FOOD WEB ARCHITECTURE AND POPULATION DYNAMICS IN LABORATORY MICROCOSMS OF PROTISTS

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Abstract.—In theory, food chain length and omnivory are pivotal elements of food web structure that can affect the population dynamics of species within the web. Long food chains are thought to be less stable than shorter food chains, and omnivores are thought to destabilize food webs, although populations of omnivores may be more stable than populations of nonomnivores. In three of four simple food webs assembled from bacteria and protists in laboratory microcosms, the abundance of bacterivorous protists varied more over time when the species occurred in longer versus shorter food chains. The abundance of protists attacked by omnivorous top predators was either more or less temporally variable than in webs where top predators fed only at one adjacent trophic level, depending on the particular combination of interacting species. The abundance of omnivorous top predators varied less over time than the abundance of top predators restricted to feeding only at an adjacent trophic level. Observations of increased temporal variation in prey abundance in longer food chains and low temporal variation in omnivore abundance agree broadly with several predictions of food web theory. The observation that different species in similar trophic positions can exhibit very different dynamics suggests that stability may depend on complex interactions between species-specific life-history traits and general patterns of food web architecture.

Links between trophic complexity and population dynamics remain largely conjectural, even though theoretical relations between complexity and stability have motivated ecological research for many years (MacArthur 1955; Elton 1958; Pianka 1966; May 1973; Goodman 1975; McNaughton 1988). For example, simple mathematical models of food webs suggest that omnivory and food chain length are key aspects of trophic complexity that can affect population dynamics, but few empirical tests of these predictions exist (Pimm 1984; Pimm and Kitching 1987; Lawton and Warren 1988; Allen-Morely and Coleman 1989).

Here we describe how the population dynamics of protists vary with food chain length and the presence or absence of omnivory by top predators in simple laboratory microcosms. In particular, we test predictions of Pimm and Lawton's (1977) models, which suggest that longer food chains are dynamically unstable relative to shorter food chains. These conclusions were based on two kinds of evidence gleaned from simulations of model food chains of different lengths: the local stability of model food chains (e.g., are populations in a particular chain

locally stable?) and the return times for model chains that were locally stable (e.g., how rapidly do populations in a locally stable food chain return to equilibrium following an arbitrarily small perturbation?). All of Pimm and Lawton's (1977) model food chains composed of four species (without omnivores) arranged in two, three, or four trophic levels were locally stable, but longer food chains exhibited longer return times after perturbations. In contrast, most (78%) of the three- or four-level chains with omnivorous top predators were locally unstable, with the remaining locally stable models having return times that were somewhat shorter than those seen for model chains of similar length without omnivores.

Early surveys of natural communities also suggested that omnivorous species were relatively rare (Pimm 1980, 1982), although recent descriptions of other natural food webs indicate that omnivores are common in some systems (Walter 1987; Sprules and Bowerman 1988; Warren 1989; Winemiller 1990; Hall and Raffaelli 1991; Polis 1991).

It seems unavoidable that any empirical tests of food web theory will be complicated by the fact that the criteria used to evaluate the stability of model systems are exceedingly difficult to measure in most experimental systems. Much food web theory involves comparisons of the classic mathematical definitions of the local stability and return times (e.g., the tendency to return to an equilibrium after a perturbation) of relatively simple multispecies models. Local stability and return times depend on the eigenvalues of the Jacobian matrix for the system of equations describing the food web, which in turn depend on the parameters of the specific equations describing each population in the community. It is notoriously difficult to estimate accurately the parameters needed to evaluate the stability of analogous experimental systems (see, e.g., Pomerantz 1981). The models also assume that interactions among species are linear and additive, which is the case in some systems (see, e.g., Vandermeer 1969) but not in others (Goodman 1975; Stoecker and Evans 1985). These problems collectively argue against the wisdom of assessing the stability of experimental systems by first fitting the parameters of an analogous model, and then using those parameters to evaluate the eigenvalues of the corresponding Jacobian matrix. Instead, we chose to directly measure aspects of the population dynamics of species that are likely to be correlated with the local stability, return times, or persistence of populations.

