Predator Diet Breadth Influences the Relative Importance of Bottom-Up and Top-Down Control of Prey Biomass and Diversity

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ABSTRACT: We investigated the effects of predator diet breadth on the relative importance of bottom-up and top-down control of prey assemblages, using microbial food webs containing bacteria, bacterivorous protists and rotifers, and two different top predators. The experiment used a factorial design that independently manipulated productivity and the presence or absence of two top predators with different diet breadths. Predators included a "specialist" predatory ciliate *Euplotes aediculatus*, which was restricted to feeding on small prey, and a "generalist" predatory ciliate *Stentor coeruleus*, which could feed on the entire range of prey sizes. Both total prey biomass and prey diversity increased with productivity in the predator-free control and specialist predator treatments, a pattern consistent with bottom-up control, but both remained unchanged by productivity in the generalist predator treatment, a pattern consistent with top-down control. Linear food chain models adequately described responses in the generalist predator treatment, whereas food web models incorporating edible and inedible prey (which can coexist in the absence of predators) adequately described responses in the specialist predator treatment. These results suggest that predator diet breadth can play an important role in modulating the relative strength of bottom-up and top-down forces in ecological communities.

Keywords: bottom-up control, diversity, predation, predator diet breadth, productivity, top-down control.

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Ecologists have long recognized the importance of bottom-up (productivity based) and top-down (predation driven) forces in structuring ecological communities. Decades of research have led to the conclusion that while productivity could largely determine patterns of species abundance and distribution (Elton 1927; Lindeman 1942; Odum 1971; White 1978; Hunter and Price 1992; Polis 1999), predators can also significantly influence populations and communities and under certain circumstances may prevail over bottom-up effects (Hairston et al. 1960; Slobodkin et al. 1967; Menge and Sutherland 1976; Fretwell 1977; Oksanen et al. 1981; Hairston and Hairston 1993, 1997; Oksanen and Oksanen 2000). Because most natural populations are affected by both bottom-up and top-down forces (Power 1992; Osenberg and Mittelbach 1996), manipulative experiments are necessary to evaluate their relative importance. Some experimental studies have simultaneously manipulated productivity and predation to assess their effects on prey assemblages (e.g., Leibold and Wilbur 1992; Steiner 2001; Worm et al. 2002), but few studies have followed the dynamics of responding organisms for more than one or two generations to distinguish transient and long-term effects. The short-term nature of most experimental studies of community organization raises questions about whether initial effects of productivity or predator manipulations are transient or will persist for longer periods of time.

Many abiotic and biotic factors could affect the relative strength of bottom-up and top-down effects (Hunter and Price 1992; Power 1992; Strong 1992; Persson 1999; Polis 1999). Among these factors, differences within trophic levels in prey edibility have received much attention, and theory shows that such differences can affect the extent of bottom-up and top-down control (Phillips 1974; Leibold 1989, 1996; Abrams 1993; Kretzschmar et al. 1993; Grover 1995; Genkai-Kato and Yamamura 2000). Linear food chain models, which assume that each trophic level consists of one homogenous (entirely edible) group, predict that abundance of the top trophic level should increase

and that of its prey trophic level should remain unchanged with increasing productivity (Oksanen et al. 1981; Abrams 1993). Essentially, the abundance of top predators is controlled from the bottom up by productivity, and the predators exert top-down control on the abundance of their prey. Two general food web models incorporate heterogeneity in edibility within the prey trophic level. The edible-inedible prey models consider two types of prey, edible and inedible, and predict that as productivity increases, edible prey abundance would remain unchanged, inedible prey abundance would increase, and the abundance of top predators can either increase or remain unchanged, depending on model configurations and assumptions (Phillips 1974; Leibold 1989; Abrams 1993; Kretzschmar et al. 1993; Grover 1995; Genkai-Kato and Yamamura 2000). Regardless of predator responses, total prey abundance always increases with productivity, a pattern consistent with bottom-up control. Unlike the edible-inedible prey model, the keystone predation model assumes that all prey species are edible to some extent (Leibold 1989, 1996). This model predicts that increased productivity will generate parallel increases in the abundance of predators and the whole prey assemblage accompanied by a turnover in prey species composition along the productivity gradient (i.e., relatively vulnerable prey species are replaced by more predation-resistant prey species with increasing productivity as predators become more abundant). As such, the prey trophic level appears to be controlled from the bottom up. Each of the three models has received some empirical support (Leibold 1989, 1996, 1999; Wootton and Power 1993; Leibold et al. 1997; Kaunzinger and Morin 1998; Bohannan and Lenski 1999, 2000; Chase et al. 2000; Steiner 2001).

Both bottom-up and top-down forces can also profoundly influence species diversity, which is another defining characteristic of ecological communities. Empirical studies show that species diversity can show complex responses to changes in productivity (Waide et al. 1999; Mittelbach et al. 2001), although it has been suggested by several ecologists that a unimodal relationship between diversity and productivity should be the norm (Rosenzweig and Abramsky 1993; Rosenzweig 1995). Predator manipulation experiments show that predation may either enhance or reduce prey diversity (reviewed by Sih et al. 1985; Olff and Ritchie 1998). Ecologists have just begun to explore how bottom-up and top-down factors interact to affect species diversity. Among the three types of food web models noted above, only the keystone predation model makes predictions about diversity. It suggests that prey species diversity should first increase and then decrease as productivity increases, producing a hump-shaped diversity curve along the productivity gradient (Leibold 1996). Empirical studies support the interdependency of bottom-up and top-down effects. Meta-analyses by Proulx and Mazumder (1998) and Worm et al. (2002) both found that the effect of grazing on plant species diversity depends on ecosystem productivity.

Because prey edibility also hinges on predator properties (an inedible species for one predator may be edible for another), predator traits may also be important in modulating the relative importance of bottom-up and top-down control of species abundance and diversity. Species-specific differences in predator effectiveness and efficiency may set the stage for either bottom-up or top-down forces to dominate (Hunter and Price 1992; Power 1992). Particularly, the diet breadth of a predator may largely determine its impacts on the prey assemblage; a generalist predator would be able to control a diverse prey assemblage effectively (top-down control), whereas a specialist predator would only consume a restricted subset (vulnerable) of the prey assemblage, exposing the remaining prey (invulnerable or unpalatable) to the influence of resources (bottom-up control).

A definitive test of the role of predator diet breadth in the bottom-up and top-down control of ecological communities requires factorial manipulations of both predator identity and the abiotic determinants of productivity. So far, few such experiments have been conducted. Among them, Leibold and Wilbur (1992) showed that phytoplankton and periphyton in ponds responded differently to nutrient enrichment in the presence of two different herbivores (*Daphnia laevis* or *Rana utricularia*). Steiner (2001) reported that *Daphnia pulex* was more effective than *Ceriodaphnia quadrangula* in controlling large grazer-resistant phytoplankton, especially under enriched conditions. Neither study examined species diversity.

Here we describe an experimental study on the importance of predator identity and diet breadth for the bottom-up and top-down control of prey biomass and diversity in aquatic microcosms containing bacteria, protists, and small metazoans. Two different top predators (the large generalist ciliate *Stentor coeruleus* and the small specialist ciliate *Euplotes aediculatus*) fed on a diverse assemblage of bacterivorous protists and metazoans along a productivity gradient. The experiment explored two questions. First, do differences in predator diet breadth affect the relative strength of bottom-up and top-down effects? Second, do the linear food chain models, the edible-inedible prey models, or the keystone predation model best characterize the experimental results? The short generation times (from hours to days) of our experimental organisms relative to our experimental duration (4 weeks) suggest that our results reflect relatively long-term persistent patterns rather than short-term transient dynamics.

