Oecologia (1998) 117:413–419

Marcel Holyoak · Sambhav Sachdev

Omnivory and the stability of simple food webs

Received: 28 December 1997 / Accepted: 22 June 1998

Abstract Traditional ecological theory predicts that the stability of simple food webs will decline with an increasing number of trophic levels and increasing amounts of omnivory. These ideas have been tested using protozoans in laboratory microcosms. However, the results are equivocal, and contrary to expectation, omnivory is common in natural food webs. Two recent developments lead us to re-evaluate these predictions using food webs assembled from protists and bacteria. First, recent modelling work suggests that omnivory is actually stabilizing, providing that interactions are not too strong. Second, it is difficult to evaluate the degree of omnivory of some protozoan species without explicit experimental tests. This study used seven species of ciliated protozoa and a mixed bacterial flora to assemble four food webs with two trophic levels, and four webs with three trophic levels. Protist species were assigned a rank for their degree of omnivory using information in the literature and the results of experiments that tested whether the starvation rate of predators was influenced by the amount of bacteria on which they may have fed and whether cannibalism (a form of omnivory) occurred. Consistent with recent modelling work, both bacterivorous and predatory species with higher degrees of omnivory showed more stable dynamics, measured using time until extinction and the temporal variability of population density. Systems with two protist species were less persistent than systems with one protist species, supporting the prediction that longer food chains will be less stable dynamically.

M. Holyoak (✉)
Entomology Department, University of California,
1 Shields Avenue,
Davis, CA 95616-8584, USA
e-mail: maholyoak@ucdavis.edu, Fax: +1-916-7521537

S. Sachdev
Gahr High School, 1111 Artesia Blvd.,
Cerritos, CA 90703, USA

Key words Cannibalism · Omnivory · Population persistence · Stability · Starvation

Introduction

In 1927 Charles Elton noted that food chains tend to consist of only three or four tropic levels (Elton 1927). Although this observation is subject to debate (Martinez 1993) it prompted valuable examinations of the relationship between trophic complexity and food web stability (reviewed by Morin and Lawler 1995). Pimm and Lawton (1977) used models with a Lotka-Volterra form to construct simple food webs with various numbers of trophic levels and amounts of omnivory, and tested these for mathematical stability. Mathematical stability was determined using the presence of stable point equilibria, quantified using the largest eigenvalue of the Jacobian matrix, and was expressed either as the frequency of real and negative eigenvalues (stable equilibria) or return time (the inverse of the absolute value of the eigenvalue for a stable equilibrium). They found that longer food chains were less often stable and that omnivory destabilized food webs. Tests of these predictions have given results that are either equivocal or opposite to expectation. Lawler and Morin (1993) and Morin and Lawler (1996) found that chains containing omnivores were not less stable than those without omnivores, and omnivorous species sometimes showed lower temporal variability in abundance than non-omnivores. As predicted, they found that species in longer food chains varied more in abundance in three of four different food webs. Contrary to the predictions of Pimm and Lawton (1977), empirical observations also show that omnivory is common in a variety of natural food webs (Polis 1991; Diehl 1993; Winemiller 1996). Here we adopt the protozoan study system of Lawler and Morin (1993; Morin and Lawler 1996) as a convenient system in which to test the hypotheses of Pimm and Lawton (1977) and more recent theoretical developments introduced below.

Three recent findings caused us to re-evaluate the effects of omnivory and food chain length on stability. First, tritrophic models show that omnivory is often stabilizing (as defined above), providing that interaction strengths are not too strong (McCann and Hastings 1997). This finding can be reconciled with the results of Pimm and Lawton (1977, 1978) by considering that their models contain random interaction strengths, which frequently include strong interactions that are destabilizing (McCann and Hastings 1997). Another difference is that McCann and Hastings (1977) used non-linear (type II) functional responses rather than linear functional responses as in Pimm and Lawton (1977). Second, Saunders (1978) and Sterner et al. (1997) tested the effect of number of trophic levels on the return time of food webs identical to those used by Pimm and Lawton (1977) except they controlled for the number of species and number of self-damping terms (where species have their own density dependence). They found that return times were longer for systems with more species and where fewer species had self-damping terms. Contrary to Pimm and Lawton (1977), Sterner et al. (1997) found that adding extra trophic levels while controlling for the number of self-damping terms produced a weak but significant increase in stability (the opposite of return time). Third, it has become clear that it is not straightforward to classify some of the protozoan species used by Lawler and Morin (1993) as omnivores or non-omnivores. Holyoak (in press) found that one of the species used in these studies (*Didinium nasutum*) is cannibalistic, whereas it was previously thought to be non-cannibalistic. Cannibalism is a special form of omnivory, where the species feeds both on itself and other food sources (Polis et al. 1989). Additionally, some predatory protozoans, e.g., *Blepharisma americanum* and some strains of *Euplotes patella*, can also feed on bacteria (Giese 1973; Zubkov and Sleigh 1996). To overcome these difficulties we directly evaluated omnivory by testing whether species were cannibalistic and whether bacterial levels influenced predator survival.