Reasonable empirical tests of food web theory hinge on identifying parallels between the dynamic behavior of model food webs and the measurable dynamics of experimental populations. There are three common empirical measures of stability: the length of time that a species persists, the temporal variability of population sizes (usually the standard deviation of the log abundance of each species over time: Williamson 1984; Connell and Sousa 1983; Redfearn and Pimm 1988; although the coefficient of variation may be more appropriate for some systems: McArdle et al. 1990), and, less directly, "return time," the time elapsed until the community returns to its previous state following a perturbation. Populations in locally unstable systems should either go extinct or exhibit temporal fluctuations associated with limit cycles and chaos (Beddington et al. 1976). These empirical measures may not correspond directly to mathematical definitions of stability, but they have the clear advantage of ease of measurement. For example, high

temporal variability in abundance need not imply local instability around an equilibrium point (Schoener 1985). However, measurement of temporal variability does allow comparisons of the relative population fluctuations of species embedded in food webs of differing architecture.

We tested whether position in the food chain affected population dynamics by comparing the mean abundance and temporal variation in abundance of two bacterivorous ciliates, *Tetrahymena pyriformis* and *Colpidium striatum,* when each was the top predator or penultimate predator in the food chain. We also compared the dynamics of a facultatively omnivorous ciliate, *Blepharisma americanum,* when it fed only as a bacterivore to its performance when it also fed omnivorously on bacteria and other bacterivorous ciliates. To assay whether an omnivore was more stable than nonomnivores, we compared the population dynamics of *Blepharisma* to the dynamics of two nonomnivorous predatory sarcodines, *Amoeba proteus* and *Actinosphaerium eichhornii*. Finally, to test whether omnivores affected prey stability, we compared the temporal variability of the two bacterivorous prey species when they were preyed on by omnivorous *Blepharisma* or nonomnivorous *Amoeba* and *Actinosphaerium*. If food webs containing omnivores tend to be unstable, populations in those food webs should vary more in abundance and/or go extinct more often than populations in food webs without omnivores.

METHODS

Food Web Assembly and Monitoring

Our detritus-based food webs (see figs. 1 and 2) contained an initially similar assemblage of bacteria that were prey for either of two species of small bacterivorous ciliates, *Colpidium* or *Tetrahymena*. Our stock cultures of each protist were initially derived from a single cell of each type, to ensure that each culture represented a single species. We constructed food webs containing each bacterivore that differed in food chain length. In short food chains (length 2) bacterivores were the top predators. In long food chains (length 3) an additional top predator fed on the bacterivores. Long food chains containing each bacterivore also differed in whether the top predator was an omnivore or nonomnivore. We determined that the omnivore (the large ciliate *Blepharisma*) could grow on a bacterial diet alone or on a combined diet of bacteria and bacterivorous ciliates (see Results and Discussion). Direct inspection of food vacuoles confirmed that the omnivore *Blepharisma* also consumed small bacterivorous ciliates. Two species of nonomnivore predators (the sarcodines *Actinosphaerium eichhornii* and *Amoeba proteus*) could not grow or persist on a bacterial diet but did grow well on a diet of small bacterivorous ciliates.

