength and 0.075% (½ strength). The lower concentrations differ because of diminished growth of *C. campylum* in 0.05% medium. Each species, then, had a high and low equilibrium level, to which they could regulate. Figure 2 shows the convergence of replicate populations of each species to both upper and lower equilibria.

Food levels alternated between high and low densities at 3 frequencies. Using the times for regulation estimated from Fig. 1, at the lowest frequency, alternating high or low food levels were held constant for 21 consecutive days. This assured the complete equilibration of populations at either level and therefore, $\tau/H < 1.0$ here. At the intermediate frequency bacterial levels alternated at 2-week intervals. In the most changeable environment, equilibria were alternated at one week intervals. For populations in this environment, then, $\tau/H > 1.0$.

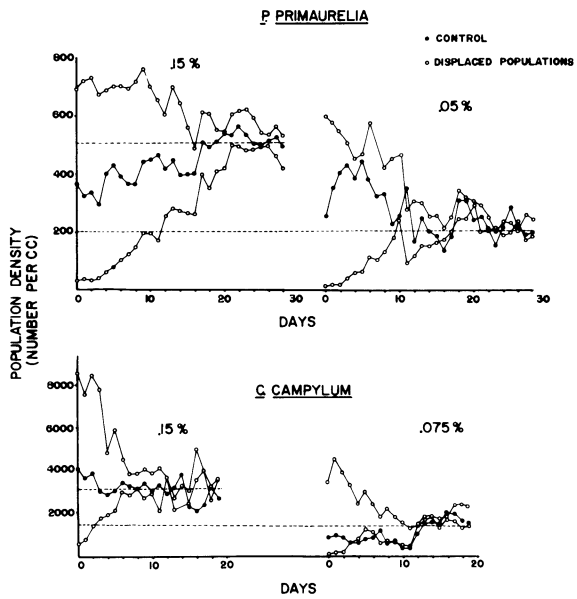

FIG. 2. Compares regulation of 2 species in full strength (0.15%) and dilute media. Populations converge to lower levels in reduced bacterial concentrations.

This experiment tests the effectiveness of these species at regulating in a changing environment. Although predictable, the equilibria of this experiment become progressively less stable in time. Figures 3 and 4 show the average for 4 replicate cultures of each species under this treatment. The frequency and magnitude of changes in the level of bacterial food supplied, as determined by the dilution of medium, are shown by the dashed line. Bacterial levels decline here as the protozoans feed and are resupplied after daily sampling. Although bacterial concentrations are comparatively constant at high or low levels, the ciliates undergo a brief initial increase after equilibria are shifted. Rather than closely tracking the changing equilibrium, the strict regulator, *C. campylum*, destabilizes in oscillations of increasing amplitude and becomes extinct after more than 175 days. On the other hand, *P. primaurelia*, a comparatively sluggish regulator, assumes more even population levels as the environment becomes more variable.

In analyzing these results it should first be stated that populations of *C. campylum* and *P. primaurelia* are limited from further increase here only by the quantity of bacterial food. Even at peak densities in these experiments, populations will increase further if

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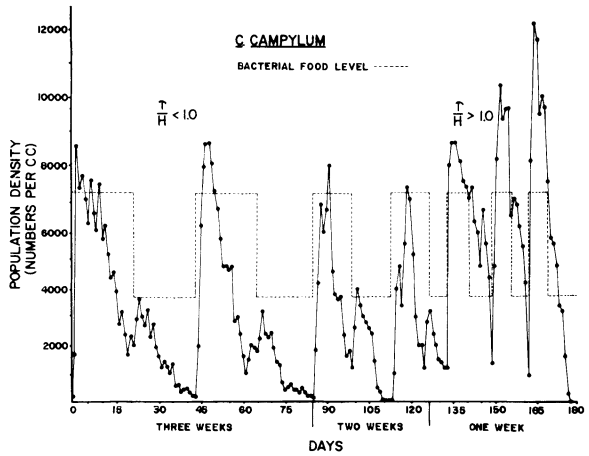

FIG. 3. *Colpidium campylum* populations regulate as bacterial concentrations fluctuate. The frequency and relative magnitude of changing levels of bacteria supplied are shown by the dashed line. Alternating bacterial levels initially vary at intervals of 3 weeks and in more variable environments at 1-week intervals.

additional bacteria are supplied. The question of interest here is: What mechanisms in these species could result in their nearly opposite responses to a shifting food supply?

The differential responses of the 2 species shown here may logically result from either of the following: (1) If *C. campylum* were a more efficient bacterial feeder than *Paramecium*, then at high densities, this species might deplete all the available bacteria. Other studies (Luckinbill 1978) have shown the opposite to be true. *Paramecium primaurelia* is a far more efficient feeder here and can grow in bacteria concentrations that are limiting for *C. campylum* populations. (2) The unequal responses of these species may result from their differences in body size. That is, the larger per capita consumption of bacteria and size of *P. primaurelia* produce a slower numerical response and sustain this species while the smaller *C. campylum* is forced to decline.