This paper uses three different indices of stability. *Mathematical stability* is defined above. In time series of abundances it is more usual to measure stability using a measure of temporal *population variability* (e.g., Connell and Sousa 1983). Modelling work by Taylor (1992) shows that population variability is a good predictor of mathematical stability in certain stochastic models of closed populations; the generality of this relationship is not known. Empirical observations suggest that closed populations that fluctuate less in abundance are usually more likely to persist (reviewed by Bengtsson and Milbrink 1995). Here we also look at *persistence time* directly because this is a more ecologically relevant measure of stability.

We conducted two experiments. First we tested for omnivory in three species of protozoan predators (which feed on other protist species) for which it was unclear if they are cannibalistic and if they can feed on bacteria. This experiment together with information in the literature allowed us to rank species for their degree of omnivory, which is used in the second experiment. Second, we assembled simple food chains in laboratory microcosms with either two or three trophic levels using either one or two ciliated protozoan species and a mixed inoculum of bacteria. Protist abundances were monitored regularly to determine temporal variability, mean abundance and time until extinction. This experiment ran for 3 weeks, which is approximately 97 prey (*Colpidium striatum*) generations. We tested the following hypotheses:

1. Omnivores and their prey have more stable dynamics than non-omnivores (McCann and Hastings 1997). This prediction would be unlikely to be met if interactions between species were strong (McCann and Hastings 1997).
2. Food webs containing more species will be less stable than food chains containing fewer species (Saunders 1978; Sterner et al. 1997).

Methods

The study organisms

All species used are free-swimming ciliated protozoa that are commonly found in fresh water. We used four bacterivores and three predatory species. Bacterivores were *Tetrahymena vorax*, *T. pyriformis*, *Colpidium striatum* and *Blepharisma americanum* (references for bacterivory: Giese 1973; Finlay 1977; Jackson and Berger 1985; Morin and Lawler 1995). Predators were *Didinium nasutum*, *Dileptus anser* and *Euplotes patella,* and these feed on other (usually bacterivorous) protists and cannot survive on bacteria alone. Although some strains of *E. patella* can survive solely on bacteria (Zubkov and Sleigh 1996), our experiments demonstrate that this is not true of the strain we used. *B. americanum* is not a strict bacterivore; it is also capable of feeding on other protists and it is cannibalistic, like *T. vorax* and *Did. nasutum* (Williams 1960, 1961; Giese 1973; Holyoak in press). Both *T. vorax* and *B. americanum* are polymorphic, with giant-celled cannibal morphs that have larger mouths (macrostome cells) than bacterivorous cells (microstomes) (Williams 1960, 1961; Giese 1973).

When food is plentiful, ciliates have a fixed time between divisions, which is the length of the cell-cycle (biomass accumulation and mitosis or meiosis) (Finlay 1977). In general, larger-bodied species have longer generation times (Finlay 1977), and take longer to starve when removed from food (Jackson and Berger 1984). *Did. nasutum*, *B. americanum* and *D. anser* are capable of forming desiccation-resistant cysts that can survive for many years (Beers 1935; Giese 1973). *Did. nasutum* does not form cysts when reared on *C. striatum*, as in the present study (Holyoak and Lawler 1996). In addition, neither *B. americanum* nor *D. anser* formed cysts in the present experiments (cysts are easily recognized). The selected predator species immobilize and ensnare their protist prey before ingestion using extrudable trichocysts (Wessenberg and Antipa 1970; Giese 1973). In addition, *D. anser* has an extensible proboscis that is used either to swipe off parts of large protist cells or to push small cells into the oral cavity (Miller 1968).

All study organisms except *T. vorax* were obtained from the Carolina Biological Supply Co. *T. vorax* came from the Algal and Type Culture Collection, strain number 30421. Prior to experimentation *Euplotes* were reared using cultures of *T. pyriformis*, and other predator species were reared on *C. striatum*.

Quantifying predator omnivory and density dependent mortality

This experiment explored the degree of omnivory in three species for which data were unavailable in the literature, *E. patella*, *Did. nasutum* and *D. anser*. Three things were tested:

1. Does the presence of additional bacteria prolong survival when no protist prey is available?
2. Can cannibalism account for differences in survival time?
3. Is survival density dependent?

