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# PRODUCTIVITY, INTRAGUILD PREDATION, AND POPULATION DYNAMICS IN EXPERIMENTAL FOOD WEBS

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*Abstract.* Theory predicts that productivity and the relative efficiency of resource utilization determine the outcome of interactions between intraguild predators and prey. Interactions between two freshwater protists, *Colpidium striatum* (the intraguild prey) and *Blepharisma americanum* (the intraguild predator), in laboratory microcosms support the predictions of intraguild predation theory. *Colpidium* competitively excluded *Blepharisma* when bacterial production was low, even though *Blepharisma* had a potential advantage conferred by its ability to consume *Colpidium*. In contrast to competitive exclusion at low productivity, *Colpidium* and *Blepharisma* coexisted for many generations at higher levels of bacterial production. Theory predicts a similar transition from competitive exclusion to coexistence as productivity increases, if intraguild predators use resources less efficiently than intraguild prey/competitors. Other experiments showed that *Colpidium* depresses bacterial densities more than *Blepharisma*, a result consistent with greater efficiency of resource utilization by *Colpidium*. These results indicate that simple mathematical models can provide important insights into the population dynamics of intraguild predators and prey under different levels of productivity.

*Key words: Blepharisma; Colpidium; competition; intraguild predation; microcosms; omnivory; population dynamics; predation; productivity; protists.*

## INTRODUCTION

Omnivory, the situation where consumers feed on more than one trophic level, appears to be common in nature (Polis et al. 1989, Polis 1991, Polis and Holt 1992, Diehl 1993, Diehl 1995, Polis and Strong 1996, Holt and Polis 1997). However, omnivory's apparent commonness runs counter to the predictions drawn from one group of food web models. This class of models suggests that omnivory will destabilize food chain dynamics (Pimm and Lawton 1977, 1978, Holt and Polis 1997). Consequently, omnivory should be rare in nature if unstable food chains fail to persist. Other work suggests that omnivory can be stabilizing in some circumstances (Matsuda et al. 1986, Fagan 1997, McCann and Hastings 1997). The disparity between observed and predicted frequencies of omnivory underscores the need for detailed studies of omnivore population dynamics (Holt and Polis 1997), which can show whether omnivore populations behave as predicted by simple models. Some models predict very different outcomes, including transitions from exclusion to coexistence, as productivity changes (Polis et al. 1989, Holt and Polis 1997). Recent reviews note the nearly complete absence of relevant long-term population dynamic information for omnivores or species involved in intraguild predation (Diehl 1993).

Intraguild predation (IGP) is a special case of om-

nivory that occurs when one guild member feeds on another (Polis and Holt 1992). Interactions among size-structured populations can lead to IGP, typically when larger individuals of ecologically similar species can consume smaller individuals (Polis et al. 1989). The apparent commonness of IGP raises important questions about conditions promoting coexistence within IGP systems. Models predict stable coexistence only when: (1) the IG prey uses a shared resource more efficiently than the IG predator, (2) the IG predator is a relatively inefficient consumer of the IG prey, and (3) the IG predator obtains more of its energy from the shared basal resource than from the IG prey (Polis et al. 1989, Holt and Polis 1997). Theory also predicts that productivity will affect the outcome of IGP (Polis et al 1989, Thingstad et al. 1996, Diehl and Kornijow 1997, Holt and Polis 1997). Low productivity can cause the IG prey to exclude the IG predator via competition; coexistence is possible at intermediate levels of productivity; and, at higher levels of productivity, the IG predator may exclude the IG prey (Polis et al. 1989, Holt and Polis 1997).

Empirical tests of ecological theory, such as the IGP theory described above, are limited by the mismatch between the short-term population dynamic data that are readily obtained from field experiments (e.g., changes in population size over one to at most several generations) and the long-term dynamics described by models (e.g., whether two species will coexist stably for many generations). The short duration of most field

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studies relative to the generation times of focal organisms compromises our ability to make strong inferences about population stability or prolonged coexistence (Connell and Sousa 1983). Unlike macro-organisms, which typically have generation times measured in months or years, the population dynamics of microorganisms over periods lasting only 1–2 mo correspond to tens or hundreds of generations (Morin and Lawler 1995). Consequently, microorganisms are ideally suited for tests of ecological theory that require knowledge of long-term population dynamics.

The experimental advantages of microorganisms are tempered by other constraints. Microbes are difficult or impossible to manipulate in natural settings, a limitation that restricts experiments to artificial arenas such as laboratory microcosms. Even so, studies of microbes have provided important insights about a host of ecological processes, including competition (Gause 1934, Vandermeer 1969), predation (Gause 1934, Luckinbill 1974, Harrison 1995), stability and complexity (Hairston et al. 1968, Lawler 1993), food web dynamics (Lawler and Morin 1993, Morin and Lawler 1996), and metapopulation dynamics (Holyoak and Lawler 1996a, b).