Methods

Our experiment used a factorial design with three predation treatments (control, no predation; *Euplotes*, specialist predation; and *Stentor*, generalist predation) repeated over 10 nutrient levels used to create differences in productivity. Additions of different amounts of protozoan pellets (a source of complex organic nutrients; Carolina Biological Supply [CBS], Burlington, NC) to well water manipulated nutrient concentration and productivity. The resulting medium supports the growth of bacteria and protists. Nutrient enrichment increases the production of bacteria (Kaunzinger and Morin 1998), the basal trophic level in our food webs. Ten nutrient levels, evenly spaced on an arithmetic scale, ranged from 0.07 to 0.7g protozoan pellets per liter of water. The experimental microcosms were 250-mL screw-capped Erlenmeyer flasks, each containing 100 mL of nutrient medium. The flasks and medium were autoclaved before use.

Sterile medium was inoculated first with three bacterial species (*Serratia marcescens*, *Bacillus cereus*, and *Bacillus subtilis*) obtained from CBS and a group of nanoflagellates collected from the Rutgers University Display Garden pond (New Brunswick, NJ). Approximately 24 h after bacterial and nanoflagellate inoculation, 16 taxa of bacterivorous protozoa and rotifers (one flagellate: *Chilomonas* sp.; two rotifers: *Lepadella* sp., *Rotaria* sp.; 13 ciliates: *Coleps* sp., *Colpidium striatum*, *Colpoda cucullus*, *Colpoda* sp., *Loxocephalus* sp., *Paramecium caudatum*, *Paramecium tetraurelia*, small *Spirostomum* sp., large *Spirostomum* sp., *Tetrahymena pyriformis*, *Tetrahymena thermophila*, *Uronema* sp., and one unidentified hypotrich) were introduced into all microcosms. Among these, *Paramecium tetraurelia* and *Tetrahymena thermophila* were obtained from the American Type Culture Collection (Rockville, MD); *Chilomonas*, *Colpidium striatum,* and *Tetrahymena pyriformis* came from CBS; and all other species were isolated from the Rutgers University Display Garden pond. All 16 species had been maintained separately in stock cultures. At least 20 individuals of each species were added to each microcosm to ensure their initial establishment. In the predation treatments, 20 individuals of each predator (either *Euplotes aediculatus* or *Stentor coeruleus*) were added to their designated microcosms 1 week after bacterivore inoculation, after bacterivores became abundant enough to support predator populations. *Euplotes aediculatus* was isolated from the Rutgers University Display Garden pond and maintained on a diet of *Colpidium*. *Stentor coeruleus* was obtained from CBS and maintained on a mixed diet of *Colpidium* and *Chilomonas*. The relatively small size of *Euplotes* ($\sim$100–150 μm) limits its ability to feed on large prey items, while the larger *Stentor* ($\sim$1,000–2,000 μm) could potentially feed on all 16 prey species. Each combination of predation treatment and nutrient level was replicated three times, yielding a total of 90 microcosms. All microcosms were kept in the dark at 22°C for the 4-week experimental period.

Each microcosm was sampled weekly by first swirling the flask to mix the contents and then using a sterile Pasteur pipette to withdraw $\sim$0.35 mL medium. The sample was distributed into 10 drops in a tared petri dish, sample volume was determined by mass using an analytical balance, and protists and rotifers were counted live with the aid of a stereoscopic microscope. Sample dilution was often necessary to count species with high densities. Ten percent (10 mL) of the volume in each microcosm was replaced with fresh medium each week to replenish the medium and to limit metabolic waste accumulation. The 10 mL of medium removed from each flask each week was also inspected to obtain a better estimate of the abundance of rare species.

The density of each protist and rotifer was recorded as the number of individuals per milliliter. We also estimated the biovolume of each bacterivorous species by randomly selecting 10 individuals in the controls and measuring their body length and width with the ocular micrometer of a compound microscope. Species volumes were calculated using the formulas in Wetzel and Likens (1991). To obtain the total biovolume of the whole prey assemblage, we simply multiplied the biovolume of each species by its density and summed all species together.

Both biovolumes and densities were log transformed to homogenize variances. Prey species richness and total prey biovolume were analyzed with repeated-measures ANOVA (rmANOVA). Prey species richness, total prey biovolume, and the density of each prey species on the final sampling date were also analyzed using ANOVA.

Results

Extinction commonly occurred in all treatments (fig. 1*A*, 1*C*, 1*E*), as indicated by a significant time effect in rmANOVAs (tables A1A, A1B, A2A, A2B in the online edition of the *American Naturalist*). By the end of the experiment, fewer than five species were present at the lowest productivity, and more than eight species remained at the three highest productivity levels in the control (fig. 2*A*). Species richness increased as productivity increased in both control and *Euplotes* treatments (fig. 1*A*, 1*C*; tables A1A, A1B; note no significant predation × productivity effect). *Euplotes* predation reduced species richness, though by only an average of one species at each productivity level (fig. 1*A*, 1*C*; tables A1A, A1B).

Compared with *Euplotes*, *Stentor* had a much stronger negative effect on prey richness that almost overwhelmed the effects of productivity (fig. 1*A*, 1*E*; tables A2A, A2B).
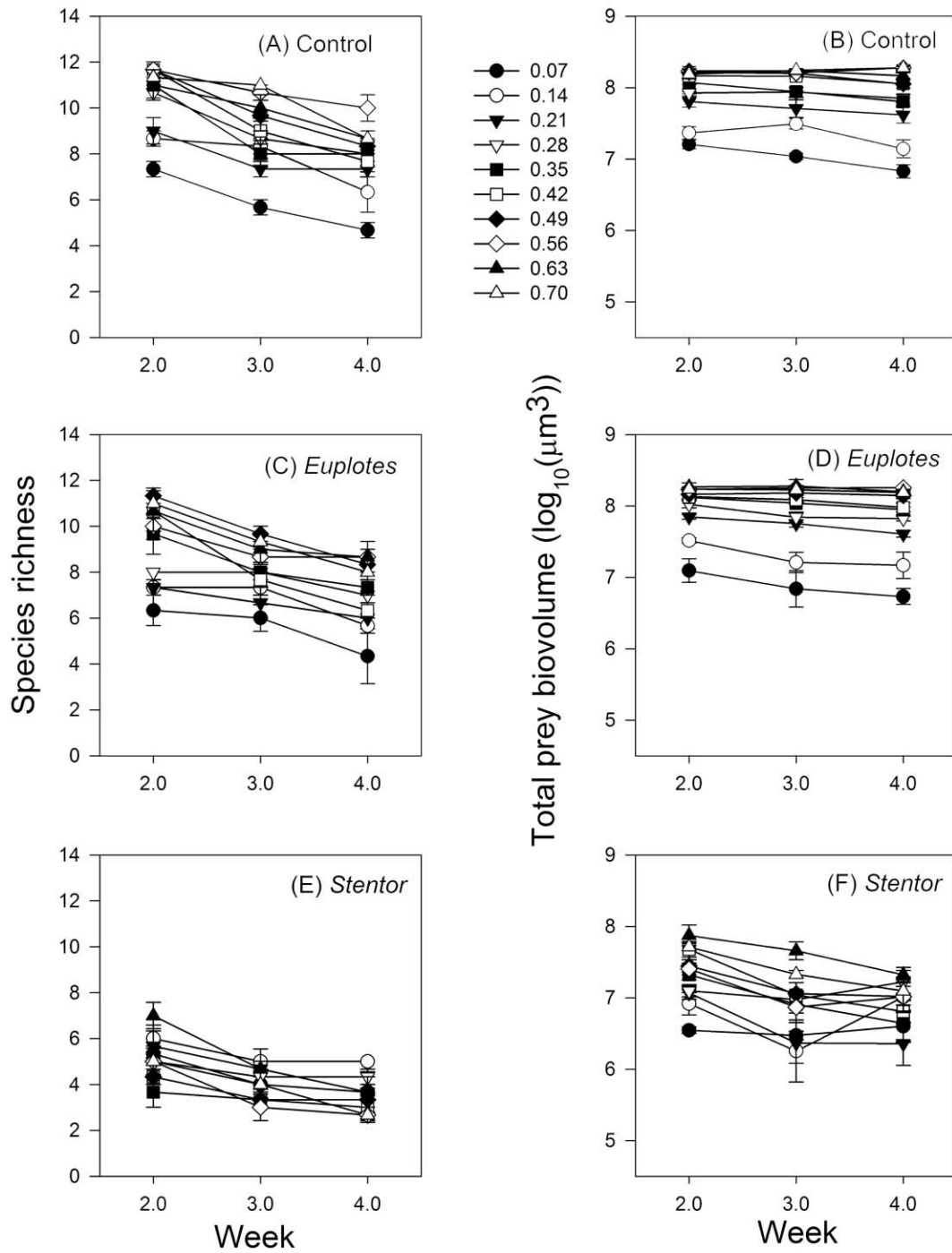
Figure 1: Responses of prey species richness (*left panels*) and total prey biovolume (*right panels*) to nutrient (productivity) manipulations through time in the control (*A*, *B*), *Euplotes* (*C*, *D*), and *Stentor* (*E*, *F*) treatments. Values are means ± 1 SE. Different symbols represent different nutrient levels (g protozoan pellets per L).
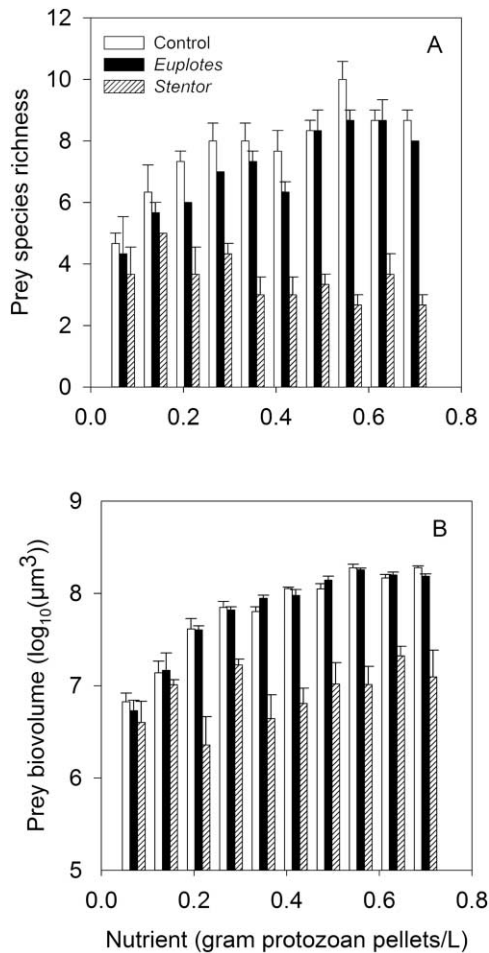
Figure 2: Effects of nutrient (productivity) and predation manipulations on (*A*) prey species richness and (*B*) total prey biovolume on the final sampling date. Values are means ± 1 SE.

