

RESOURCE AND TOP-PREDATOR REGULATION IN THE PITCHER PLANT (*SARRACENIA PURPUREA*) INQUILINE COMMUNITY

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Abstract. The effects of top-down and bottom-up forces on species abundance and diversity were quantified in the inquiline communities found in the water-filled leaves of the pitcher plant, *Sarracenia purpurea*. A press field experiment was conducted in which the abundances of resources (dead ants) and the top predators (larva of the mosquito *Wyeomyia smithii*) were each maintained at three levels in a factorial design for 23 d. Abundances of mites, rotifers, protozoans, and bacteria increased significantly with prey addition. Protozoan species richness also increased with increasing resource levels, whereas additional resources did not affect bacterial species richness. Increases in top-predator density decreased rotifer abundance but increased bacterial abundance and species richness. Increases in bacterial abundance and richness indicate that a trophic cascade occurs via the larvae, rotifer, and bacteria pathway; omnivory appears to be not strong enough to affect the trophic cascade. Top-down and bottom-up forces both had strong, but different, effects on the abundance and richness of intermediate trophic levels. For most components of the inquiline community, species richness and population sizes are resource limited, whereas predator limitation targets a limited set of groups.

Key words: bacteria; bottom-up effects; omnivory; protozoans; rotifers; *Sarracenia purpurea*; species diversity; top-down effects; trophic cascade; *Wyeomyia smithii*.

INTRODUCTION

Ecologists have frequently tried to determine the degree to which populations are regulated by bottom-up (resource) and top-down (predation) forces (Elton 1927, Lindeman 1942, Hairston et al. 1960, Paine 1966, Power 1992, Persson et al. 1996). Recently, both theory (Oksanen et al. 1981, Leibold 1996) and experimental work (e.g., McQueen et al. 1989, Wootton and Power 1993, Balciunas and Lawler 1995, Bohannan and Lenski 1999, 2000, Diehl and Feiel 2000) have sought to integrate these two forms of regulation, and the current consensus is that most populations are regulated by some mixture of the two (Power 1992, Osenberg and Mittlebach 1996). The central questions are therefore under what conditions will either of these factors dominate in a system (Hunter and Price 1992) and when must the actions of both be considered. Furthermore, since resources and predation may vary, spatial and temporal heterogeneity must be incorporated into our understanding of community structure (Hunter and Price 1992).

Early models of resource and predator regulation of populations predicted that increased productivity is expected to increase biomass or abundance at all trophic levels (Elton 1927, Lindeman 1942). In general, empirical studies indicate that biomass of higher trophic levels increases with productivity (Begon et al. 1990). In contrast, top-down regulation models predict that

predators will directly suppress prey populations, which may then have a positive indirect effect on the trophic level below the prey (Hairston et al. 1960, Carpenter et al. 1985). This pattern can vary, however, depending on food-chain length, productivity levels, habitat type, and community composition (Oksanen et al. 1981, Strong 1992, Wootton and Power 1993, Polis and Strong 1996, Leibold et al. 1997).

The relative roles of bottom-up and top-down processes can be obscured by various factors. Omnivory can diffuse the effects of both resource and predator regulation in communities (Diehl 1993, Polis and Strong 1996), and models that address the coexistence of species that interact both as competitors and as predator and prey predict that predator and prey should differ in resource use efficiency (Holt and Polis 1997, Diehl and Feiel 2000). Differences among species within a trophic level can also complicate the patterns of abundance observed in communities (Leibold 1989, Hunter and Price 1992, Bohannan and Lenski 1999). Species within a trophic level that are more resistant to predators may compensate for decreased abundance of less resistant species by increasing in abundance. It is unclear how trophic cascades might be affected; compensation may prevent a trophic cascade (Strong 1992).