We did not perform similar tests on bacterivores because starving bacterivores would have necessitated killing bacteria, and this proved to be difficult because antibiotic solutions caused *B. americanum* to encyst and were variably toxic to the other bacterivores.

Only predators in groups can be cannibalistic. However, adding extra predator individuals to allow cannibalism also increases the total biomass present, which might improve conditions for bacterial growth. If predators were capable of feeding on bacteria, their time until starvation might increase, not because of cannibalism, but because burst cells or additional excretion could cause bacteria to increase in abundance. This difficulty was overcome by having a treatment, called the *biomass control*, where burst predator cells were added to starving groups of predators to increase biomass without raising the likelihood of cannibalism.

Groups of predators of each species were placed into sterile well plates containing 1 ml of bacterized nutrient solution per well. Bacterized medium was made in the following way:

1. A sterile Protozoan Pellet (Carolina Biological Supply Co.) was placed in 1 l of 50:50 autoclaved spring: distilled water.
2. The supernatant was decanted after 24 h and used in step 4.
3. A mixed (and unidentified) flora of bacteria were obtained by filtering a little over 5 ml of a *C. striatum* culture through a 5-μm nylon syringe filter that retained protists but allowed bacteria to pass through.
4. The medium was bacterized by placing 5 ml of filtrate in 1 l of sterile nutrient solution and incubating at room temperature (approximately 23°C) for 24 h.

Each species was placed in groups of 1 (30 replicates), 10 (3 replicates for *E. patella* and *Did. nasutum*, 5 replicates for *D. anser*), and in biomass controls of 10 live cells plus 20 burst dead cells (3 replicates) and 30 live cells (3 replicates). Cells were killed and burst by heating in a microwave oven. Numbers of cells in each well were counted daily under a binocular microscope until no cells remained. For each species, a multivariate analysis of variance (MANOVA) was used to test for differences in the proportion surviving in different treatments. Proportions (p) surviving were arcsine square-root transformed $[\sin^{-1}(\sqrt{p})]$ to make them normally distributed (tested using a χ^2-test). The proportion alive each day was a dependent variable in the MANOVA, and treatment was a single factor. Individual ANOVAs for each day identified the days with significant ($P < 0.05$) differences between treatments in the proportion alive, and least significant difference tests identified the treatments that differed within each day.

Population persistence and dynamics

Eight combinations of protist species were each placed in five 32-ml polypropylene bottles containing 30 ml of nutrient solution and were monitored either until extinction or for a maximum of 21 days. The bottles initially contained 29 ml of bacterized nutrient solution made as described in the previous experiment. A sterilized millet seed was also placed in each bottle to provide a slow release of nutrients for bacteria to feed on, providing food for the bacterivores. This experiment used five replicates of each of eight different combinations of ciliate species:

1. *Tetrahymena vorax* (105 cells ml^{-1})
2. *Blepharisma americanum* (10 cells ml^{-1})
3. *Colpidium striatum* (2728 cells ml^{-1})
4. *Tetrahymena pyriformis* (8520 cells ml^{-1})
5. *Blepharisma* and *Colpidium* (10 cells per drop and 2528 cells ml^{-1}, respectively)
6. *Didinium* and *Colpidium* (258 cells per drop and 2528 cells ml^{-1}, respectively)
7. *Dileptus* and *Colpidium* (14 cells per drop and 2528 cells ml^{-1}, respectively)
8. *Euplotes* and *Colpidium* (35.68 cells per drop and 2528 cells ml^{-1}, respectively)

The bacterivores (except *Blepharisma* in treatment 5) were introduced to bottles in 1 ml of medium that contained the species at the rates indicated above. After 2 days a drop of medium containing the predators was added to treatments 5, 6 and 8, and after a further 2 days *D. anser* were added to treatment 7 – the extra 2 days were necessary because of variation in the time taken to remove contaminant protist species from cultures obtained from Carolina Biological. Predators were introduced after prey to give the prey (*C. striatum*) time to increase in density before predators were added.

On Mondays, Wednesdays and Fridays, a 3-ml sample of each bottle was removed after mixing the contents with a pipette. The sample was killed with a drop (0.032 ml) of Lugol's iodine solution, and we counted the number of cells under a dissection microscope. Bacterivores were counted in each of three drops from a Pasteur pipette of 0.032 ml each, and if fewer than three individuals were present the entire 3 ml was censused. Predators were counted in the entire 3-ml sample. The entire bottle contents were checked for the presence of a species if that species was absent from a 3-ml sample. Extinctions only occurred for predators, and although cysts were occasionally observed for *D. anser* and *B. americanum* these were infrequent and on no occasion were motile protists absent and cysts present. The 3 ml of solution from each bottle was replaced with the same volume of fresh sterile nutrient solution. Sterile technique was used throughout the experiment. Sampling continued for 21 days after predator addition. Mean room temperature was 23.8°C (SD 0.6°C, from 23 daily measurements).