Although there was an overall significant positive effect of increasing productivity on species richness when the control and *Stentor* treatments were examined together (fig. 1*A*, 1*E*; tables A2A, A2B), responses in the two treatments differed, as indicated by the significant interaction between predation and productivity (tables A2A, A2B). There was a strong positive response in the predator-free control (fig. 1*A*; one-way rmANOVA, productivity: $F = 15.24$, df = 9, 20, $P < .0001$) and a weaker but significant response in the *Stentor* treatment (fig. 1*E*; one-way rmANOVA, productivity: $F = 2.79$, df = 9, 20, $P = .0267$). By the end of the experiment, the effects of productivity disappeared in the *Stentor* treatment (one-way ANOVA, productivity: $F = 1.77$, df = 9, 40, $P = .1387$) as prey richness remained roughly constant (fewer than four species on average) along the productivity gradient (fig. 2*A*).

Responses of total prey biovolume were similar to those

of species diversity. Total prey biovolume increased significantly with productivity in both control and *Euplotes* treatments, and *Euplotes* did not affect total prey biomass (figs. 1*B*, 1*D*, 2*B*; tables A3A, A3B in the online edition of the *American Naturalist*). Conversely, *Stentor* strongly reduced total prey biomass and eliminated any effects of productivity (figs. 1*B*, 1*F*, 2*B*; tables A4A, A4B in the online edition of the *American Naturalist*). By the end of the experiment, total prey biomass remained essentially con-
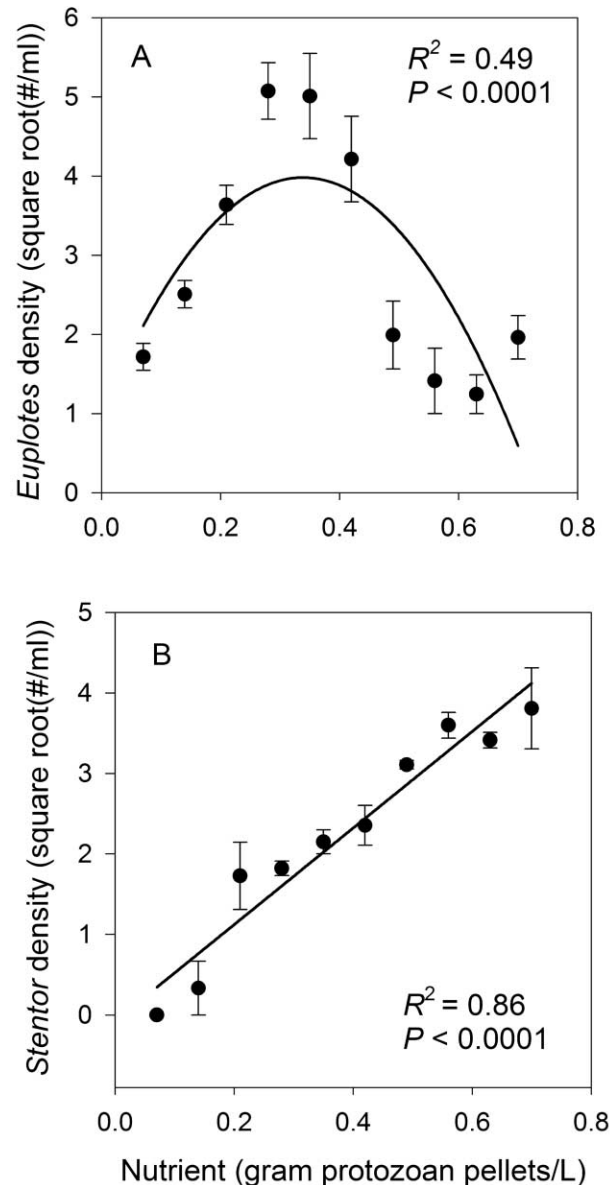

Figure 3: Effects of nutrient (productivity) manipulations on the abundance of (*A*) *Euplotes* and (*B*) *Stentor* on the final sampling date. Values are means ± 1 SE. Regressions were performed based on individual replicates rather than the mean values.

stant along the productivity gradient in the *Stentor* treatment (fig. 1*B*; one-way ANOVA, productivity: $F = 1.44$, df $= 9, 40$, $P = .2370$).

Productivity affected the abundance of *Euplotes* (one-way rmANOVA, productivity: $F = 7.86$, df $= 9, 20$, $P < .0001$) and *Stentor* (one-way rmANOVA, productivity: $F = 11.69$, df $= 9, 20$, $P < .0001$). Interestingly, *Euplotes* abundance on the final sample date displayed a hump-shaped pattern along the productivity gradient, and a quadratic curve explained almost 50% of the variation (fig. 3*A*). In contrast, *Stentor* abundance on the final sample date showed a significantly positive linear relationship with productivity (fig. 3*B*, linear regression: $R^2 = 0.86$, $P < .0001$).