Species diversity is another measure of bottom-up and top-down regulation in communities (Paine 1966, Menge and Sutherland 1976, Tilman 1982, Rosenzweig and Abramsky 1993, Leibold 1996). The relationship between productivity and diversity shows different patterns (none, increasing, decreasing, unimodal) in the-

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PLATE 1. (Left) The field site at the Sumatra Savannah in the Appalachian National Forest. (Right) A leaf of *Sarracenia purpurea* which contains the inquiline community. Photographs by Jamie Kneitel.

oretical and empirical work, and numerous mechanisms have been used to explain these patterns (e.g., Rosenzweig and Abramsky 1993, Waide et al. 1999). Similarly, the relationship between predation and diversity may produce different patterns. For example, keystone predation is predicted to produce a unimodal relationship between predation and diversity (Paine 1966). These predictions arise from theoretical and empirical work that addresses the diversity of one trophic level in response to a single force (productivity or predation). Other models, though, have incorporated greater complexity. Menge and Sutherland (1976) addressed systems with omnivory and predicted that predation would be more important in maintaining diversity in lower trophic levels, whereas competition would be more important in higher trophic levels. Leibold (1996) incorporated both bottom-up and top-down effects on population abundance and diversity into a three-trophic-level system. This model incorporated different densities of productivity and competitors with species character differences in resource utilization and predator resistance. The net result was that diversity had a unimodal relationship with both productivity and predator density. However, most models address diversity at a single trophic level; there have been no predictions of the expected diversity in multiple trophic levels, nor were the consequences of trophic cascades on diversity addressed.

The inquiline community that occurs inside the leaves of the pitcher plant *Sarracenia purpurea* (see Plate 1) has been used for several studies (Addicott 1974, Fish and Hall 1978, Bradshaw and Creelman 1984, Heard 1994, Cochran-Stafira and von Ende 1998). These natural microcosms are easy to work with because they are discrete communities that are easily manipulated, and the organisms present have short generation times (Addicott 1974). The supply of energy in this system consists of allochthonous material in the

form of insects and other invertebrates that fall into the water-filled leaves and drown. Bacteria and mites make up the bottom, detritivorous trophic level (Fig. 1). The second trophic level is composed of rotifers (most commonly, *Habrotrocha rosa*) and protozoans, which filter feed or graze on the bacteria. Rotifers also feed on smaller protozoans, but this probably occurs less frequently (J. M. Kneitel, *personal observation*). The omnivorous top predator, the pitcher-plant mosquito *Wyeomyia smithii* (Coq.), grazes on surfaces and filter feeds on protozoans, rotifers, and bacteria (Heard 1994; Fig. 1). Other species, including larvae of other dipterans, copepods, and cladocerans, are also occasionally found in these communities (Heard 1994, Harvey and Miller 1996).

Two previous pitcher-plant studies focused on top-down effects of mosquito larvae on protozoan and bacterial species richness and reached somewhat different conclusions. Addicott (1974) found that increasing mosquito-larvae densities produced a monotonically decreasing level of protozoan species richness. In contrast, Cochran-Stafira and von Ende (1998), in a laboratory study of pitcher-plant communities, found that

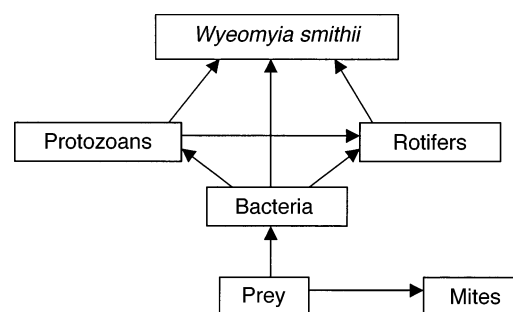


FIG. 1. Simplified food-web organization in *Sarracenia purpurea* pitchers. Directions of arrows refer to direction of consumption.

W. smithii predation facilitated the coexistence of protozoan and bacterial competitors, thereby increasing species diversity. A number of factors could have contributed to the observed differences: differences in experimental setting, length of experiment, natural protozoan species richness, resource levels, and predator densities (Cochran-Stafira and von Ende 1998). It, therefore, remains unclear how predation levels may interact with other factors, such as productivity, in affecting the composition of this community.