The densities of each species were used to calculate the mean $\ln(1 + \text{density of cells } ml^{-1})$ and the coefficient of variation (CV) of density for each species in each of the treatments. To avoid comparing time series of different lengths, only the time up until the first predator extinctions was considered (12 days). CVs cannot readily be interpreted if the samples have different slopes for power law plots according to Taylor (1961; see McArdle et al. 1990). For each species in each treatment we calculated regression slopes of ln(variance of density) against ln(mean density). We compared CVs only when both species had significant ($P < 0.05$) slopes (indicating that the slope value is in some sense reliable), and where the slopes did not differ in value in Student's t-tests. Comparison of variability from populations with different Taylor's power law relationships would risk confounding differences in temporal variability with differences in mean density.

Results

Predator omnivory and density dependent mortality

Figure 1 shows the proportion of predators alive after various periods of starvation and Table 1 gives statistical analyses of these data. All three species (*E. patella*, *Did. nasutum* and *D. anser*) showed density-dependent survival. After 100–193 h of starvation, *Euplotes* survival was significantly greater for groups of 10 and 30 individ-

uals than for single predators. A greater proportion of *Dileptus* were alive from groups of 30 than for groups of 10 individuals after 94–204 h starvation, and survival was also greater for groups of 10 cells than for isolated individuals after 94–204 h starvation. For *Didinium* there were complex effects of group size on survival: after 24–49 h starvation the proportion alive was greater in groups of 1 and 30 individuals than in groups of 10 individuals.

There was also an effect on survival of all three species of adding extra predator biomass. Because the results are complex to interpret we present the results separately for each species.

Results were most straightforward for *Dileptus*, where more individuals were alive after 94–204 h starvation in groups of 30 individuals and in the biomass controls than in groups of 10 individuals, which also survived better than isolated individuals during this period (Fig. 1, Table 1).

For *Euplotes*, survival was lower in groups of 30 individuals than in groups of 10 individuals after 100 h of starvation, and after 193 h of starvation the biomass controls had a greater proportion of *Euplotes* alive than either the groups of 10 or 30 cells (Fig. 1, Table 1). Altogether this suggests that *Euplotes* starvation is slowed by additional biomass on which bacteria can grow.

Survival of *Didinium* showed more complex effects of predator biomass. Survival (after 24–49 h starvation) was greater in groups of 30, in isolated individuals, and in the biomass controls than in groups of 10. The greater survival of groups of 10 with 20 dead cells than just 10 live cells suggests that *Didinium* were feeding on bacteria and did benefit from additional biomass. After 24 h there was a significantly greater proportion of *Didinium* alive in wells started with single cells than in wells of the biomass controls, which is consistent with cannibalism reducing densities in larger groups. Overall the results for *Didinium* are consistent with initial negative effects of cannibalism on survival that are ameliorated by extra predator biomass in larger groups of *Didinium*.

These results together with information from the literature enable us to rank species by their degree of omnivory (Table 2). The least omnivorous species, *T. pyriformis* and *C. striatum,* can only feed on bacteria and were assigned an omnivory score of 1. *D. anser* and *E. patella* are capable of feeding on two food sources, bacteria and bacterivores, and were therefore given an omnivory score of 2. Both *T. vorax* and *B. americanum* are capable of feeding on other bacterivores; however, when there were no other bacterivores present they can only feed on two food sources, bacteria and themselves (cannibalism). These species were assigned an omnivory rank of 3 because their less usual food source (cannibalism) has a larger impact on survival than bacterivory in *D. anser* and *E. patella* (authors' personal observations; Fig. 1; Williams 1960, 1961; Giese 1973). When with bacterivores, both *B. americanum* and *Did. nasutum* can feed on three kinds of prey (bacteria, *C. striatum* and themselves). A higher omnivory score was assigned to *B. americanum* than *Did. nasutum* because cannibalism is more frequent in the former species (authors' personal observations) and *B. americanum* can divide on bacteria alone, whereas *Did. nasutum* cannot.