We inspected the responses of individual prey species to explore why *Euplotes* abundance declined at high productivity levels. *Euplotes* negatively affected the abundance of five small-bodied species (*Uronema*, *Chilomonas*, *Loxocephalus*, *Colpidium*, and *Coleps*) out of the 12 prey species present at the end of the experiment (fig. 4). This is not unexpected, considering that the relatively small size of *Euplotes* made it function as a gape-limited predator. We also found that *Colpidium* was eliminated from low to medium productivities but coexisted with *Euplotes* at high productivities (fig. 4). *Colpidium* was probably the principle energy source for *Euplotes* because other prey species were either too small (i.e., *Uronema*) or too scarce (i.e., *Chilomonas*, *Loxocephalus*, and *Coleps*) to contribute much to its nutrition. Closer examination revealed that individual cell size of *Colpidium* increased substantially with productivity (fig. 5, linear regression: $R^2 = 0.43$, $P < .0001$). Therefore, it is likely that a productivity-mediated increase in *Colpidium* size rendered them invulnerable to *Euplotes* and led to the observed *Euplotes* decline at high productivity levels. The abrupt increase in *Colpidium* abundance at the upper end of the productivity gradient in microcosms with *Euplotes* is consistent with its reaching a size threshold that rendered it invulnerable to predation by *Euplotes* (fig. 4).

Responses of individual prey species also confirmed that *Stentor* had a broader impact than *Euplotes* on the prey assemblage. *Stentor* significantly reduced the abundance of 11 of 12 species at the end of the experiment, while *Euplotes* reduced the abundance of only five species (fig. 4). *Stentor* eliminated *Chilomonas*, *Loxocephalus*, *Colpidium*, *Colpoda*, *P. tetraurelia*, and one species of *Spirostomum* across the productivity gradient, while *Euplotes* only drove one species, *Loxocephaulus*, to extinction. *Euplotes* had a positive effect on *P. tetraurelia* (fig. 4), probably because of the competitive release of this species from those negatively affected by *Euplotes*.

We classified the diverse prey assemblage into either the edible or inedible group in the *Euplotes* treatments, based on our prior knowledge about its diet breadth, which is consistent with observed responses of individual species to *Euplotes* predation. Focusing on the final date of the experiment, *Euplotes* did not affect the total biovolume of the inedible group (fig. 6; two-way ANOVA, predation: $F = 0.22$, df $= 1, 40$, $P = .6445$), which responded positively to increasing productivity in both control and *Euplotes* treatments (fig. 6; two-way ANOVA, productivity: $F = 84.13$, df $= 9, 40$, $P < .0001$). For the edible group, we focus on responses from low to medium productivities (0.07–0.42 g protozoan pellets/L), where *Colpidium* individuals were completely vulnerable and *Euplotes* abundance increased with productivity. Within this productivity range, *Euplotes* significantly reduced total biovolume of the edible group (fig. 6; two-way ANOVA, predation: $F = 213.16$, df $= 1, 24$, $P < .0001$). The response of the edible group in the *Euplotes* treatment differed from that in the control (fig. 6; two-way ANOVA, predation × productivity: $F = 11.43$, df $= 5, 24$, $P < .0001$). When each predation treatment was examined separately, the edible group increased with productivity in the control (one-way ANOVA, productivity: $F = 64.36$, df $= 5, 12$, $P < .0001$) and was unaffected by productivity in the *Euplotes* treatment (one-way ANOVA, productivity: $F = 1.68$, df $= 5, 12$, $P = .2131$).

To examine whether species composition varied with productivity, we calculated prey compositional similarity among communities differing in productivity, using the Jaccard similarity index (Jaccard 1912). Jaccard similarity indexes calculate the proportion of species shared between two different communities, in this case between two different productivity levels. The analysis was conducted separately for each predation treatment. All replicates at each productivity level were pooled for the analysis. Prey compositional similarity declined as the difference in productivity increased in both control and *Euplotes* treatments but remained relatively constant in the *Stentor* treatment (fig. 7). The decline in prey compositional similarity is not caused by species turnover but is caused by a simple nested pattern where species present at the lower end of the productivity gradient were a subset of those present at the upper end (fig. 4).