This paper describes interactions between productivity and the outcome of intraguild predation in simple microbial food webs. Many protists are facultative omnivores, feeding either on bacteria, or on other small protists that consume only bacteria. The omnivore considered here is the freshwater ciliate Blepharisma americanum (Perty) (see Giese 1973). Blepharisma is occasionally cannibalistic (Giese 1973), a situation readily recognized by the distinctive pink food vacuoles containing the pigment blepharismin that occur in cannibalistic individuals. The conditions in this study did not produce noticeable levels of cannibalism. The smaller ciliate Colpidium striatum (Stokes) potentially competes with Blepharisma for bacteria. Blepharisma readily consumes Colpidium, an interaction that is easily confirmed by observations of Colpidium in food vacuoles. Three food web configurations, with or without IGP, can be created by culturing each ciliate (Colpidium or Blepharisma) with or without the other.

IGP arises in different ways in size-structured populations of protists and metazoans. Size structure in metazoan populations results from an extended somatic growth period between birth and maturity. Many invertebrates pass through a series of developmental instars. Vertebrates with indeterminate growth, including fishes and amphibians, also have size-structured populations. IGP then occurs when larger individuals consume smaller ones. In protists, opportunities for intraguild predation, namely the presence of potential prey species, actually induce the size structure that facilitates IGP. Chemical cues produced by prey (Buhse 1966, Giese 1973), or starvation (Giese 1973), induce development of large predator or cannibal morphs that consume other guild members. Predatory morphs typically have enlarged cell sizes and a larger cytostome (the cellular equivalent of a mouth). Unlike the situation in most size-structured metazoan populations, larger predator morphs can transform into smaller bacterivores, usually after cell division. This developmental plasticity allows omnivorous protists to respond rapidly to short-term variation in resource availability. This form of developmental omnivory also creates polymorphic populations containing strictly bacterivorous microstomes and macrostomes that feed on both bacteria and other ciliates.

Little is known about the impact of IGP on protist population dynamics. Previous work shows that omnivores reach higher population densities and sometimes exhibit more stable population dynamics than non-omnivores (Lawler and Morin 1993, Morin and Lawler 1996). Omnivores sometimes exclude their IG prey competitors (Lawler and Morin 1993), and other times coexist with prey. The different outcomes of IGP observed for the same species in different experiments suggest the possibility of alternate states, or dependence on subtle differences in productivity or initial conditions. Models suggest that both alternate community patterns and strong effects of productivity can occur in simple food webs with IGP (Holt and Polis 1997).

## MATERIALS AND METHODS

Experimental manipulations of productivity and food web composition permitted comparisons of predator and prey dynamics with or without IGP. Simple differences in food web composition determined whether IGP could occur. Each of two ciliate species, Colpidium striatum or Blepharisma americanum, were bacterivores when established in microcosms with bacteria and a single ciliate species. Addition of both ciliate species to the same microcosm created situations where Blepharisma could consume both Colpidium and bacteria, creating a simple food web with IGP. Blepharisma involved in IGP increase in cell size and develop an enlarged cytostome, resulting in a distinctive macrostome morph (Giese 1973). Ciliate prey can be readily observed in food vacuoles within macrostomes. Differences in nutrient concentration created differences in bacterial densities, which provided a direct means of altering productivity. Bacteria formed the basal trophic level of all of these simple food webs.

A second set of short-term experiments quantified effects of nutrient concentration on bacterial densities, and also measured the relative ability of ciliate populations at carrying capacity to reduce bacterial abundance. Differences in bacterial densities resulting from ciliate grazing were used to assess the impact of each species on resource levels. Greater reductions in resource levels (bacterial densities) by a grazer would indicate both a greater impact on resource abundance and a greater ability to persist at low resource levels.

Microcosms.—Replicates of three food web config-

urations were established in 250-mL glass bottles containing 100 mL of medium. Productivity was manipulated by varying the initial concentration of the medium, using either 0.28 or 1.12 g of "protozoan pellets" (Carolina Biological Supply, Burlington, North Carolina) per liter of sterile well water. Basic culture methods were similar to those described by Lawler and Morin (1993). Lids allowed some air circulation, while restricting evaporation, and limiting contamination. Culture vessels and media were autoclaved before use. The design used four replicates of each distinct food web, at each of two levels of productivity, for a total of 24 microcosms. Replacement of 10% of the total volume with fresh medium every 7 d provided additional nutrients.