The effects of resource addition in this system have not been studied. In addition, variation among pitcher communities in resource (prey) and predator levels is high (Harvey and Miller 1996; J. M. Kneitel, *personal observation*). Resource and predator heterogeneity has been found to have strong community-wide effects in other pitcher plants and phytotelmata (Kitching 1987, Naeem 1988, 1990). Therefore, understanding the consequences of this heterogeneity on community composition is an important step in developing a sharper image of trophic dynamics in communities. We used a press experiment (Bender et al. 1984) that was long enough relative to the generation times of all of the organisms involved to evaluate consistent effects of top-down and bottom-up forces on the rest of the community (mite, rotifer, protozoan, and bacterial abundance and protozoan and bacterial species richness).

METHODS

Field sites

Sarracenia purpurea (also called *S. rosea*, Naczi et al. 1999), the purple pitcher plant, occurs in bogs and wetlands from Florida to Canada. This study was conducted in a population of *Sarracenia purpurea* at the Sumatra Savannah in the Apalachicola National Forest along Road 118, 3 km N of Sumatra, Florida (see Plate 1). The site is a bog that has been burned every other year for the last 10 yr and receives ~165 cm of rainfall annually. The vegetation is dominated by *Aristida stricta*, as well as other common bog species (*Xyris fibriata*, *Eriocaulon compressum*, and *Rhexia virginica*), and includes several other carnivorous plants (*Sarracenia flava*, *S. pinnatifida*, and *Drosera capillaris*).

Experimental design

The 3×3 factorial design included three levels of resource input (none, low [5 ants], and high [25 ants]) and three levels of predator (*Wyeomyia smithii* larvae of similar size) addition (none, low [2 larvae], and high [10 larvae]). Low levels were approximately half the mean and high levels approximately twice the mean of natural prey (mean = 8.9, 1 SD = 13.6, $N = 15$) and predator levels (mean = 4.1, 1 SD = 5.2, $N = 15$) in pitchers (J. M. Kneitel, *unpublished data*). Therefore, the treatments represented almost the full range of natural resource and predator densities.

One replicate of each of the nine treatments was

randomly applied within each of five haphazardly located blocks. Dead, autoclaved fire ants (*Solenopsis invicta*) were used as prey because they are the most common insect prey found in local pitchers (Miller et al. 1994; J. M. Kneitel, *personal observation*). To initiate the communities, fluid was collected from ~90 pitcher-plant leaves, pooled in a common vat, and filtered to remove all mosquito larvae and prey items. Protozoan species typically found in the inquiline community, *Bodo*, *Colpidium*, and *Colpoda*, were among the species also present in this experiment. Then, 15-mL aliquots of this mixture were drawn out, placed in separate vials, and randomly assigned to treatments. The water-holding capacity of *Sarracenia* leaves was quite variable (up to 50 mL) depending on leaf size and precipitation. After the appropriate numbers of larvae and ants were added, the treatment aliquots were poured into the 45 leaves in the field. The treatment leaves were approximately equal size and had been washed out with sterile water just prior to use. Mesh cloth (1 mm) was placed over the mouths of the treated pitchers to prevent further prey entry or colonization by mosquito larvae. Protozoan and rotifer colonization into experimental pitchers could have occurred during the course of the experiment; however, it was not possible to determine whether increases in protozoan and rotifer population densities resulted from immigration or reproduction.