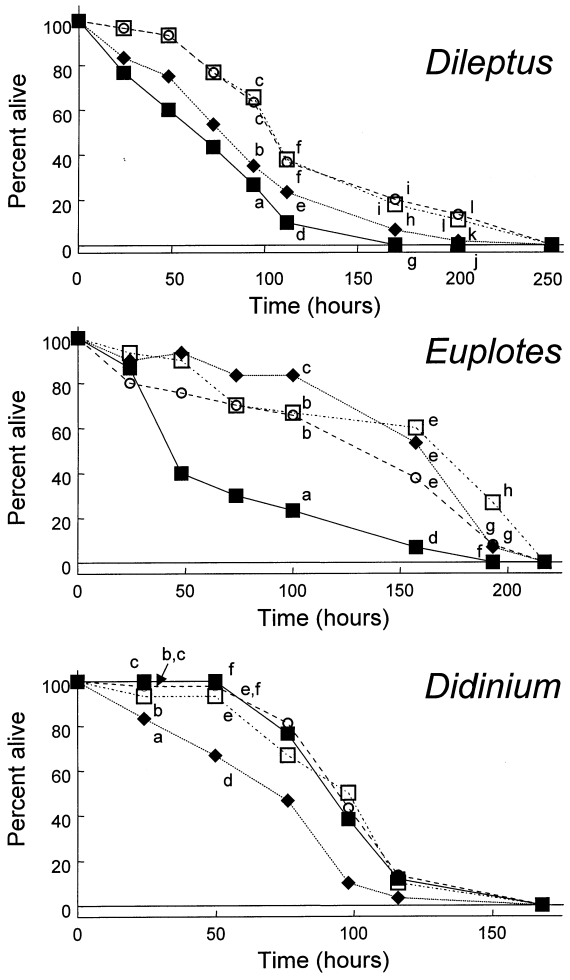

Fig. 1 The mean percentage of predators alive when starved in groups of various sizes. *Filled square symbols* and *solid lines* are for isolated predators, *solid diamond symbols* and *dotted lines* are for groups of 10 live predators, *open circles* and *dashed lines* are for groups of 30 live predators, and *open squares* and *dot-dashed lines* are for "biomass controls" that had 10 live and 20 dead predators. Points with the same *letter* beside them did not differ ($P > 0.05$) in the proportion alive in least significant difference tests for that species on that day. Proportions were arcsine square-root transformed, and results are only given where there was at least one significant difference at $P < 0.05$

Population persistence and dynamics

All bacterivores persisted for the duration of the experiment (21 days, *c.* 97 *C. striatum* generations) when no predators were present. Fig. 2A and the analysis of variance in Table 3 show that predator persistence times were shorter in less omnivorous predator species. Persistence times were also significantly longer in systems with fewer protozoan species (Fig. 2A, Table 3). For bacterivores without predators, a comparison of persistence times was

Table 1 MANOVA of the effect of group size on the proportion alive after various periods of starvation. MANOVAs were conducted separately for each species using arcsine square-root transformed proportions for each day as a dependent variable. In both univariate and multivariate tests the dependent variables were the proportion alive at durations of starvation indicated below for univariate tests (*df* degrees of freedom). Normality and homogeneity of variances were checked prior to analysis

Multivariate tests Species	Effect	Wilk's λ	*df 1*	*df 2*	*P*
Dileptus	Group size	0.0084	21	92	$<1\times10^{-6}$
Euplotes	Group size	0.116	18	85	$<1\times10^{-6}$
Didinium	Group size	0.139	15	97	$<1\times10^{-6}$

Univariate tests Species	Dependent variable	Mean square effect	Mean square error	*F*	*df 1*	*df 2*	*P*
Dileptus	Time = 24	0.101	0.357	0.28	3	38	0.84
	Time = 48	0.261	0.471	0.56	3	38	0.65
	Time = 72	0.259	0.480	0.54	3	38	0.66
	Time = 94	1.206	0.178	6.79	3	38	0.001
	Time = 112	0.973	0.002	426.7	3	38	$<1\times10^{-6}$
	Time = 170	0.370	0.004	101.0	3	38	$<1\times10^{-6}$
	Time = 204	0.209	0.003	78.4	3	38	$<1\times10^{-6}$
Euplotes	Time = 24	0.060	0.250	0.24	3	35	0.87
	Time = 48	0.991	0.515	1.92	3	35	0.14
	Time = 73	0.884	0.454	1.95	3	35	0.14
	Time = 100	1.129	0.390	2.99	3	35	0.049
	Time = 157	1.112	0.139	8.00	3	35	0.001
	Time = 193	0.319	0.005	65.4	3	35	$<1\times10^{-6}$
Didinium	Time = 24	0.128	0.010	13.3	3	39	$<1\times10^{-5}$
	Time = 49	0.354	0.006	59.1	3	39	$<1\times10^{-6}$
	Time = 76	0.227	0.393	0.58	3	39	0.63
	Time = 98	0.160	0.515	0.31	3	39	0.82
	Time = 116	0.030	0.228	0.13	3	39	0.94

not possible because all species persisted for the duration of the experiment.