Community assembly involved additions of standard inocula of each species to microcosms containing freshly prepared bacterized medium. Inoculation with *Serratia marcescens, Bacillus cereus,* and *Bacillus subtilis* standardized initial bacterial species composition. *Colpidium* and *Blepharisma* grow readily on a diet of these bacteria. Bacterivores were added 24 h after the bacteria.

Short-term experiments designed to measure effects of nutrient concentration and grazers on bacterial abundance consisted of three grazing treatments, *Colpidium, Blepharisma,* or no ciliates, conducted at two different nutrient concentrations consisting of either 0.28 g or 1.12 g of "protozoan pellets" per liter of sterile well water. These experiments used the same microcosm protocol described above. After *Colpidium* and *Blepharisma* reached stable population densities, as determined by daily counts of ciliate abundance, bacterial densities were sampled by removing small volumes of medium from each microcosm with a sterile micropipette. Plate counts of serially diluted subsamples measured bacterial abundance under different regimes of nutrient concentration and grazing (Rashit and Bazin 1987, Allen-Morely and Coleman 1989). Plate counts provide accurate measures of the bacteria deliberately added to this system. Use of only culturable bacteria avoids the usual concerns about enumerating unculturable bacteria in natural systems (Daly 1979).

*Data.*—Microcosms were subsampled every 2–3 d for the 60-d duration of the main experiment to monitor ciliate population dynamics. Sampling involved withdrawing ~0.50 mL of medium from a thoroughly mixed microcosm with a sterile pipette. Protists were identified and counted live with the aid of a stereoscopic microscope. Each sample consisted of 10 ~0.04-mL subsamples (drops) placed on a tared plastic petri plate. The sample volume was rapidly determined by mass (to 0.0001 g precision) using an electronic balance. Counts standardized per unit volume provided estimates of average protist densities. Sampled medium was replaced with an equal volume of fresh sterile medium. On average, only ~0.5% of the entire community was removed in each sample.

*Statistical analysis.*—For each ciliate species, a two-factor ANOVA tested the effects of IGP and productivity on (1) the $\log_{10}$ of average abundance over time, (2) the $\log_{10}$ of maximum abundance, (3) persistence time (d), and (4) the coefficient of variation for abundance over time. MANOVAs of all four variables measured for each species provide statistically conservative tests of the overall responses of both species. Average abundance and the coefficient of variation included only data collected up through observed extinctions, and excluded data collected during the initial logarithmic phase of population growth. Average abundance provides a measure of secondary production, while the coefficient of variation provides a relatively unbiased measure of temporal variation in population dynamics (McArdle et al. 1990). Similarly, a two-factor ANOVA tested for effects of different consumers (none, *Colpidium, Blepharisma*) and nutrient levels on log-transformed bacterial abundances.

RESULTS

*Effects of productivity in the absence of IGP*

Populations of both *Colpidium* and *Blepharisma* increased when feeding on bacteria. *Colpidium* increased more rapidly than *Blepharisma,* and also reached higher population densities (Figs. 1 and 2). *Colpidium* attained maximal population densities after only 2–4 d of growth, while *Blepharisma* required 8–18 d to reach maximal abundance. Elevated productivity increased both the mean and maximum density of *Blepharisma* (Tables 1, 2, and 5). Mean abundance of *Colpidium* did not respond to productivity, although maximum abundance did (Tables 1 and 2). *Colpidium* apparently responded to reduced productivity by decreasing in cell size rather than by decreasing in abundance, a result noted in other studies (Balciunas and Lawler 1995), but not quantified here. *Colpidium* also displayed more variable population dynamics in communities with elevated productivity (Figs. 1 and 2; Tables 3 and 5). In all but one of the replicates containing a single ciliate species, populations persisted through the entire 60–d duration of the study (Figs. 1 and 2, Tables 4 and 5). *Blepharisma* abundance declined sharply in a few replicates toward the end of the experiment, perhaps in response to deteriorating conditions in the microcosms. These declines would have made a minor contribution to measures of average abundance, but would not have affected analyses of other responses.