The experimental microcosms were covered 240-mL glass jars containing 100 mL of initially sterile medium (0.56 g of Carolina Biological Supply protozoan pellets per liter of well water) plus two sterile wheat seeds to provide additional nutrients. We used five replicate microcosms for each food chain containing *Colpidium* and four replicate microcosms for food chains containing either *Tetrahymena* or *Blepharisma* feeding only as a bacterivore. Microcosms initially received
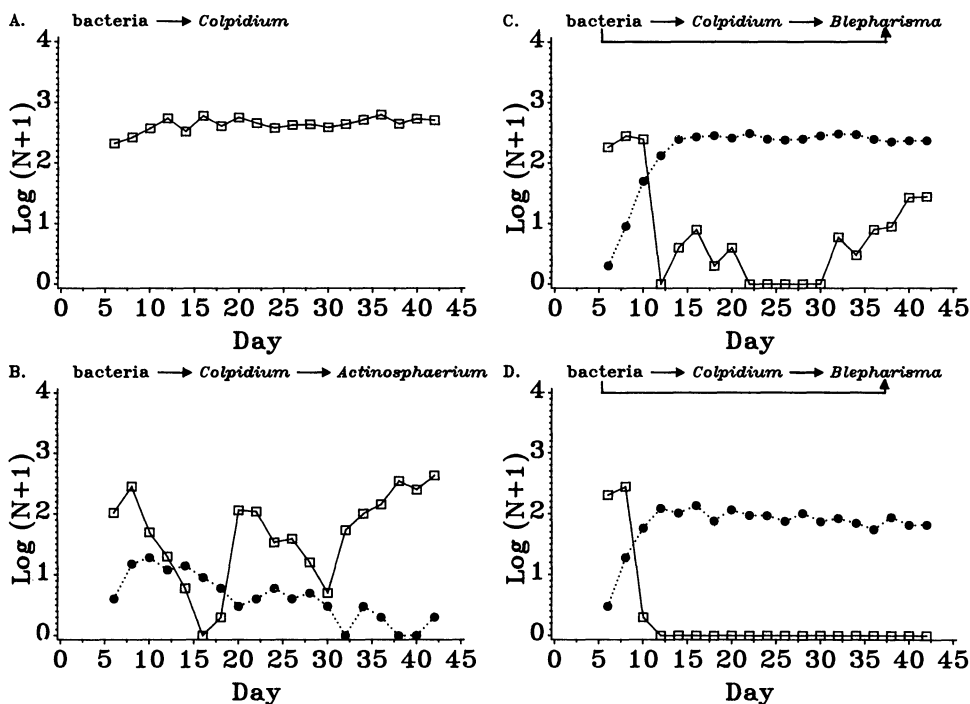
FIG. 1.—Examples of population dynamics in representative replicates of different experimental food webs containing the bacterivore *Colpidium. Open squares* denote *Colpidium* densities. *Solid circles* denote densities of predators feeding on *Colpidium*. Important trophic connections in each food chain are sketched in each panel. *A, Colpidium* in short food chains without another top predator; *B, Colpidium* with *Actinosphaerium; C, Colpidium* persisting with *Blepharisma; D, Colpidium* going extinct with *Blepharisma* persisting.

a standardized inoculum of bacteria (*Enterobacter aerogenes* and *Escherichia coli*) and a bacterivore (*Colpidium* or *Tetrahymena*). After a 2-d time lag to allow prey to become sufficiently abundant to support predators, randomly selected subsets of the microcosms received standard inocula of different top predators (omnivores, *Blepharisma,* or nonomnivores, *Amoeba* or *Actinosphaerium*). The resulting food webs are diagrammed in figures 1 and 2. Other microcosms without these top predators served as controls for bacterivore dynamics in the absence of higher trophic levels. Microcosms were placed in a spatially randomized array on a lab cart, where they experienced ambient conditions of light and temperature. Addition of a sterile wheat seed to each microcosm every week provided supplemental nutrients.