Stability can also be estimated using the temporal variability of density. In the present analysis persistence times and the CV of either predator or prey density were not significantly correlated ($r = -0.36$, $n = 20$, $P \gg 0.05$, and $r = -0.43$, $n = 20$, $P \gg 0.05$, respectively); this analysis was limited to the bottles with predators because there were no bacterivore-only bottles where slopes of Taylor's power law regressions were comparable, and such comparisons might therefore confound changes in mean density with changes in temporal variability. Using the criteria described in the methods, three comparisons of CVs were made:

1. Predatory *E. patella* that is less omnivorous than *B. americanum* when feeding on *C. striatum*
2. The prey species *C. striatum*, when being fed on by either *E. patella* or the more omnivorous *Did. nasutum*
3. The prey species *C. striatum* when being fed on by either *D. anser* or the most omnivorous predator, *B. americanum*.

The outcomes of these comparisons were:

1. As predicted, predatory *E. patella* had a significantly higher coefficient of variation in a Student's *t*-test than the more omnivorous *B. americanum* when with *C. striatum* ($t_8 = 14.3$, $P < 0.001$; Fig. 2B).

Table 2 Rankings of the degree of omnivory of species in experimental treatments. Omnivory scores ranged from 1 (least omnivorous) for species that feed only on bacteria to 5 for species that feed frequently on all available food sources. An explanation of the omnivory scores is given in the Results (section on Predator omnivory and density dependent mortality) (*n.a.* not applicable)

Protist species present	Prey			Omnivory score
	Bacteria	Self	*C. striatum*	
Colpidium striatum	Yes	No	n.a.*	1
Tetrahymena pyriformis	Yes	No	n.a.	1
T. vorax	Yes	Yes	n.a.	3
Blepharisma americanum	Yes	Yes	n.a.	3
B. americanum with *C. striatum*	Yes	Yes (frequent)	Yes	5
Didinium. nasutum with *C. striatum*	Yes	Yes (infrequent)	Yes	4
Euplotes patella with *C. striatum*	Yes	No	Yes	2
Dileptus anser with *C. striatum*	Yes	No	Yes	2

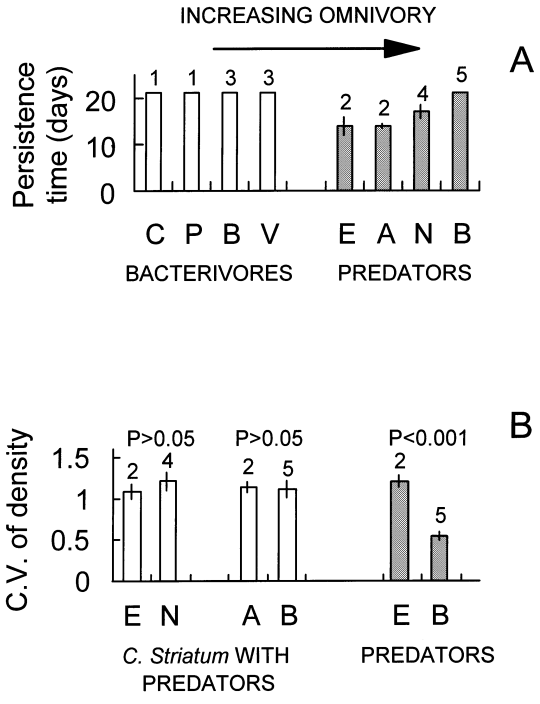

Fig. 2 **A** Persistence times of prey and predators in three trophic level systems, and **B** temporal variability of species with different degrees of omnivory. Mean persistence times of 21 days indicate that the species did not go extinct during the experiment. *Figures above bars* are the omnivory scores from Table 2. **B** shows the coefficient of variation of density for predators (*shaded bars*), and *Colpidium striatum* (*unshaded bars*) when with the predator species indicated beneath the bar. In **B** bars are grouped together for species that had similar slopes in Taylor's power law regressions, making the CVs comparable, and are not shown for other species. *Figures above bars* show the omnivory score for the predator species present and *P*-values are from Student's *t*-tests (species letter codes are: C *C. striatum*, P *Tetrahymena pyriformis*, B *Blepharisma americanum*, V *T. vorax*, E *Euplotes patella*, A *Dileptus anser*, N *Didinium nasutum*). All *bars* show the mean value ± 1 SE. Sample sizes are 5 except for *B. americanum* without other protist species, where the sample size was 1 because other bottles became contaminated

2. *C. striatum* did not differ in its CV when with *E. patella* or *Did. nasutum* ($t_8 = 0.54$, $P \gg 0.05$; Fig. 2B).
3. *C. striatum* also did not differ in its CV when with *B. americanum* or *D. anser* ($t_8 = 1.96$, $0.05 > P > 0.1$; Fig. 2B); however, the trend was towards the more omnivorous *B. americanum* causing its prey to have more stable dynamics. Each of these three comparisons gave similar results if *F*-tests were used to compare variances.