*Effects of omnivory and productivity on population dynamics*

The outcome of interactions between *Blepharisma* and *Colpidium* depended on productivity. *Colpidium* excluded *Blepharisma* after ~40 d of interaction in three out of four replicates at the lower level of productivity (Fig. 1), despite the fact that *Blepharisma* could consume *Colpidium*. At higher levels of produc-
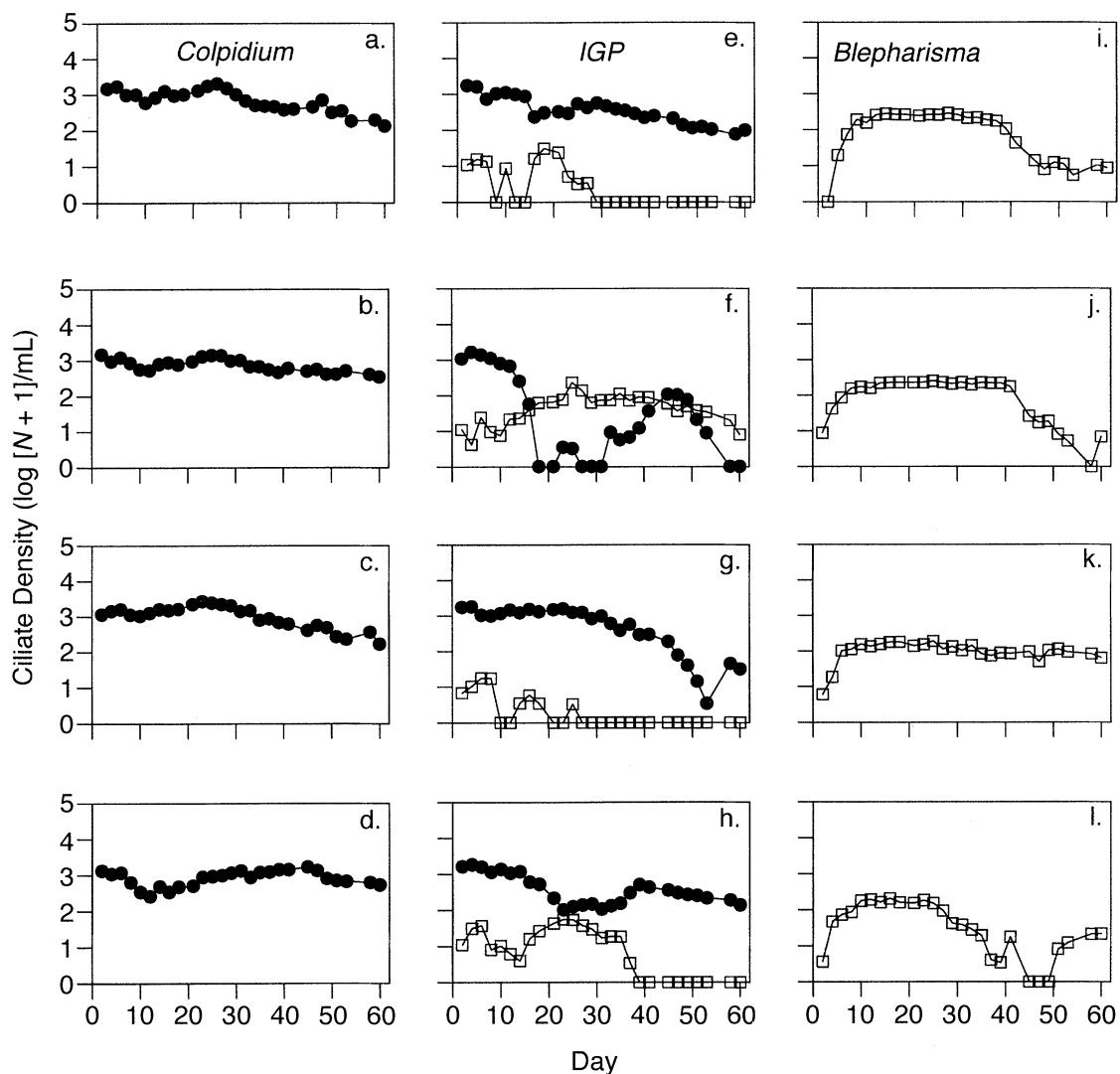
FIG. 1. Population dynamics of *Colpidium* (solid circles) and *Blepharisma* (open squares) in the low nutrient treatment. Each panel corresponds to dynamics observed in a single microcosm.

tivity, *Colpidium* and *Blepharisma* coexisted for nearly the entire duration of the study (Figs. 1 and 2). A significant productivity × IGP interaction in the ANOVA for *Blepharisma* persistence time confirms these different dynamic responses to productivity (Tables 4 and 5). Interactions with the other guild member reduced the average abundance of *Colpidium* and *Blepharisma* at both levels of productivity (Table 1), suggesting that any benefits obtained by *Blepharisma* from consuming *Colpidium* were more than offset by competition with the survivors.