Sampling

Pitchers were sampled every 2–3 d for 23 d for a total of 10 census dates. This sampling frequency and length was sufficient to capture any significant population growth of the organisms measured. For field censuses, each community was gently mixed, then emptied into a sterile petri dish. A dissecting microscope was used in the field to count mites and determine whether prey and predators were at their proper treatment levels. Treatment levels were adjusted as necessary. The mesh cloth prevented mosquitoes from ovipositing in pitchers, but mortality and pupation sometimes changed predator numbers. In these cases, larvae (taken from the original mixture which was stored in our laboratory at room temperature) were added, and it was later tested whether treatments had any effect on loss of larvae. Generally, mesh was also effective in maintaining prey treatment levels. In several cases, fire ants entered pitchers despite the mesh and had to be removed. These pitchers did not exhibit any increase or drastic change in their bacterial community following these accidental invasions. More prey was added to maintain original treatments when the original prey items had sufficiently decomposed that exoskeleton segments detached from each other. After examination, each community was replaced and remixed before a 0.25-mL aliquot was taken for laboratory analysis.

For bacterial abundance and richness measurements, a subsample (0.05 mL) was first serially diluted with

TABLE 1. Treatment means (with 1 SE in parentheses) for percentage larva loss, pH, and dissolved oxygen (DO) in pitcher plant inquiline communities.

Dependent variable	Predator level	Resource level		
		None	Low	High
Larva loss (%)	low	26 (5.62)	30.2 (4.21)	28.9 (5.15)
	high	32.2 (4.36)	33.3 (5.73)	31.1 (4.68)
pH	none	5.90 (0.31)	6.70 (0.33)	6.37 (0.17)
	low	5.63 (0.48)	5.95 (0.42)	6.70 (0.20)
	high	6.61 (0.08)	6.19 (0.23)	6.76 (0.27)
DO (mg/L) [†]	none	5.10 (0.15)	3.35 (0.80)	4.17 (0.23)
	low	4.37 (0.13)	4.81 (0.21)	3.20 (0.51)
	high	4.53 (0.23)	2.73 (0.80)	3.03 (0.67)

[†] Significant resource effect, $F_{2,22} = 4.01$, $P = 0.03$.

sterile saline buffer and 0.1 mL of a 10^{-5} dilution was then spread on Luria-broth agar plates (Cochran-Stafira and von Ende 1998). These plates were incubated in a growth chamber at 26°C for 48 h, and abundance and colony types (richness) were recorded. Colony types were distinguished using color, texture, and growth form. There may have been some error in distinguishing among the different types, but this method was used because many bacterial species are undescribed and their identities were not required for the purposes of this study. Protozoans (abundance and species richness) and rotifers (abundance) were sampled with a hemacytometer under a compound microscope (at 100×). Rotifers primarily consisted of *Habrotrocha rosa* and protozoans were identified to genus (Patterson 1996). Rotifer, protozoan, and bacterial abundances were log transformed to normalize data. Upon final completion of sampling at day 23, fluid in each leaf was measured for pH and dissolved oxygen (mg/L).

Resource addition increased abundances of many species, and treatments with more individuals may have artificially shown greater species richness (Gotelli and Graves 1996). Therefore, to compare treatments directly while controlling for abundance differences, rarefaction was conducted to estimate species richness of protozoa and bacteria (EcoSim, version 6, Acquired Intelligence and Kesey-Bear, Burlington, Vermont, USA; Gotelli and Entsminger 2001). For strict comparisons, the minimum number of individuals sampled must exceed $S + 1$, where S is the number of species in the most species-rich sample (Tipper 1979). This criteria was met, but some replicates contained fewer individuals. In these cases, the total species richness was used, which was generally 0 to 2 species. Each replicate was sampled 100 times and the mean number of species was used as our estimate. Rarefaction curves were generated for each replicate on each time period and the final point in each curve was used as the dependent variable in our analyses.

Statistical analyses

Analysis of variance with repeated measures (ANCOVAR) was used for all dependent variables to test for

treatment effects over a discrete time period (Joyner 1985, Potvin et al. 1990, SAS Institute 1990). In all tests, compound symmetry (homogeneity of the variance-covariance matrix) was rejected (Mauchly's test, $P < 0.001$), so a Huynh-Feldt test was used to determine whether the symmetry assumption could be relaxed (Potvin et al. 1990). This violation was mild (mite abundance, $e = 0.86$; rotifer abundance, $e = 1.11$; protozoan abundance, $e = 0.80$; protozoan richness, $e = 1.17$; bacterial richness, $e = 0.88$) except for bacterial abundance ($e = 0.68$), where caution should be used in interpreting results.