Discussion

All of the significant results were in agreement with theoretical predictions that more omnivorous species and their prey will show more stable dynamics (McCann and Hastings 1997), and that food webs containing more species are less stable (Saunders 1978; Sterner et al. 1997). Increased stability was shown both by persistence times and (where statistics permit) using the coefficient of variation of density. [Two of the comparisons of coefficients of variation of density were not significant at $P < 0.05$. This might be because comparisons of measures of population variability have low power (Gaston and McArdle 1994) and the present sample size was only five populations of each treatment]. The significant results suggest that recent theory is on the right track. This finding also accords with the demonstration by Fagan (1997) that terrestrial arthropod populations were more resistant to changes in density when an aphicide was applied in field experiments.

An important finding of this study is that a number of protozoan species that were previously thought to be specialized predators are actually feeding to some extent on bacteria. Starvation times of both *D. anser* and *Did. nasutum* increased when more predator biomass was present, which would have provided more organic material on which bacteria could grow and the predators could feed. Burbanck and Eisen (1960) also showed that *Did. nasutum* showed a number of growth deformities when reared on *Paramecium aurelia* that had been fed on one of a number of species of bacteria, whereas *Did. nasutum* fed on several bacterial species grew normally. This result suggests that either the *P. aurelia* were not a normal food stuff when fed monobacterially, or that *Did. nasutum* has to feed on bacteria as well as bacterivores for normal growth. A gradation between species that can divide on bacteria alone and those that require bacterivorous prey to divide might be expected because *T. vorax*, *B. americanum* and some strains of *Euplotes* can survive and divide when feeding on either bacteria or bacterivores (Giese 1973; Morin and Lawler 1995; Zubkov and Sleigh 1996). The involvement of predatory ciliates in the bacterial loop in natural water bodies is a topic that merits further investigation.

Cannibalism is an interesting form of omnivory because it usually is also a strong form of density dependence (Polis 1981; Crowley and Hopper 1994). Sterner et al. (1997) found that the number of self-damping

Table 3 Analysis of variance of persistence times in treatments with different numbers of protist species and with various degrees of omnivory (*df* degrees of freedom). Prior to analysis homogeneity of variances was checked using Bartlett's tests and normality was checked using a χ^2-test

Independent variable	Sums of squares	*df*	Mean square	*F*	*P*
Number of protist species	114.0	1	114.0	29.1	$< 1 \times 10^{-5}$
Omnivory score	363.3	4	90.8	23.2	$< 1 \times 10^{-6}$
Error	121.6	31	3.92		

species in Pimm and Lawton's (1977) food webs had a strong influence on food web stability (return time). Given that most of the omnivorous species in this study are also cannibals, and that cannibals often show strong self-regulation, the two sets of theory both give equivalent predictions about the increased stability of the protist food webs considered.

An interesting question that arises from the experiments on predator survival rate is whether the predators alter bacterial population dynamics. Two alternatives are that:

1. Adding extra biomass increased predator survival (in *E. patella, Did. nasutum* and *D. anser*) because some predators died and burst, releasing nutrients on which bacteria could grow.
2. Adding extra predators created a stronger microbial loop promoting bacterial growth, possibly through extra nutrients released by predators feeding (e.g., Bratbak and Thingstad 1985).

These two alternatives are not mutually exclusive, and to distinguish between them would require counts of bacteria, which are not currently available.

In conclusion, this paper agrees with recent theory (McCann and Hastings 1997; Sterner et al. 1997) in showing that omnivory stabilizes simple food webs. As expected, adding additional species to food webs shortened persistence times.

Acknowledgements We thank Sharon P. Lawler, Kevin McCann, and Peter Morin for discussions and comments. We appreciate the support of Julie Oliver of the UC Davis NSF Young Scholar's Program (NSF-YSP) during this study. This project was supported by NSF DEB 96–29876 to M.H. and Susan Harrison. S.S.'s involvement was supported by the NSF-YSP.