### Effects of grazers and productivity on bacterial densities

Both initial nutrient concentration and different ciliate species affected bacterial densities (Fig. 3). Bacterial densities increased in response to increased nutrient con-

centrations, indicating that nutrient manipulations altered bacterial production (Table 6). Ciliate grazing significantly reduced bacterial densities, with *Colpidium* driving bacterial densities to lower levels than *Blepharisma* (Fig. 3, Table 6). Significant interactions between productivity and grazing treatments indicated that productivity altered the ability of grazers to reduce bacterial densities. In general, both ciliates drove bacterial densities to lower levels in the low-productivity treatments, and *Colpidium* reduced bacteria to a greater extent than *Blepharisma* in the lower productivity regime. The results are consistent for both sampling dates, which bracket the peak period of ciliate abundance. These results suggest that both *Colpidium* and *Blepharisma* have some form of direct intraspecific density dependence that might be mediated by factors such as the buildup of waste products in the culture medium.
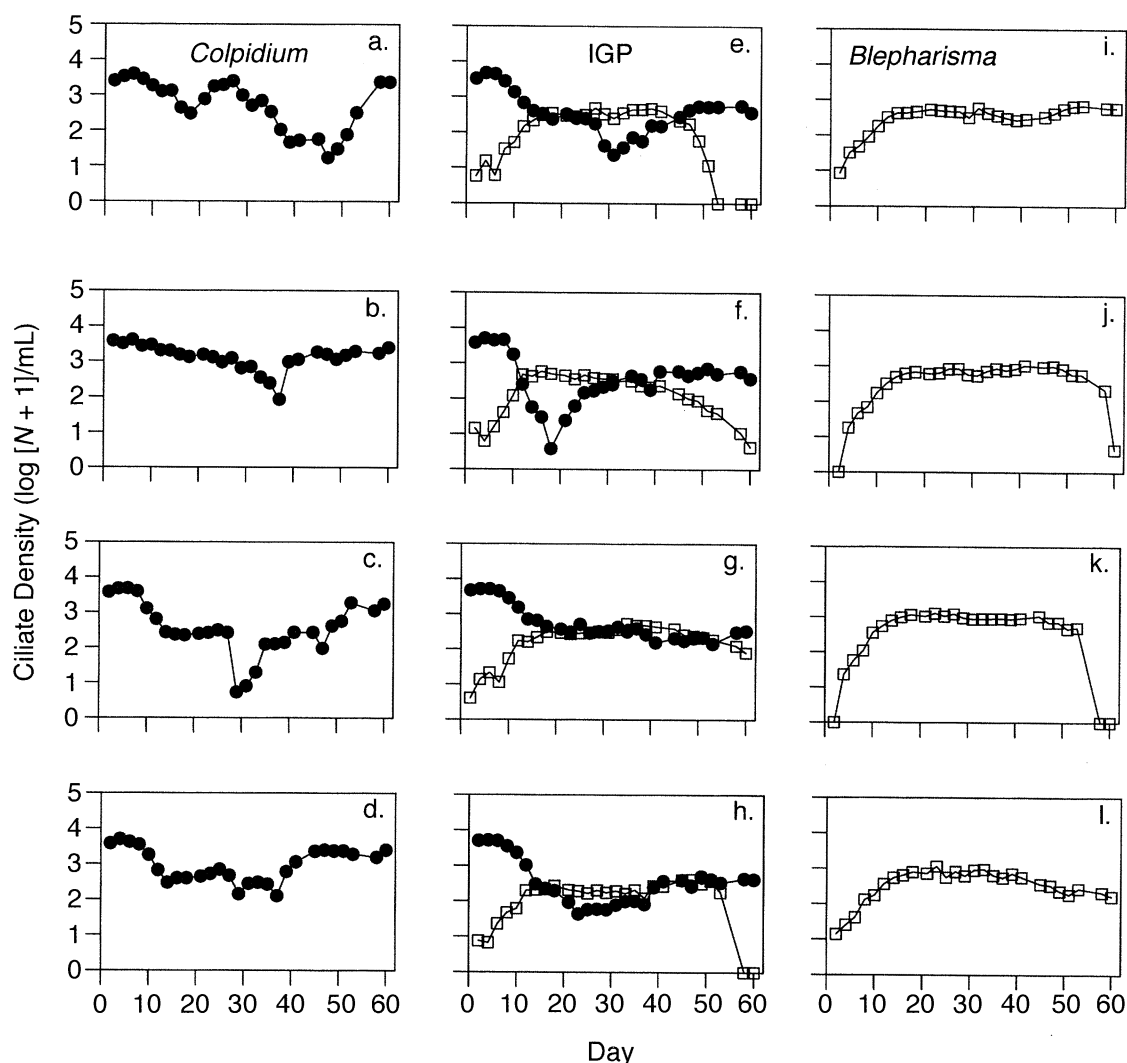
FIG. 2. Population dynamics of *Colpidium* (solid circles) and *Blepharisma* (open squares) in the high nutrient treatment. Each panel corresponds to dynamics observed in a single microcosm.