   Colpidium, Tetrahymena, and *Blepharisma* are all actively swimming ciliates that tend to be distributed throughout the water column in the microcosms. The sarcodines *Amoeba* and *Actinosphaerium* do not swim about in the water column and tend to be restricted to the substrate, in this case the bottom and walls of the microcosms. Despite these differences in microhabitat use, all of the protists were readily suspended in the water column by vigorously swirling the contents of each microcosm for the purposes of sampling.
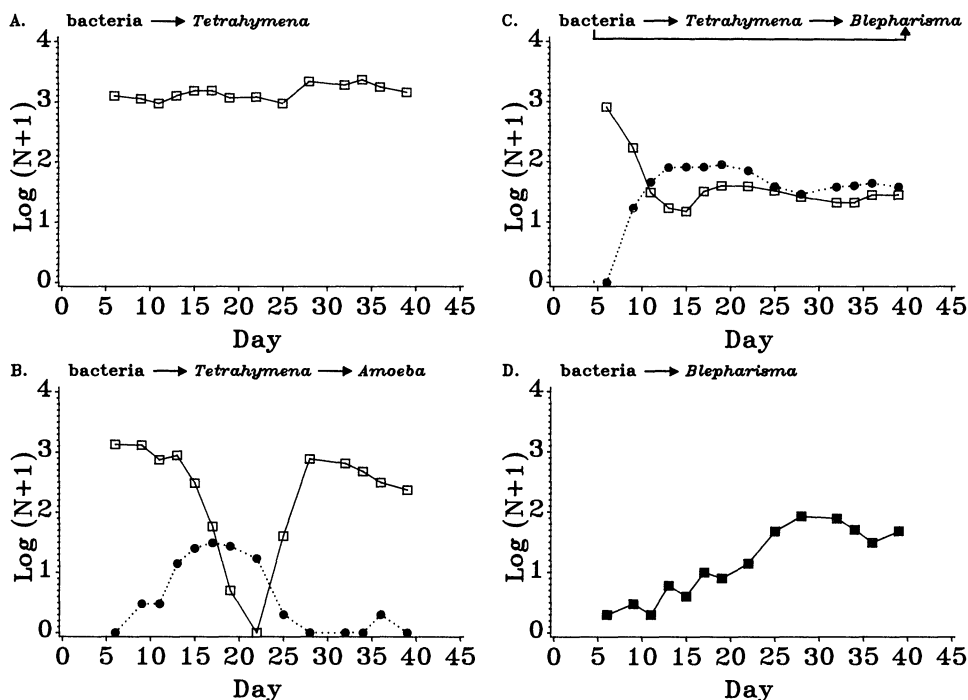
FIG. 2.—Examples of population dynamics in representative replicates of different experimental food webs containing the bacterivore *Tetrahymena*. *Open squares* denote *Tetrahymena* densities. *Solid circles* denote densities of predators feeding on *Tetrahymena*. A, *Tetrahymena* in short food chains without another top predator; B, *Tetrahymena* with *Amoeba*; C, *Tetrahymena* with *Blepharisma*; D, *Blepharisma* feeding on bacteria without *Tetrahymena*.

We sampled each microcosm at approximately 2-d intervals, beginning 6 d after the introduction of the first species. Sampling involved first swirling the contents of each jar to suspend the protists in the water column, and then withdrawing a small volume of medium and suspended organisms with a sterile pasteur pipette. We counted the protists in 10 separate standard pipette drops with the aid of a stereoscopic microscope. Ten drop subsamples had an average volume of 0.31 mL and consequently comprised a very small fraction of the microcosm volume. We did not monitor the abundance of bacteria in this study, and we limit our analysis to the dynamics of protists.

We used counts of protists over time to estimate the standard deviation over time of the logarithm of abundance per sample, as one empirical measure of relative stability. The short generation times of protists (max 1–2 d) ensure that sampling at 2-d intervals measured population dynamics rather than the long-term persistence of individuals (see Connell and Sousa 1983). All microcosms experienced a similar regime of small perturbations including the weekly addition of food and the physical disturbance caused by regular mixing and subsampling.

We also estimated r (the intrinsic rate of increase) for each of the bacterivore species. Because the population growth of bacterivores had already leveled off when we began to sample the microcosms, we estimated values of r for bacteri-

vores in other small, readily counted subcultures. We isolated one to two cells of *Colpidium* and one to five cells of *Tetrahymena* in 25 μL of standard protozoan medium contained in capillary tubes. We prepared five replicate capillary tubes for each species. The capillary tubes were submerged under mineral oil in petri dishes to prevent evaporation and to improve optical resolution for subsequent sampling. We counted the cells twice per day until population growth began to level off (approximately 3 d) and used the log-linear phase of growth to estimate r using the equation

$$[\ln(N_t) - \ln(N_0)]/t = r ,$$

where N_0 is the initial number of protists per sample and N_t is the number of protists per sample after t hours.