Discussion

Our results clearly show that the relative importance of bottom-up and top-down regulation of prey assemblages depends critically on the identity and diet breadth of predators. Prey species richness and total prey biovolume both increased with productivity where a relatively specialized predator fed on a limited subset of prey. However, prey diversity and total prey biovolume showed little or no response to productivity where generalist predators consumed nearly the entire range of prey species. The striking
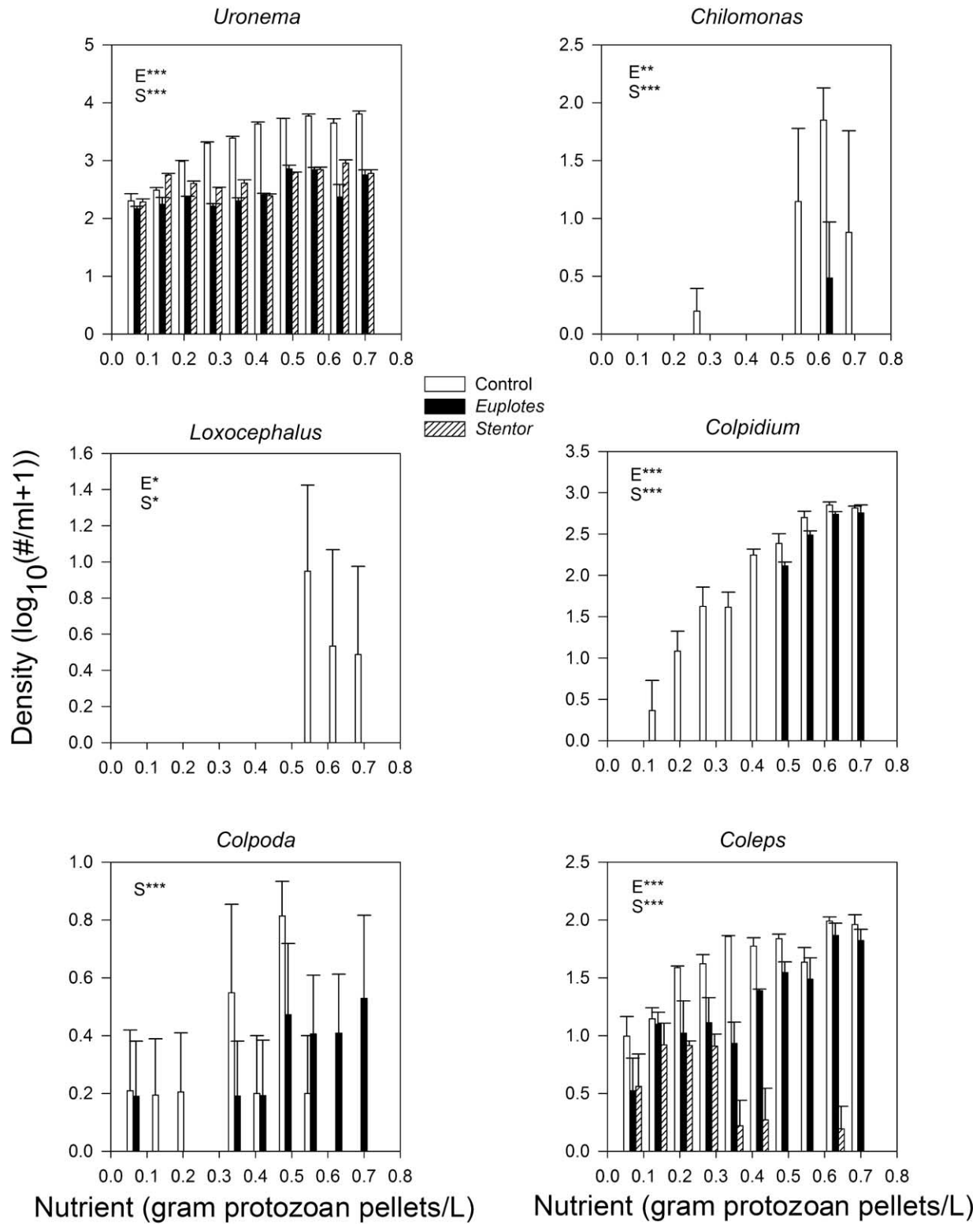
Figure 4: Effects of nutrient (productivity) and predation manipulations on the abundance of 12 prey species present on the final sampling date. Values are means of the density of each species ± 1 SE. Species are listed in the increasing order according to their body size, that is, *Uronema* < *Chilomonas* < *Loxocephalus* and so forth. The effects of predation from *Euplotes* (*E*) or *Stentor* (*S*), if significant, are indicated in each panel. One asterisk, $P < .05$; two asterisks, $P < .01$; three asterisks, $P < .001$.
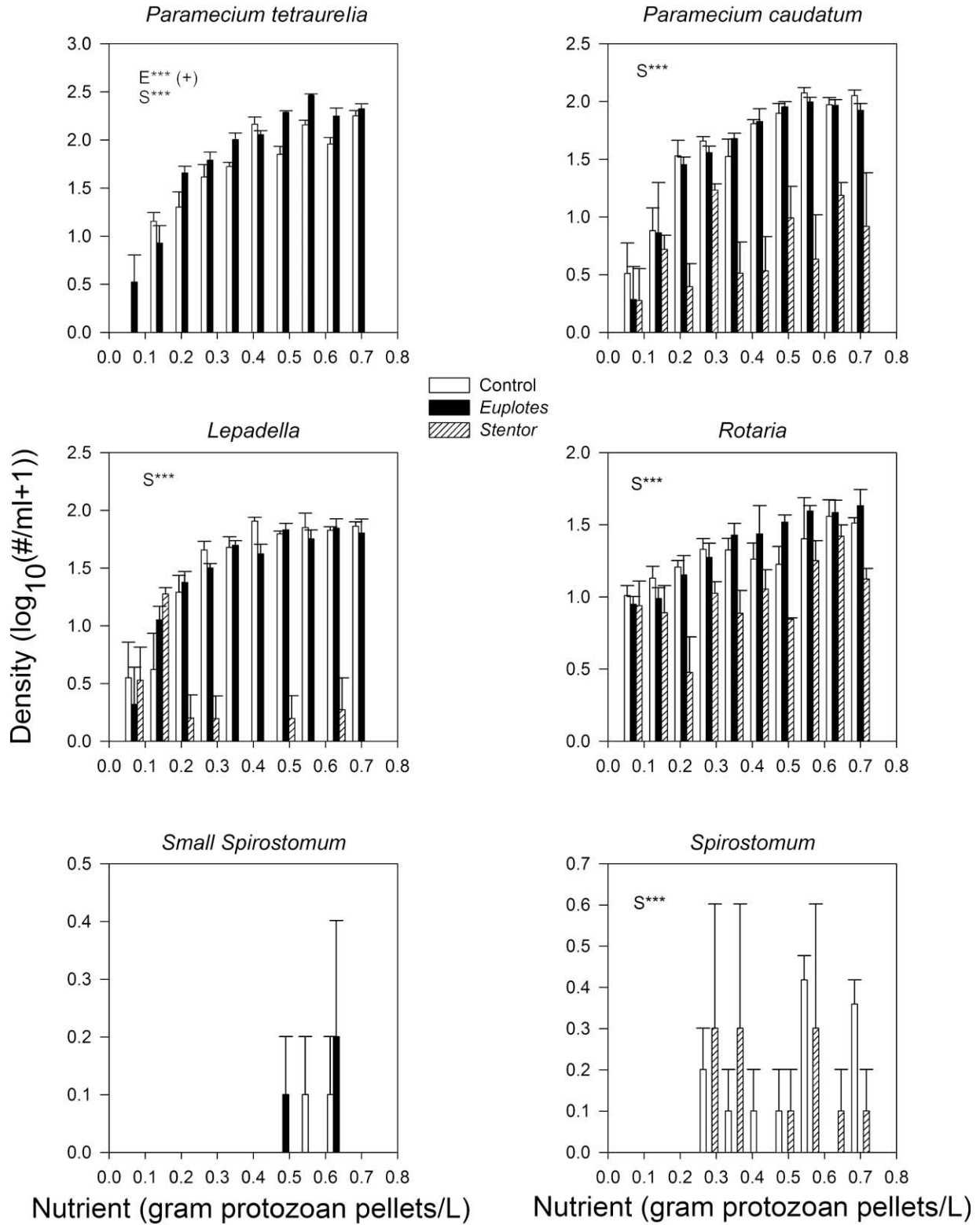
Figure 4: (*Continued*) Note that *Euplotes* had a significant positive effect on *Paramecium tetraurelia*, as indicated by E^{***} (+)
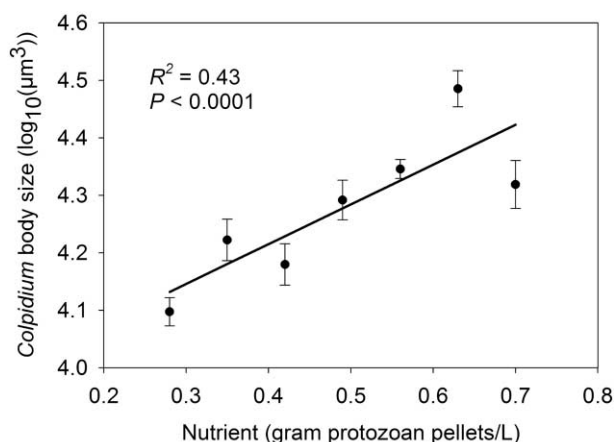
Figure 5: Effects of nutrient (productivity) manipulations on the cell size of *Colpidium*. Values are means ± 1 SE. The regression was performed based on individual replicates. Cell sizes were not measured for the three lowest nutrient levels because of the difficulty of finding enough individuals.

difference between the impacts of these two predators on prey diversity and biomass strongly supports the position of Hunter and Price (1992), who argue that species identity may be as important as productivity and the number of trophic levels in determining the impact of consumers on population and community dynamics.

High prey species richness is sometimes thought to dampen top-down effects of predators, making bottom-up effects of resource limitation especially prominent in species-rich communities (Strong 1992; Polis and Strong 1996). The rationale is that, among other things, heterogeneity in prey edibility may promote compensatory responses among species that buffer the effects of top-down forces. Both the edible-inedible prey model and the keystone predation model fit within this framework. Two experimental studies also provide support for the hypothesis (Bohannan and Lenski 1999; Steiner 2001). In both studies, increased productivity caused prey abundance to increase in heterogeneous food webs, while prey abundance remained essentially unchanged in homogenous food chains without invulnerable prey. Our relatively diverse food webs produced mixed results. Prey species richness apparently buffered the impact of the gape-limited specialist predator *Euplotes* because total prey biovolume increased with productivity. Strong top-down effects, however, still prevailed in the presence of the generalist predator *Stentor*, as shown by the insensitivity of total prey biovolume to productivity at the end of the experiment. The strong top-down effect of *Stentor* suggests that high prey diversity may not necessarily weaken top-down control in communities dominated by generalist predators.

Likewise, in freshwater pelagic communities, generalist herbivores like *Daphnia* are generally more effective than other more specialized zooplankton in controlling phytoplankton biomass (Leibold 1989; Carpenter and Kitchell 1993; Steiner 2001). Recent surveys also suggest that generalist predators may exert strong top-down effects in highly diverse communities (Pace et al. 1999; Halaj and Wise 2001).

A linear food chain model provides a reasonable description of how prey assemblages respond to increased productivity in the presence of generalist predators. Top predator abundance increased while total prey abundance remained unchanged as productivity increased, just as in simple linear food chains where a single edible species occupies the intermediate trophic level (Kaunzinger and Morin 1998). Despite the presence of considerable diversity in the intermediate trophic level of our study, these relatively complex food webs behaved like homogenous linear food chains. These results show that apparent taxonomic complexity may not necessarily preclude the existence of functional trophic levels and simple trophic dynamics (Hairston and Hairston 1993, 1997; Oksanen and Oksanen 2000).