## DISCUSSION

### Effects of productivity on IGP

The interactions observed between *Colpidium* and *Blepharisma* are broadly consistent with the predictions of simple models of intraguild predation (Polis et al 1989), assuming that the IG predator is much less ef-

ficient than its IG prey/competitor in resource use. Those models predict competitive exclusion of the predator by its intraguild prey at low resource levels, coexistence at intermediate resource levels, and exclusion of the prey by the predator at even higher resource levels. Apparently, the resource levels used in this study bracket the low to middle region of this range.

TABLE 1. Average over time of log-transformed ciliate abundance (a measure of secondary production). Entries are means (1 SD in parentheses) of log-transformed abundances (log $[N + 1/\text{mL}]$) for four replicate microcosms.

| Species | Productivity | Food web configuration | | ANOVA | | |
|---------|--------------|------------------------|------|-------|------------|-------------|
| | | No IGP | IGP | IGP | Productivity | Interaction |
| *Colpidium* | 0.5× | 2.889 (0.067) | 2.260 (0.602) | $F_{1,12} = 7.00$ | $F_{1,12} = 0.51$ | $F_{1,12} = 1.27$ |
| IG prey | 2.0× | 2.820 (0.257) | 2.567 (0.102) | $(P = 0.0214)$ | $(P = 0.4898)$ | $(P = 0.2814)$ |
| *Blepharisma* | 0.5× | 1.817 (0.269) | 1.026 (0.455) | $F_{1,12} = 18.75$ | $F_{1,12} = 66.99$ | $F_{1,12} = 1.99$ |
| IG predator | 2.0× | 2.749 (0.132) | 2.347 (0.074) | $(P = 0.0010)$ | $(P = 0.0001)$ | $(P = 0.1834)$ |

TABLE 2. Maximum of log-transformed ciliate abundance. Entries are means (1 SD in paretheses) of the maximum observed in each of four replicate microcosms.

| Species | Productivity | Food web configuration | | ANOVA | | |
| | | No IGP | IGP | IGP | Productivity | Interaction |
| --- | --- | --- | --- | --- | --- | --- |
| *Colpidium* | 0.5× | 3.281 (0.113) | 3.237 (0.019) | $F_{1,12} = 0.05$ | $F_{1,12} = 162.96$ | $F_{1,12} = 2.53$ |
| IG prey | 2.0× | 3.635 (0.050) | 3.692 (0.018) | $(P = 0.8328)$ | $(P = 0.0001)$ | $(P = 0.1376)$ |
| *Blepharisma* | 0.5× | 2.361 (0.083) | 1.710 (0.480) | $F_{1,12} = 14.22$ | $F_{1,12} = 41.31$ | $F_{1,12} = 1.90$ |
| IG predator | 2.0× | 2.999 (0.116) | 2.696 (0.064) | $(P = 0.0027)$ | $(P = 0.0001)$ | $(P = 0.1931)$ |

Attempts to grow *Blepharisma* at even higher resource levels were unsuccessful, perhaps because of the osmotic problems caused by increased nutrient concentrations. *Blepharisma* is sensitive to increased osmolarity of growth medium (Geise 1973). Consequently, it is unclear whether conditions leading to predominance by *Blepharisma* can be created by direct manipulations of nutrient concentration. Other studies using nutrient concentrations within the range of those used here show that *Blepharisma* can sometimes exclude *Colpidium* (Lawler and Morin 1993). For example, Lawler and Morin found that *Blepharisma* excluded *Colpidium* in three of five replicate communities established at a level of productivity intermediate to that used in the present study. In other initially similar replicates, *Blepharisma* and *Colpidium* coexisted. Reasons for the different outcomes of these different two experiments are unknown.

The apparent exclusion of *Blepharisma* by *Colpidium* at lower levels of productivity deserves comment, since it seems counterintuitive for a prey to competitively exclude its predator. One contributing factor is that *Colpidium* drives bacterial populations to lower levels than *Blepharisma*. In the parlance of mechanistic competition theory (Volterra 1928, Armstrong and McGhee 1980, Tilman 1982, Holt et al. 1994), *Colpidium* generates a lower equilibrium value of resource abundance, $R^*$, than does *Blepharisma*. In such settings, simple competition models predict that *Colpidium* will exclude *Blepharisma*. However, *Blepharisma* can also consume *Colpidium*. Why doesn't this apparent advantage prevent the exclusion of *Blepharisma*? One possibility is that *Colpidium* densities were not sufficient to sustain *Blepharisma* populations at the lower productivity level. The observation that average *Colpidium* densities were similar at both productivity