Hypotheses and Statistical Analysis

We reasoned that if longer food chains or chains with greater degrees of omnivory tended to be either locally unstable systems or locally stable systems with long return times, then the dynamics of some of the populations within those chains should manifest statistical evidence of instability or long return times. Because most of our populations persisted for the duration of the experiment, we focused on differences in temporal variation in abundance, as measured by the standard deviation of the log of abundance over time, using a nonparametric Kruskal-Wallis test.

We also reasoned that food chain length and position within the food chain should have predictable effects on the population sizes of species on similar trophic levels. In our food chains consisting of two or three trophic levels, species of bacterivores on the second trophic level should be more abundant when they were not consumed by species on a higher trophic level (Hairston et al. 1960; Oksanen et al. 1981). All else being equal, top predators located on higher trophic levels should also be less abundant than top predators located on lower levels, because of the attenuation of energy passed up through the food chain. Omnivores that potentially feed on multiple trophic levels should also be more abundant when feeding closer to the base of the food chain. We tested for effects of differences in food chain composition or trophic position on the average abundance of protists with a repeated-measures ANOVA of the logarithm of sampled counts of protists over time.

RESULTS AND DISCUSSION

Effects of Community Structure on Abundance

Species abundances depended on food chain structure and position within the food chain. Predators reduced the abundance of both bacterivorous prey species relative to microcosms without predators (table 1; figs. 1 and 2; repeated-measures ANOVA for *Colpidium, F = 95.07, df = 2,12, P = .0001*; for *Tetrahymena, F = 34.82, df = 2,9, P = .0001*). In one longer food chain configuration, *Colpidium* went extinct rapidly in three of five replicate food chains where it interacted with *Blepharisma*. *Blepharisma* increased more rapidly and had higher

TABLE 1

MEAN PROTIST ABUNDANCE, MEASURED BY THE MEAN WITHIN REPLICATES OVER TIME OF THE
LOGARITHM OF THE NUMBER OF CELLS + 1 PER 0.31-ML SAMPLE

	PREDATOR		
	None	Blepharisma	Actinosphaerium
A. Colpidium (mean abundance)*	2.6873	.4507	1.4460

	PREDATOR		
	None	Blepharisma	Amoeba
B. Tetrahymena (mean abundance)†	2.9876	1.5263	2.0110

	PREY	
	Bacteria	Tetrahymena and Bacteria
C. Blepharisma (mean abundance)‡	1.1439	1.5604
D. Blepharisma (maximum abundance)§	1.9800	1.9912

NOTE.—Significance levels (P) for ANOVAs indicate differences in average abundance over time for the same species in different kinds of webs. Statistical comparisons specifically refer to differences in mean values among columns in the table.

* Values are means of the means; ANOVA; $F = 95.07$; df $= 2,9$, $P = .0001$.
† Values are means of the means; ANOVA; $F = 31.57$; df $= 2,9$, $P = .0001$.
‡ Values are means of the means; ANOVA; $F = 43.86$; df $= 1,6$, $P = .0006$.
§ Values are means of the maxima; ANOVA; $F = 0.03$; df $= 1,6$, $P = .8739$.

mean abundance (averaged over all sampling dates) when feeding as an omnivore than as a bacterivore (repeated-measures ANOVA for *Blepharisma*, $F = 43.86$, df $= 1,6$, $P = .0006$). Maximum population sizes were almost identical when *Blepharisma* fed as an omnivore or as a bacterivore (ANOVA, $F = 0.03$, df $= 1,6$, $P = .8757$), despite the potentially greater amount of energy available at the lower trophic level (Hutchinson 1959; Hastings and Conrad 1979).

The results for *Blepharisma* do not support hypotheses based on ecological energetics that predict that omnivores should be able to attain higher population levels and possibly greater stability when feeding at lower trophic levels. Instead, our data are more consistent with Stenseth's (1985) contention that predators may sacrifice efficiency to feed on diverse prey types. Perhaps *Blepharisma* is not as efficient a bacterivore as it is a predator, and the energy and resources in *Tetrahymena* are either more readily harvested or assimilated than those in bacteria. Alternatively, *Blepharisma* may perform best on a mixed diet of bacteria and small ciliates, as appears to be the case for some omnivores in other systems (Walter 1987).