Linear food chain models do not provide a good description of situations where the abundance of top predators and total prey both increase with productivity in the specialist predation treatment. Concordant increases in the abundance of predators and prey are consistent with both the edible-inedible prey model and the keystone predation model. However, an increase in species richness (figs. 1*C*, 2*A*) without substantial turnover in species composition (figs. 4, 7) along the productivity gradient is inconsistent with the keystone predation model, which predicts a unimodal change in species richness together with serial species replacements as productivity increases (Leibold 1996). The observed increase in predator and inedible prey abundance together with unchanged edible prey abundance as productivity increases (fig. 6) are consistent with edible-inedible prey models where prey species are able to coexist without predators (Leibold 1989; Kretzschmar et al. 1993), but they are inconsistent with models where predation is required for prey species coexistence (Phillips 1974; Abrams 1993; Grover 1995). The first group of models predicts correlated increases in the abundance of predators and inedible prey (Leibold 1989; Kretzschmar et al. 1993), while the second group predicts increased abundance of inedible prey but not predators as productivity increases (Phillips 1974; Abrams 1993; Grover 1995). In our experiment, prey coexistence in the absence of predation may be due to their differential use of the basal resource, which contained three bacteria species and nanoflagellates inoculated at the start of the experiment and an unknown number of additional bacteria entering the microcosms
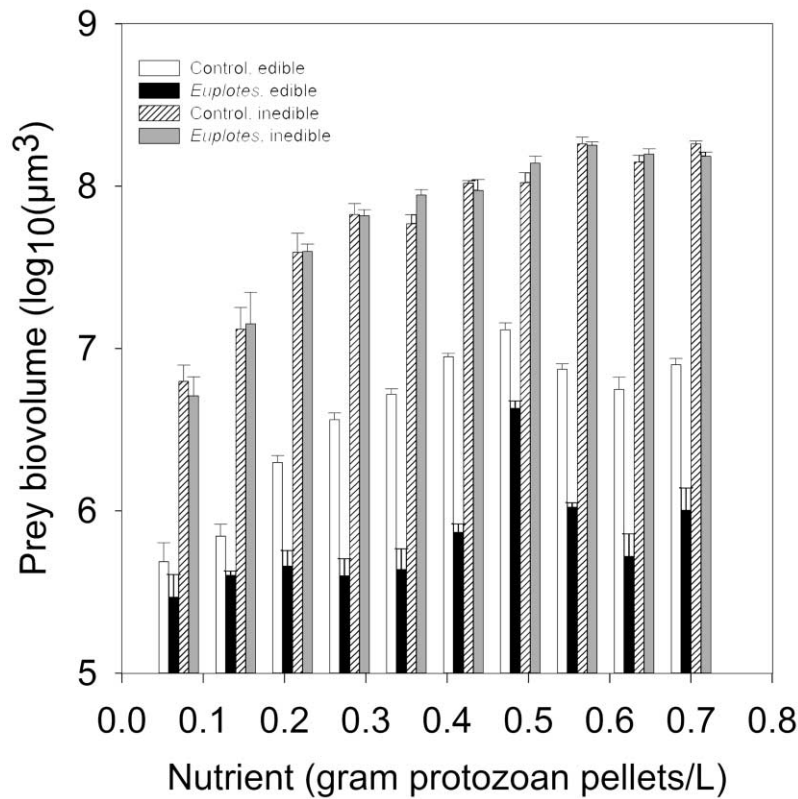
Figure 6: Effects of nutrient (productivity) and *Euplotes* predation on the abundance of edible and inedible prey species on the final sampling date. Values are means ± 1 SE

during the experimental period. We know that two prey, *Colpidium* and *Paramecium tetraurelia,* have limited overlap in resource use (Jiang and Morin 2004). Differential resource use is also suggested by the lack of compensatory responses when several prey species abundances were reduced by *Euplotes* predation; only *P. tetraurelia* increased its abundance in response (fig. 4). Overall, data from the *Euplotes* predation treatment are in good agreement with one of the edible-inedible prey models.

Using correlative evidence, several researchers have shown that patterns in freshwater pelagic communities and grasslands are consistent with the keystone predation model (Leibold et al. 1997; Leibold 1999; Chase et al. 2000). Our results do not support this model, probably because model assumptions were not met in our experiment. First, the keystone predation model assumes that prey species compete for a single limiting resource (Leibold 1996). This is often true for both phytoplankton in aquatic systems and plants in terrestrial environments. Our protists and rotifers competed for multiple resources, including multiple species of bacteria and nanoflagellates. This fundamental difference between detritus-based microbial

communities and producer-based communities may be one reason why patterns predicted by the keystone predation model failed to emerge. Second, the keystone predation model assumes a trade-off between prey competitive ability and resistance to predation. This trade-off probably does not exist when organisms compete for multiple resources. Clearly, the relevance of the keystone model to ecological communities should be experimentally tested in algal or plant-based systems where critical assumptions about competitive interactions are mostly likely to hold (see Steiner 2001 for a preliminary exploration).

The positive relationship between species richness and productivity seen in our predator-free controls can be explained by the "more individuals hypothesis" (Rosenzweig and Abramsky 1993; Abrams 1995; Srivastava and Lawton 1998; Gaston 2000), which posits that increasing productivity should support more individuals of each species, buffering species against local extinction. Our results show that most species increased in abundance as productivity increased, and several rare species were present only at high productivities (fig. 4). The positive trend of diversity along the productivity gradient has often been discounted
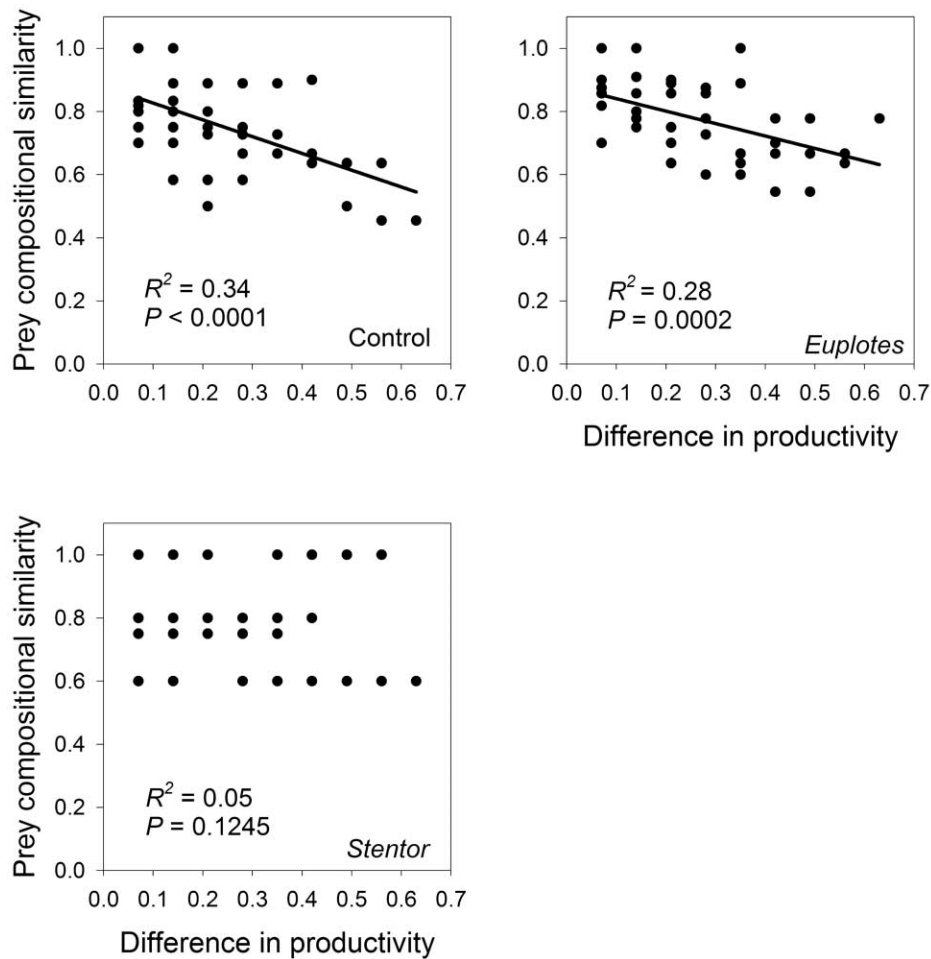
Figure 7: Prey compositional similarity (Jaccard similarity index) between communities with different productivity levels for the control, *Euplotes*, and *Stentor* treatments. The index was calculated with presence/absence data at each productivity level with all replicates pooled. Linear regression results: control, $y = 0.88 - 0.39x$, $R^2 = 0.34$, $P < .0001$; *Euplotes* predation treatment, $y = 0.88 - 0.53x$, $R^2 = 0.28$, $P = .0002$; *Stentor* predation treatment, $y = 0.85 - 0.22x$, $R^2 = 0.05$, $P = .1245$.