Two-way ANOVA (SAS Institute 1996) was used to test treatment effects on mosquito larvae loss, pitcher pH, and pitcher dissolved oxygen after assumptions of normality were tested.

RESULTS

Two pitcher-plant leaves (one each from no predator/low prey and high predator/no prey treatments) were damaged near the end of the experiment and were deleted from subsequent analyses. The mean pitcher volume at the end of the experiment was 7.67 mL (1 SD = 4.10), and this variation did not differ among treatments (ANOVA, $df = 34$, $F = 1.01$, $P = 0.444$). Treatment levels had no effect on number of larvae lost (to mortality or pupation; range 26.0–33.3%) or on pH (range 5.63–6.76) in the pitchers, but dissolved oxygen decreased significantly with prey addition (Table 1).

Resource effects

Prey addition caused significant increases in all abundance and diversity variables, except for mosquito larval loss and bacterial species richness (Table 2). Mites increased in abundance with prey addition at all predator levels (Fig. 2a). Rotifer abundance (primarily *Habrotrocha rosa*) also increased with prey addition when predators were absent or at low predator levels (Fig. 2b), but at high predator levels, they were most abundant in the low-prey-density treatment. Protozoan abundance increased with increasing prey levels across all predator levels (Fig. 2c). Few patterns were observed with individual protozoan species, except *Col-*

TABLE 2. Statistical summary of ANOVA results for the between-subject effects of predator, resource, and predator \times resource interaction for each of the dependent variables.

Dependent variable	Source	df	F	P
Mite abundance	Predator	2	1.58	0.220
	Resource	2	4.74	0.015*
	Predator \times Resource	4	0.28	0.890
	Error	34		
Rotifer abundance	Predator	2	33.65	<0.001***
	Resource	2	8.83	<0.001***
	Predator \times Resource	4	1.22	0.319
	Error	34		
Protozoan abundance	Predator	2	0.40	0.673
	Resource	2	10.02	<0.001***
	Predator \times Resource	4	0.57	0.684
	Error	34		
Bacterial abundance	Predator	2	3.09	0.059
	Resource	2	3.45	0.043*
	Predator \times Resource	4	0.88	0.485
	Error	34		
Protozoan species richness	Predator	2	1.36	0.269
	Resource	2	17.28	<0.001***
	Predator \times Resource	4	2.78	0.042*
	Error	34		
Bacterial species richness	Predator	2	4.24	0.023*
	Resource	2	1.40	0.260
	Predator \times Resource	4	0.82	0.521
	Error	34		

* $P < 0.05$; *** $P < 0.001$.

pidium was found to increase with resource addition (ANOVAR: $df = 36$, $F = 6.12$, $P = 0.005$). Bacteria showed the smallest percentage increase in response to prey addition (10%, Fig. 2d, compared to rotifers 66% and protozoans 59%), which is somewhat surprising as the response of rotifers and protozoans must depend on bacteria.

Resource effects on protozoan species richness were similar to the strong pattern observed in protozoan abundance: prey addition doubled protozoan species richness (Table 2, Fig. 3a). In contrast, bacterial species richness was not significantly affected by increased resource levels (Table 2, Fig. 3b).

Predator effects

Predator addition had no significant effect on mite and protozoan abundances (Table 2, Fig. 2a, c). However, one protozoan species, *Bodo*, had low abundance at no and high predation levels and almost a two-fold increase at low predation levels (ANOVAR: $F_{2,34} = 3.39$, $P = 0.045$). Increases in predator density significantly decreased rotifer abundance, by 60% (Table 2, Fig. 2b). There was an 18% increase in bacterial abundance with increased predator densities, which was nearly significant ($P = 0.059$; Table 2, Fig. 2d).