levels argues against this idea. Another possibility is that *Colpidium* was nutritionally deficient, and only served as supplementary prey when bacteria were abundant. Tests of this idea would require culturing *Blepharisma* on a diet of *Colpidium,* with few or no bacteria present, a situation that is technically difficult to arrange. What is clear is that any advantage gained by the consumption of *Colpidium* is not sufficient to offset the reduced bacterial densities encountered at lower levels of productivity. The third possibility is that although *Colpidium* densities were similar in the two different productivity regimes, a smaller cell size for *Colpidium* at lower productivity may have made them less suitable prey for *Blepharisma*. Although cell size was not measured in this experiment, other studies have shown that individual *Colpidium* decrease in size in less productive settings (Balciunas and Lawler 1995). Balciunas and Lawler (1995) showed that reduction of nutrient concentration to 33% of baseline levels caused *Colpidium* length to decrease from 62.8 to 41.3 μm, a substantial change in cell size.

### Effects of productivity on population dynamics

Increased productivity can have destabilizing effects on population dynamics via the paradox of enrichment noted in some predator–prey models (Rosenzweig 1971). Increased productivity increased the temporal variability of *Colpidium* population dynamics in food webs with or without IG predators, suggesting that this result does not depend strongly on interactions with such predators. *Blepharisma* responded differently to increased productivity, as shown by the increased stability of the *Colpidium–Blepharisma* interaction in the higher productivity treatment. These different responses of different species to the same productivity manipulation caution against making blanket state-

TABLE 3. Mean coefficients of variation for abundance over time (1 SD in parentheses), a measure of variation in population dynamics.

| Species | Productivity | Food chain configuration | | ANOVA | | |
| | | No IGP | IGP | IGP | Productivity | Interaction |
| --- | --- | --- | --- | --- | --- | --- |
| *Colpidium* | 0.5× | 52.28 (10.31) | 110.23 (46.76) | $F_{1,12} = 14.81$ | $F_{1,12} = 9.46$ | $F_{1,12} = 0.0$ |
| IG prey | 2.0× | 98.68 (35.01) | 155.85 (7.79) | $(P = 0.0023)$ | $(P = 0.0096)$ | $(P = 0.979)$ |
| *Blepharisma* | 0.5× | 69.45 (30.00) | 96.89 (18.52) | $F_{1,12} = 4.02$ | $F_{1,12} = 19.26$ | $F_{1,12} = 0.63$ |
| IG predator | 2.0× | 34.28 (11.45) | 46.12 (12.61) | $(P = 0.0680)$ | $(P = 0.0009)$ | $(P = 0.4411)$ |

TABLE 4. Mean persistence time (d; 1 SD in parentheses), another measure of stability. Maximal persistence time was 60 d, the duration of the experiment. Ellipses (⋯) indicate where ANOVA statistics could not be estimated because of no variation among replicates.

| Species | Productivity | Food chain configuration | | ANOVA | | |
| | | No IGP | IGP | IGP | Productivity | Interaction |
| --- | --- | --- | --- | --- | --- | --- |
| *Colpidium* | 0.5× | 60 (0) | 60 (0) | ⋯ | ⋯ | ⋯ |
| IG prey | 2.0× | 60 (0) | 60 (0) | ⋯ | ⋯ | ⋯ |
| *Blepharisma* | 0.5× | 60 (0) | 40 (14.2) | $F_{1,12} = 8.53$ | $F_{1,12} = 7.73$ | $F_{1,12} = 7.73$ |
| IG predator | 2.0× | 60 (0) | 59 (1.0) | ($P = 0.0128$) | ($P = 0.0167$) | ($P = 0.0167$) |

ments about how enrichment affects the stability of predator–prey interactions.

Other examples of predator–prey interactions among protists without IG predation exhibit dynamics that are consistent with the paradox of enrichment (Luckinbill 1973, 1974, Balciunas and Lawler 1995; M. Holyoak, *unpublished manuscript*), although the proximal mechanisms that create instability are not always those considered by Rosenzweig (1971). The different responses of systems with and without IGP to enrichment suggest that food webs containing different amounts of IG predation may respond rather differently to variation in productivity.