because it can simply represent the increasing portion of a unimodal curve, which has been suggested as the universal pattern at local scales (Rosenzweig and Abramsky 1993; Rosenzweig 1995). However, empirical evidence for positive diversity-productivity relationships has begun to emerge. For example, Kaspari et al. (2000) found that both ant densities and ant species richness increased from unproductive deserts to highly productive rain forests. The positive trend persisted across three orders of magnitude of productivity. In an experimental study, Stevens and Carson (2002) also found that plant species richness increased with light availability in light-limited plant communities. Note that the productivity-diversity relationship may also depend on the spatial scale examined, with some studies reporting that the positive relationship is observed at large regional scales (among habitats) and the hump-

shaped relationship at small local scales (among communities; Chase and Leibold 2002; Steiner and Leibold 2004). Our study examined diversity at local scales and found a positive relationship, and it is unclear whether a hump-shaped pattern might emerge if larger productivity gradients were used. This seems unlikely, given that species turnover, which often accompanies the hump-shaped productivity-diversity relationship (Leibold et al. 1997; Leibold 1999; Chase et al. 2000), did not occur in our experiment.

Both predation treatments reduced prey species richness. Previous studies have found that predation may either enhance or reduce prey diversity (reviewed by Sih et al. 1985; Olff and Ritchie 1998; Proulx and Mazumder 1998). The impacts of predation on prey species diversity can be affected by many factors such as prey preference

(Lubchenco 1978), the strength of interaction among prey species (Addicott 1974), nutrient status of the system (Proulx and Mazumder 1998; Worm et al. 2002), and whether the system is open or closed to species dispersal (Shurin 2001). For example, Addicott (1974) found that predation from the mosquito larvae *Wyeomyia smithii* reduced the richness of its protist and rotifer prey in pitcher plant inquiline communities. He suggested that the negative predation effect was probably caused by weak competition among prey species. This reasoning could probably account for the negative impact of predation on prey diversity found in our experiments. Prey species used different resources and only one prey species (*P. tetraurelia*) responded positively when the abundances of several prey species were reduced by *Euplotes* predation, suggesting relatively weak competition among prey species.

Nutrient status may also alter the impact of predators on prey diversity. Recent surveys have revealed a reversal of grazing impact on plant species richness under contrasting nutrient conditions; grazing generally reduces plant species richness in nutrient-poor environments and enhances richness in nutrient-rich environments (Proulx and Mazumder 1998; Worm et al. 2002). In this study, little interactive effect of productivity and predation on prey diversity was found in the *Euplotes* treatment (tables A1A, A1B), and the negative effect of predation on prey diversity was actually more pronounced at higher productivities in the *Stentor* treatment (fig. 2A). It is probably that the fundamental difference between our multi-resource detritus-based communities and single-limiting-resource plant-based communities may again account for the disparity. Clearly, more studies are needed to explore the generality of the grazing reversal phenomenon across different ecosystem types and to elucidate its causal mechanisms.

We focused on the effects of predation on diversity and did not manipulate dispersal. For any local natural community embedded in its regional metacommunity, species diversity is influenced both by local species interactions and by dispersal between local communities (MacArthur and Wilson 1967; Leibold et al. 2004). Species dispersal may interact with predation to determine diversity in these communities. For example, Shurin (2001) found that fish predation reduced prey zooplankton diversity in the absence of prey dispersal and increased diversity in the presence of dispersal because zooplankton immigration from the regional species pool more than compensated for the predator-induced species loss in the dispersal treatment. Although our experiments focused on local factors within communities, we recognize the potential importance of regional factors in regulating species diversity and community structure and encourage future studies to consider them simultaneously.

One point of concern is that predator diet breadth effects were evaluated by examining only two predator species; thus the possibility of confounding predator identity with predator diet breadth cannot be ruled out. An ideal solution to this problem would be to use as many predatory species with differential diet breadths as possible, but this may not be logistically possible in many systems. Nevertheless, our experiment demonstrated the drastically different impacts of generalist and specialist predators on how the prey assemblage responded to productivity. Obviously, more studies should be conducted to compare and contrast the effects of predators with different diet spectra. Another caveat is that our experimental communities were not constructed with any specific natural communities in mind, and the experimental organisms do not come from a single source. Despite this caveat, we believe that our general findings may be extrapolated to natural systems for the following two reasons. First, in general, predator diet breadth is strongly correlated with body size, with larger predators feeding on a wider range of prey than smaller ones (Cohen et al. 1993). In our experiment, the generalist predator *Stentor* was much larger than the specialist predator *Euplotes*. We suggest that systems dominated by large generalist predators or small specialist predators may show responses to productivity similar to those seen in our experiment. Second, many of our experimental organisms come from a single pond, and *Euplotes* and the same *Stentor* species (*Stentor coeruleus*) are two common predatory ciliates in this pond (L. Jiang, personal observation). Our findings may therefore be applicable to this particular pond community. There is also some evidence that many microbial species are not limited by dispersal and tend to have a cosmopolitan distribution (Finlay 2002), suggesting that communities similar in composition to our experimental communities almost certainly exist elsewhere in nature.

Conclusions

Recent theoretical and empirical studies of how food webs respond to nutrient enrichment have emphasized the importance of differences in edibility within the prey assemblage (e.g., Leibold 1989, 1996; Grover 1995; Hansson et al. 1998; Bohannan and Lenski 1999, 2000). Prey edibility, however, depends on both prey and predator properties. We show that changes in predator identity and diet breadth can result in qualitatively different responses of both prey diversity and total prey biomass to increasing productivity. This highlights the importance of trait heterogeneity within the predator trophic levels, further strengthening the notion that food web heterogeneity may affect the relative importance of bottom-up and top-down control of community dynamics (Hunter and Price 1992; Power

1992; Polis and Strong 1996; Persson 1999). We expect that natural communities dominated by generalist predators and specialist predators would exhibit different responses to nutrient enrichment. Future studies on food webs must consider heterogeneity in the traits of both predators and prey to gain a more complete understanding of mechanisms structuring communities and to make better predictions about how communities will respond to anthropogenic perturbations that alter productivity and top predators.

Acknowledgments

Literature Cited

Abrams, P. A. 1993. Effects of increased productivity on the abundances of trophic levels. American Naturalist 141:351–371.

———. 1995. Monotonic or unimodal diversity-productivity gradients: what does competition theory predict? Ecology 76:2019–2027.

Addicott, J. F. 1974. Predation and prey community structure: an experimental study of the effect of mosquito larvae on the protozoan communities of pitcher plants. Ecology 55:475–492.

Bohannan, B. J. M., and R. E. Lenski. 1999. Effect of prey heterogeneity on the response of a model food chain to resource enrichment. American Naturalist 153:73–82.

———. 2000. The relative importance of competition and predation varies with productivity in a model community. American Naturalist 156:329–340.