Effects of Food Chain Structure on Variability and Persistence

Food chain structure also affected temporal variability in population size. The population dynamics of both bacterivores, *Colpidium* and *Tetrahymena,* varied more with the addition of a predator in three out of four different food webs (figs. 1 and 2; table 2). The single exception involved webs where *Blepharisma* fed on

TABLE 2

TEMPORAL VARIATION IN PROTIST ABUNDANCE, MEASURED BY WITHIN-REPLICATE STANDARD DEVIATIONS
OVER TIME OF THE LOGARITHM OF THE NUMBER OF CELLS + I PER 0.31-ML SAMPLE

	PREDATOR			
	None	Blepharisma	Actinosphaerium	P
A. *Colpidium*, less first three dates*	.114	.540	.646	.0172
B. *Colpidium*, all 19 dates*	.150	.815	.672	.0138
C. Predator, less first three dates†	· · ·	.128	.324	.0163
D. Predator, all 19 dates†	· · ·	.412	.357	.9168

	PREDATOR			
	None	Blepharisma	Amoeba	P
E. *Tetrahymena*, less first three dates‡	.255	.250	.922	.0244
F. *Tetrahymena*, all 14 dates‡	.240	.563	.976	.0073
G. Predator, less first three dates†	· · ·	.237	.557	.0209
H. Predator, all 14 dates†	· · ·	.488	.548	.1489

NOTE.—Significance levels (*P*) for Kruskal-Wallis tests indicate differences in SDs for species in webs with different top predators. Statistical comparisons specifically refer to differences in mean values among columns in the table. Standard deviations excluding the first three sample dates eliminate the initial phase of predator population growth from estimates of temporal variation.
* Values are mean *Colpidium* SD.
† Values are mean predator SD.
‡ Values are mean *Tetrahymena* SD.

Tetrahymena. Following an initial decline as *Blepharisma* increased, *Tetrahymena* abundance varied temporally about as much as in the control webs without *Blepharisma* or other top predators (fig. 2; table 2). Other examples of increasingly variable dynamics in longer food chains have been observed in previous studies of relatively simple protist communities (Gause 1934; Hairston et al. 1968).

The greater temporal variation in abundance of bacterivores in longer food chains where they were consumed by top predators is consistent with predictions of decreased local stability or prolonged return times in food chains of increased length (Pimm and Lawton 1977) or in food webs of increased species richness (May 1972).

We might expect greater temporal variation in abundance to translate into a greater probability of extinction over an even longer temporal scale or with greater environmental variation (see, e.g., Beddington et al. 1976). Indeed, the single situation where we observed extinctions was one characterized by high temporal variation in abundance of *Colpidium*. *Colpidium* populations varied more in webs with the omnivore *Blepharisma* than in webs with the nonomnivore *Actinosphaerium* (fig. 1; table 2). *Colpidium* also went extinct rapidly in three of five replicates containing *Blepharisma*, while it persisted in all five replicate webs with *Actinosphaerium*. In the two replicates where *Colpidium* persisted with *Blepharisma*, its dynamics were slightly more variable, but not significantly so,

than in webs where it persisted with *Actinosphaerium*. Examples in figure 1 in which populations appear to go extinct and then reappear simply resulted when densities temporarily fell below one cell per sampled volume. The dynamics of *Colpidium* are consistent with reduced stability or prolonged return times in microcosms where top predators were omnivores (*Blepharisma*) rather than nonomnivores (*Actinosphaerium*).

The bacterivore *Tetrahymena* persisted in all replicate microcosms, but unlike *Colpidium* its populations varied more widely in webs with a nonomnivore top predator (*Amoeba*) than in webs with the omnivore (*Blepharisma*) (fig. 2; table 2). *Tetrahymena* differed from *Colpidium* in its slower hourly rate of exponential increase ($r = 0.0916$, SD $= 0.0124$ vs. $r = 0.1342$, SD $= 0.0069$), smaller cell size, and greater maximum potential population size (see figs. 1 and 2). It is unclear whether these life-history differences contributed to the different dynamics of *Tetrahymena* and *Colpidium* when they interacted with *Blepharisma*.