References

Beers CD (1935) The viability of ten-year-old *Didinium* cysts (infusoria). Am Nat 71:521–524

Bengtsson J, Milbrink G (1995) Predicting extinctions: interspecific competition, predation and population variability in experimental *Daphnia* populations. Oecologia 101:397–406

Bratbak G, Thingstad TF (1985) Phytoplankton-bacteria interactions: an apparent paradox? Analysis of a model system with both competition and commensalism. Mar Ecol Prog Ser 25:23–30

Burbanck WD, Eisen JD (1960) The inadequacy of monobacterially-fed *Paramecium aurelia* as food for *Didinium nasutum*. J Protozool 7:201–206

Connell JH, Sousa WP (1983) On the evidence needed to judge ecological stability or persistence. Am Nat 121:789–824

Crowley PH, Hopper KR (1994) How to behave around cannibals: a density-dependent dynamic game. Am Nat 143:117–154

Diehl S (1993) Relative consumer sizes and the strengths of direct and indirect interactions in omnivorous feeding relationships. Oikos 68:151–157

Elton C (1927) Animal ecology. Macmillan, New York

Fagan WF (1997) Omnivory as a stabilizing feature of natural communities. Am Nat 150:554–467

Finlay BJ (1977) The dependence of the reproductive rate on cell size and temperature in freshwater protozoa. Oecologia 30:75–81

Gaston KJ, McArdle BH (1994) The temporal variability of animal abundances: measures, methods and patterns. Philos Trans R Soc Lond B Biol Sci 345:335–358

Giese AC (1973) *Blepharisma*: the biology of a light-sensitive protozoan. Stanford University Press, Stanford

Holyoak M (in press) Unexpected effects of nutrient enrichment on predator-prey metapopulation dynamics. Ecology

Holyoak M, Lawler SP (1996) Persistence of an extinction-prone predator-prey interaction through metapopulation dynamics. Ecology 77:1867–1879

Jackson KM, Berger J (1984) Survival of ciliate protozoa under starvation conditions and at low bacterial levels. Microb Ecol 10:47–59

Jackson KM, Berger J (1985) Life history attributes of some ciliated protozoa. Trans Am Microsc Soc 104:52–63

Lawler SP, Morin PJ (1993) Food web architecture and population dynamics in laboratory microcosms of protists. Am Nat 141:675–686

Martinez ND (1993) Effects of resolution on food web structure. Oikos 66:403–412

McArdle BH, Gaston KJ, Lawton JH (1990) Variation in the size of animal populations: patterns problems and artifacts. J Anim Ecol 59:439–454

McCann K, Hastings A (1997) Re-evaluating the omnivory-stability relationship in food webs. Proc R Soc Lond Ser B 264:1249–1254

Miller S (1968) The predatory behaviour of *Dileptus anser*. J Protozool 15:313–319

Morin PJ, Lawler SP (1995) Food web architecture and population dynamics: theory and empirical evidence. Annu Rev Ecol Syst 26:205–229

Morin PJ, Lawler SP (1996) Effects of food chain length and omnivory on population dynamics in experimental food webs. In: Polis G, Winemiller K (eds) Food webs: integration of patterns and dynamics. Chapman and Hall, New York, pp 218–230

Pimm SL, Lawton JH (1977) Number of trophic levels in ecological communities. Nature 268:329–331

Pimm SL, Lawton JH (1978) On feeding on more than one trophic level. Nature 275:542–544

Polis GA (1981) The evolution and dynamics of intraspecific predation. Annu Rev Ecol Syst 12:225–251

Polis GA (1991) Complex trophic interactions in deserts: an empirical critique for food web theory. Am Nat 138:123–155

Polis GA, Myers CA, Holt RD (1989) The ecology and evolution of intraguild predation: potential competitors that eat each other. Annu Rev Ecol Syst 20:297–330

Saunders PT (1978) Population dynamics and the length of food chains. Nature 272:189–190

Sterner RW, Bajpai A, Adams T (1997) The enigma of food chain length: absence of theoretical evidence for dynamic constraints. Ecology 78:2258–2262

Taylor AD (1992) Deterministic stability analysis can predict the dynamics of some stochastic population models. J Anim Ecol 61:241–248

Taylor LR (1961) Aggregation, variance and the mean. Nature 189:732–735

Wessenberg H, Antipa G (1970) Capture and ingestion of *Paramecium* by *Didinium nasutum*. J Protozool 17:250–270

Williams NE (1960) The polymorphic life history of *Tetrahymena patula*. J Protozool 7:10–17

Williams NE (1961) Polymorphism in *Tetrahymena vorax*. J Protozool 8:403–410

Winemiller K (1996) Factors driving temporal and spatial variation in aquatic food webs. In: Winemiller KO, Polis G (eds) Food webs: integration of patterns and dynamics. Chapman and Hall, New York, pp 298–312

Zubkov MV, Sleigh MA (1996) Bacterivory by the ciliate *Euplotes* in different states of hunger. FEMS Microbiol Ecol 20:137–147