Carpenter, S. R., and J. F. Kitchell. 1993. The trophic cascade in lakes. Cambridge University Press, Cambridge.

Chase, J. M., and M. A. Leibold. 2002. Spatial scale dictates productivity-biodiversity relationship. Nature 416:427–230.

Chase, J. M., M. A. Leibold, A. L. Downing, and J. B. Shurin. 2000. The effects of productivity, herbivory, and plant species turnover in grassland food webs. Ecology 81:2485–2497.

Cohen, J. E., S. L. Pimm, P. Yodzis, and J. Saldana. 1993. Body sizes of animal predators and animal prey in food webs. Journal of Animal Ecology 62:67–78.

Elton, C. S. 1927. Animal ecology. Sidgwick & Jackson, London.

Finlay, B. J. 2002. Global dispersal of free-living microbial eukaryote species. Science 296:1061–1063.

Fretwell, S. D. 1977. The regulation of plant communities by food chains exploiting them. Perspectives in Biology and Medicine 20:169–185.

Gaston, K. J. 2000. Global patterns in biodiversity. Nature 405:220–227.

Genkai-Kato, M., and N. Yamamura. 2000. Profitability of prey determines the response of population abundances to enrichment. Proceedings of the Royal Society of London B 267:2397–2401.

Grover, J. P. 1995. Competition, herbivory, and enrichment: nutrient-based models for edible and inedible plants. American Naturalist 145:746–774.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control and competition. American Naturalist 94:421–425.

Hairston, N. G., Jr., and N. G. Hairston Sr. 1993. Cause-effect relationships in energy flow, trophic structure, and interspecific interactions. American Naturalist 142:379–411.

———. 1997. Does food web complexity eliminate trophic-level dynamics. American Naturalist 149:1001–1007.

Halaj, J., and D. H. Wise. 2001. Terrestrial trophic cascades: how much do they trickle? American Naturalist 157:262–281.

Hansson, L. A., C. Bronmark, P. Nystrom, L. Greenberg, P. Lundberg, P. A. Nilsson, A. Persson, et al. 1998. Consumption patterns, complexity and enrichment in aquatic food chains. Proceedings of the Royal Society of London B 265:901–906.

Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology 73:724–732.

Jaccard, P. 1912. The distribution of flora in the alpine zone. New Phytologist 11:37–50.

Jiang, L., and P. J. Morin. 2004. Temperature-dependent interaction strength explains unexpected responses to environmental warming in competitive communities. Journal of Animal Ecology 73:569–576.

Kaspari, M., S. O'Donnell, and J. R. Kercher. 2000. Energy, density, and constraints to species richness: ant assemblages along a productivity gradient. American Naturalist 155:280–293.

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

Kretzschmar, M., R. M. Nisbet, and E. McCauley. 1993. A predator-prey model for zooplankton grazing on competing algal populations. Theoretical Population Biology 44:32–66.

Leibold, M. A. 1989. Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. American Naturalist 134:922–949.

———. 1996. A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence, and diversity patterns in communities. American Naturalist 147:784–812.

———. 1999. Biodiversity and nutrient enrichment in pond plankton communities. Evolutionary Ecology Research 1:73–95.

Leibold, M. A., and H. M. Wilbur. 1992. Interactions between food-web structure and nutrients on pond organisms. Nature 360:341–343.

Leibold, M. A., J. M. Chase, J. B. Shurin, and A. L. Downing. 1997. Species turnover and the regulation of trophic structure. Annual Review of Ecology and Systematics 28:467–494.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7:601–613.

Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. Ecology 23:399–418.

Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preferences and algal competitive abilities. American Naturalist 112:23–39.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, NJ.

Menge, B., and J. P. Sutherland. 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. American Naturalist 110:351–369.

Mittelbach, G. G., C. F. Steiner, S. M. Scheiner, K. L. Gross, H. L. Reynolds, R. B. Waide, M. R. Willig, et al. 2001. What is the observed relationship between species richness and productivity? Ecology 82:2381–2396.

Odum, E. P. 1971. Fundamentals of ecology. Saunders, Philadelphia.

Oksanen, L., and T. Oksanen. 2000. The logic and realism of the hypothesis of exploitation ecosystems. American Naturalist 155:703–723.

Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemela. 1981. Exploitation ecosystems in gradients of primary productivity. American Naturalist 118:240–261.

Olff, H., and M. E. Ritchie. 1998. Effects of herbivores on grassland plant diversity. Trends in Ecology & Evolution 13:261–265.

Osenberg, C. W., and G. G. Mittelbach. 1996. The relative importance of resource limitation and predator limitation in food chains. Pages 134–148 *in* G. A. Polis and K. O. Winemiller, eds. Food webs: integration of patterns and dynamics. Chapman & Hall, London.

Pace, M. L., J. J. Cole, S. R. Carpenter, and J. F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. Trends in Ecology & Evolution 14:483–488.

Persson, L. 1999. Trophic cascades: abiding heterogeneity and the trophic level concept at the end of the road. Oikos 85:385–397.

Phillips, O. M. 1974. The equilibrium and stability of simple marine biological systems. II. Herbivores. Archiv für Hydrobiologie 73:310–333.

Polis, G. A. 1999. Why are parts of the world green? multiple factors control productivity and the distribution of biomass. Oikos 86:3–15.

Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. American Naturalist 147:813–846.

Power, M. E. 1992. Top-down and bottom-up forces in food webs: do plants have primacy? Ecology 73:733–746.

Proulx, M., and A. Mazumder. 1998. Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. Ecology 79:2581–2592.

Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press, Cambridge.

Rosenzweig, M. L., and Z. Abramsky. 1993. How are diversity and productivity related? Pages 52–65 *in* R. E. Ricklefs and D. Schluter, eds. Species diversity in ecological comminutes: historical and geographical perspectives. University of Chicago Press, Chicago.

Shurin, J. B. 2001. Interactive effects of predation and dispersal on zooplankton communities. Ecology 82:3404–3416.

Sih, A., P. Crowley, M. McPeek, J. Petranka, and K. Strohmeier. 1985. Predation, competition, and prey communities: a review of field experiments. Annual Review of Ecology and Systematics 16:269–311.

Slobodkin, L. B., F. E. Smith, and N. B. Hairston. 1967. Regulation in terrestrial ecosystems, and the implied balance of nature. American Naturalist 101:109–124.

Srivastava, D. S., and J. H. Lawton. 1998. Why more productive sites have more species: an experimental test of theory using tree-hole communities. American Naturalist 152:510–529.

Steiner, C. F. 2001. Effects of prey heterogeneity and consumer identity on the limitation of trophic-level biomass. Ecology 82:2495–2506.

Steiner, C. F., and M. A. Leibold. 2004. Cyclic assembly trajectories and scale-dependent productivity-diversity relationships. Ecology 85:107–113.

Stevens, M. H. H., and W. P. Carson. 2002. Resource quantity, not resource heterogeneity, maintains plant diversity. Ecological Letters 5:420–426.

Strong, D. R. 1992. Are trophic cascades all wet? differentiation and donor-control in speciose ecosystems. Ecology 73:747–754.

Waide, R. B., M. R. Willig, C. F. Steiner, G. Mittelbach, L. Gough, S. I. Dodson, G. P. Juday, et al. 1999. The relationship between productivity and species richness. Annual Review of Ecology and Systematics 30:257–300.

Wetzel, R. G., and G. E. Likens. 1991. Limnological analyses. Springer, New York.

White, T. C. R. 1978. The importance of relative shortage of food in animal ecology. Oecologia (Berlin) 33:71–86.

Wootton, J. T., and M. E. Power. 1993. Productivity, consumers, and the structure of a river food chain. Proceedings of the National Academy of Sciences of the USA 90:1384–1387.

Worm, B., H. K. Lotze, H. Hillebrand, and U. Sommer. 2002. Consumer versus resource control of species diversity and ecosystem functioning. Nature 417:848–851.