The abundance of the omnivore *Blepharisma* varied less than that of nonomnivorous predators located on the third trophic level. After initially rapid population growth, *Blepharisma* populations seemed quite stable, showing little variation even when populations of its prey species, like *Colpidium,* varied wildly or went extinct (table 2; fig 1). In contrast, populations of the predators *Actinosphaerium* and *Amoeba* had multiple or single peaks and did not appear particularly stable relative to populations of omnivorous *Blepharisma*. The lower variability of the omnivore populations presumably reflected their ability to feed on bacteria when ciliate prey become scarce, while the dynamics of nonomnivores were tightly linked to fluctuations in the abundance of ciliates on which they preyed.

Trophic position did not strongly affect variability in abundance of the omnivore *Blepharisma*. Although populations of *Blepharisma* varied more when they were restricted to feeding on bacteria than when they could feed on both bacteria and bacterivorous ciliates (nonparametric ANOVA on standard deviations, Kruskal-Wallis $P = .0209$), this difference was simply because of the slower growth of the populations feeding only on bacteria (fig. 2). We found little evidence that populations of *Blepharisma* were more stable when feeding lower in the food chain. If anything, *Blepharisma* populations were more stable when given the opportunity to feed at a higher trophic level, since their low initial abundance when feeding as bacterivores could conceivably increase their risk of extinction in early phases of community development.

The differences in population dynamics in our systems occurred in the absence of explicitly contrived experimental perturbations of the microcosms. Such perturbations, which might be achieved by pulsed nutrient additions (see, e.g., Luckinbill 1974; DeAngelis 1992) or temperature shocks (see, e.g., Allen-Morely and Coleman 1989), could yield further information about whether systems with more intrinsically variable dynamics are also less stable in the sense that they might be less likely to resist or recover from perturbations. Even in the absence of experimental perturbations, the dynamics of our systems probably represent both the intrinsic properties of the interacting populations and their responses to small uncontrolled fluctuations in the laboratory. It can also be argued that the different

dynamics of bacterivores in the presence or absence of top predators correspond to measures of dynamics in response to another kind of perturbation, namely the presence or absence of an additional species in the web.

CONCLUSIONS

Food web theory attempts to predict the dynamic consequences of food web architecture in natural systems. The greatest obstacle to empirical tests of food web theory is that it is extraordinarily difficult to measure the dynamics of the complex natural systems that provide the current descriptions of food web structure. In contrast, laboratory microcosms containing organisms with short generation times can yield important insights about the dynamics of complex systems (Gause 1934; Hairston et al. 1968; Vandermeer 1969; Maguire 1977; Luckinbill 1979; Dickerson and Robinson 1984, 1985; McNaughton 1988; Kareiva 1989). Microcosms containing bacteria and protists offer systems where both food web architecture and population dynamics can be rigorously studied.

Our results provide some tentative support for the prediction that population fluctuations and extinctions will increase with increasing food chain length (Pimm and Lawton 1977), even if one does not assume that the observed dynamics necessarily reflect the properties of the specific mathematical models used in previous theoretical studies. The dynamics of our omnivore also support the contention that species feeding on multiple prey taxa located in different trophic levels will endure fluctuations in prey abundance better than specialists feeding on fewer types of prey (MacArthur 1955). Convincing generalizations about the dynamics of omnivores and their impact on the rest of the food web will require studies of additional species, to rule out other complicating factors, such as differences among predators in prey encounter rates (Luckinbill 1973, 1974). We also recognize that our findings depend on a very small sample of species, while the theoretical predictions represent the average behavior of a very large number of simulated food webs. The critical point is that simple food webs composed of real organisms can exhibit some of the phenomena predicted by simple mathematical models.

Convincing statements about the generality of these patterns will require examination of many more species assembled in various trophic combinations. Similarly, statements about the relative stability of these systems, relating either to local stability or return times, will also benefit from observations of the responses of comparable systems to explicit experimental perturbations.

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Associate Editor: John Pastor