Although this hypothesis seems compatible with results thus far, comparing survivorship in declining experimental populations is made difficult by the disparate densities the 2 species reach. But if the hypothesis is correct, then comparing the survivorship of the species in exhausted medium should show *C. campylum* to be highly inferior to equal densities of *Paramecium*. To test this, 50 *P. primaurelia* and 50 *C. campylum* were introduced separately into 0.5 cc of sterile, filtered, aged (Sonneborn 1970) Cerophyl, in each of 3 1.0 cc depression spot plates. Populations were censused daily and replaced in the same medium.

Figure 5 compares the average of 3 replicates for each species and shows their decline in depleted medium. Both species undergo a brief initial increase. The cause of this is uncertain but it probably results from reinoculation of the aged medium from bacteria introduced with the cells. *Colpidium campylum* is more seriously affected by the low bacterial level and becomes extinct after 14 days. *Paramecium*, however, declines comparatively little and other experiments have shown such populations to persist for several weeks before extinction. *Colpidium campylum* then, becomes extinct here because it is more sensitive to a reduced food level and declines before an adequate supply is restored.

Implicitly, these results suggest also that the stability or instability of this system is fixed by the frequency of change in the environment and is relatively unrelated to the amplitude that oscillating populations experience here. That is, if the principal determinant of whether such a system shall continue or become extinct is simply the length of time a species can starve

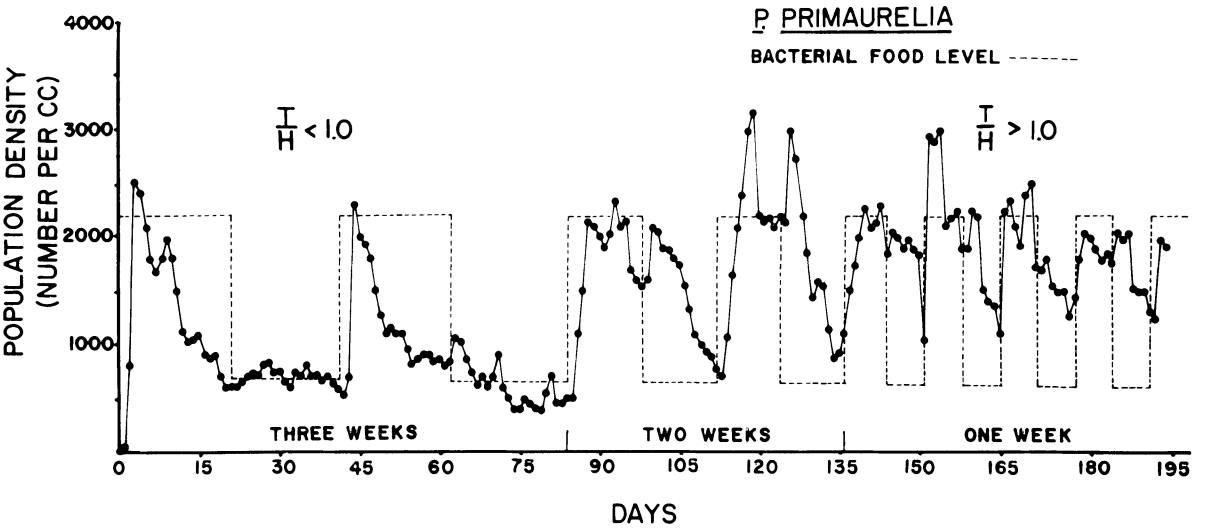

FIG. 4. *Paramecium primaurelia* populations assume a more even density as bacterial levels fluctuate more frequently.

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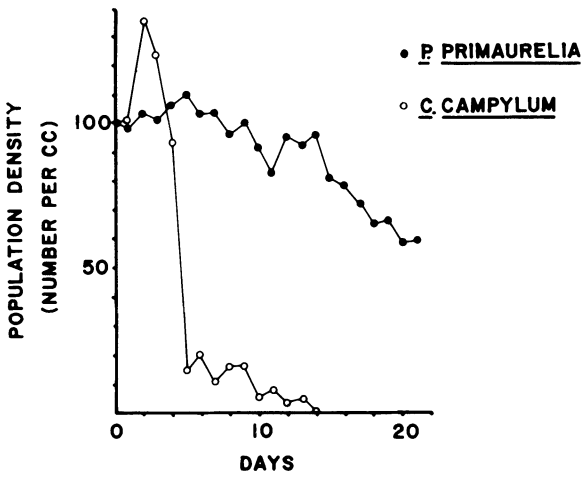

FIG. 5. *Colpidium campylum* declines rapidly to extinction in depleted medium while *Paramecium* responds more slowly.