### Food chain theory

Causal relations between productivity and food chain length remain controversial. Some models predict nonlinear relations between food chain length and productivity, with food chain length eventually decreasing at sufficiently high levels of productivity (Abrams and Roth 1994, Holt and Polis 1997) Some surveys of natural patterns find little support for effects of productivity on chain length (Pimm and Lawton 1977, Pimm 1982). Other experimental manipulations suggest that the available energy and its efficiency of transfer between trophic levels plays an important role in food chain length (Jenkins et al. 1992, Wootton and Power 1993). At face value, interactions between *Colpidium* and *Blepharisma* support a positive relation between productivity and food chain length, although not for the simple reasons of efficiency of energy transfer that

TABLE 5. MANOVAs for the effects of IGP and productivity on responses of *Colpidium* and *Blepharisma*.

| Factor | Wilks' lambda | P |
| --- | --- | --- |
| *Colpidium* | | |
| IGP | 0.2703 | 0.0034 |
| Productivity | 0.0680 | 0.0001 |
| Interaction | 0.5706 | 0.1182 |
| *Blepharisma* | | |
| IGP | 0.2574 | 0.0093 |
| Productivity | 0.0582 | 0.0001 |
| Interaction | 0.3577 | 0.0381 |

*Note:* The MANOVA provides a test statistic that is adjusted for the analysis of four different variables (average density, maximum density, persistence time, and coefficient of variation for abundance).
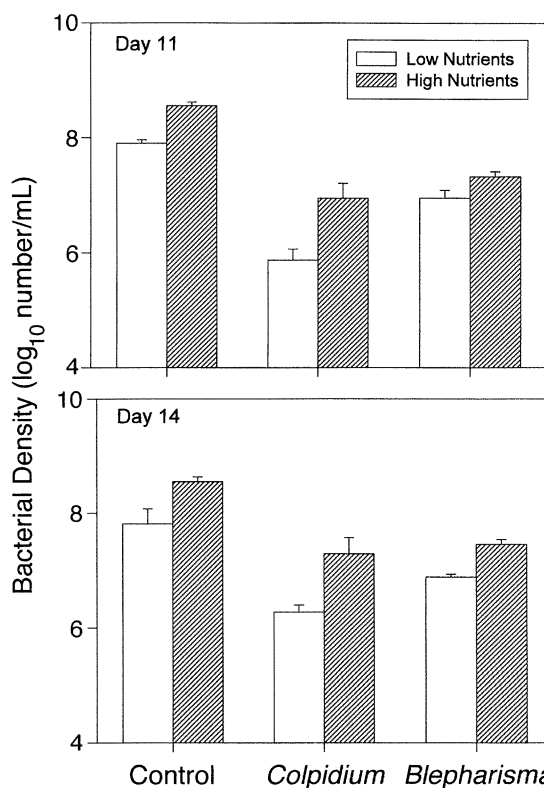
are usually invoked (Lawton 1989). Increased productivity led to an effective increase in food chain length, since the IG predator *Blepharisma* was able to persist with *Colpidium* only at the higher level of productivity. This increased productivity was accompanied by an increase in bacterial standing stocks by a factor of ~4.6–4.9, but did not lead to a significant increase in *Colpidium* abundance. Of course, the standing stock of *Colpidium* is also not a direct measure of productivity, per se, although it might be expected to increase in more productive situations without predators that consume *Colpidium* (Oksanen et al. 1981). As noted previously, other studies show that *Colpidium* cell sizes



FIG. 3. Effects of nutrient manipulations (low vs. high) and different consumers (*Colpidium, Blepharisma,* or none) on bacterial abundance. Samples on two consecutive dates correspond to time periods when *Blepharisma* and *Colpidium* both attained maximal abundance.

TABLE 6. ANOVA for effects of ciliate grazing and nutrient concentration on bacterial abundance.

| Source | df | Mean square | $F$ | $P$ |
|---|---|---|---|---|
| Day 11 | | | | |
| Nutrients | 1 | 3.6842 | 158.82 | 0.0001 |
| Grazing | 2 | 8.3986 | 362.06 | 0.0001 |
| Interaction | 2 | 0.3070 | 13.24 | 0.0001 |
| Error | 24 | 0.0232 | | |
| Day 14 | | | | |
| Nutrients | 1 | 4.4481 | 147.75 | 0.0001 |
| Grazing | 2 | 5.2108 | 173.08 | 0.0001 |
| Interaction | 2 | 0.1254 | 4.17 | 0.0280 |
| Error | 24 | 0.0301 | | |

increase with increasing nutrient concentrations (Balciunas and Lawler 1995). This suggests that the food quality of individual *Colpidium* may have changed in ways missed by the simple enumeration of cell densities, and consequently a bottom-up effect on *Colpidium* quality cannot be ruled out as a cause of greater food chain length in more productive settings. Clearly, future experiments should monitor both population dynamics and changes in the sizes of interacting organisms, to identify the proximal causes of responses to altered productivity. Alternately, the maintenance of longer food chains in higher productivity environments may have been mediated via a direct effect on bacterial abundance, which provided a greater abundance of alternate prey for *Blepharisma*. Regardless of the precise mechanism involved, this result illustrates how responses to productivity in food webs containing omnivores can depart in important ways from the predictions made by models that ignore omnivory (Oksanen et al. 1981).

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