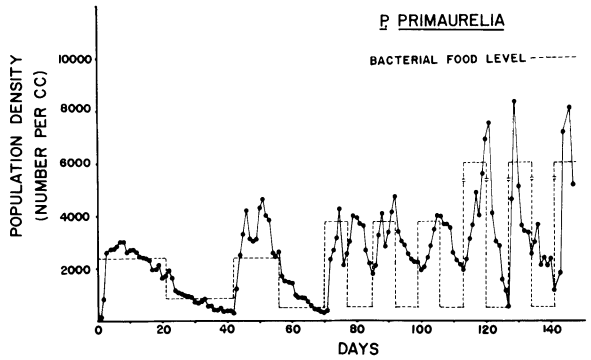

FIG. 6. *Paramecium primaurelia* responds to changing concentrations of bacterial food that progressively vary in both amplitude and frequency.

at the population nadir, then so long as the frequency of equilibrium reversals remains constant, *P. primaurelia* should persist regardless of how wildly populations are made to oscillate.

To test this prediction, replicate populations of *P. primaurelia* were treated as before with food levels alternating between high and low at 3-week intervals initially, to intervals of 1 week finally. These populations were also, however, made to oscillate in progressively more violent fashion by varying the levels of bacteria to which cultures adjusted. That is, the amplitude of the equilibrium level was varied here as well as the frequency.

Four replicate populations of *Paramecium* were allowed to adjust their densities in 0.25% Cerophyl (Sonneborn 1970). Then equilibria were alternated between high and low at 3-week intervals and over a 3-fold range in concentration from 0.25% Cerophyl at the high level, down to 0.08% strength at the lower level. This was followed by alternating bacterial levels at 2-week intervals and over a 5-fold range. Bacterial concentrations varied here from 0.25% strength Cerophyl diluted to a lower concentration of 0.05%. As Fig. 6 shows in each case, experimental populations at first fluctuate but then assume progressively more even numbers. Therefore, in the final oscillations, food levels alternated at 1-week intervals, but the upper equilibrium was enriched far above that of the 0.25% concentration media by the addition of extra bacteria. To obtain the enriched medium, 2 loopfuls of *Enterobacter aerogenes* were suspended in 5 cc bacterized Cerophyl. At first, approximately 0.15 cc of this was added to each culture in addition to the fresh bacterized Cerophyl. In the 3 final oscillations of this experiment, 0.5 cc of this heavily enriched medium was fed to cultures instead of the standard Cerophyl preparation. Dilution counts of viable bacteria plated on Cerophyl-agar were compared for these populations at their nadir (1.5×10^6 cells/cc), with those resuspended in heavily bacterized medium (4.6×10^8 cells/cc). Hence levels of bacteria here varied over a 300× range in concentration (broken dashed line of Fig. 6). In sum, in this experiment equilibria became less stable in 2 ways, the amplitude increased from a 3-fold initial range to a 300-fold range, and, concomitantly, the frequency increased from 1/6 to ½ cycle per week.

As Fig. 6 indicates, even under these extreme changes in amplitude, *Paramecium* populations begin to stabilize and assume more even densities. As in the previous experiment, large numbers of small recently divided individuals with diminished energy reserves are the first to starve after bacteria are depleted. Only larger individuals survive population crashes and at the nadir of oscillations these cells predominate. They gradually decline in size until bacteria are again replenished. Although *P. primaurelia* temporarily destabilizes, it readily survives fluctuating equilibria that are several orders of magnitude more severe than in previous experiments where *C. campylum* became extinct.

CONCLUSIONS

These experiments have shown the following: (1) Species respond differently to changing environments; one species that rapidly regulates its population density becomes highly unstable when tracking a fluctuating equilibrium, whereas a slower regulating species becomes more stable, and assumes relatively even population densities. (2) The comparatively large size and greater individual consumption of bacteria by *Paramecium* sustains this species through periods of depleted food supply during the wide fluctuations of equilibria here. (3) The differential effects of this environment are determined here more by the frequency of environmental fluctuations than by their magnitude.

The species chosen were selected for use as representatives of several comparatively similar species

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that reflect the spectrum of characters examined. Two things are evident: (1) The dynamics of a species in adjusting to stable equilibria may be totally unrepresentative of its performance in changing environments. That is, strong regulatory ability neither assures that constant population numbers will be maintained nor that populations will hold closely to a varying equilibrium. (2) Changes in population size are not necessarily indicative of the dynamics of the controlling equilibrium. This is particularly well shown by the fact that *Paramecium* holds relatively even densities, although equilibrium levels fluctuate widely.

Acknowledgments

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