Predator addition had no effect on protozoan species richness (Table 2, Fig. 3a). A predator by resource interaction was detected with protozoan species richness (Table 2). At low resource levels, richness decreased with increasing predator levels, but at low and high resource levels, the response was variable (Fig. 3b).

Increasing predator density significantly increased bacterial species richness by 15% (Table 2).

DISCUSSION

The effects of both predators (top-down) and resources (bottom-up) were detected in the inquiline community of *Sarracenia purpurea*. The abundances of mites, rotifers, protozoans, and bacteria all increased in response to prey addition (Table 2), suggesting that all were resource limited to some degree. Only two variables (rotifer abundance and bacterial species richness) changed significantly in response to increased predator levels, although bacterial abundance was marginally affected by predation (Table 2). Rotifer abundance was strongly negatively affected by increases in predator density, but bacterial abundance and richness increased with increasing predator addition (Figs. 2, 3b).

Increased resource levels were also related to changes in abiotic factors in the community, for example with decreased levels of dissolved oxygen (Table 1). This is the expected relationship between oxygen levels and prey: an increase in the resource base increases organismal abundance, which means increased oxygen consumption for respiration. The pH levels found in this experiment were consistent with previous studies (Fish and Hall 1978).

The results of this experiment support bottom-up theoretical predictions about community regulation, in which abundance at each trophic level is a function of resource availability (Elton 1927, Lindeman 1947).

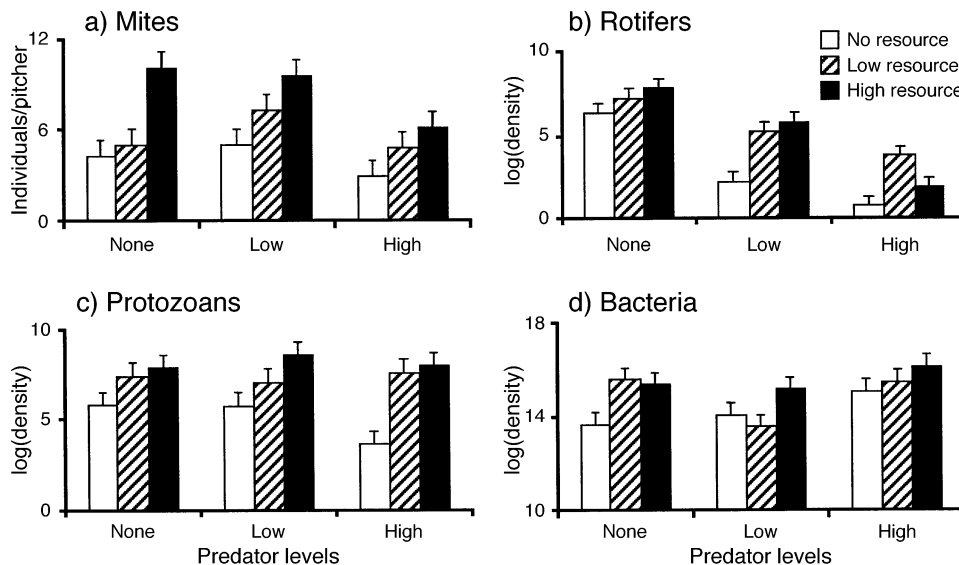


FIG. 2. Mean abundance over time (+1 SD) for (a) mites, (b) rotifers, (c) protozoans, and (d) bacteria in each of the nine treatments. Values for rotifers, protozoans, and bacteria were measured in individuals/mL and log-transformed.

Abundance increased at all trophic levels with resource addition (Fig. 2). Interestingly, the effects on abundances were larger at the middle trophic level (protozoans and rotifers) when compared with the basal trophic level (bacteria), even though protozoans and rotifers primarily feed upon bacteria. Resource limitation has been found to be more important at higher trophic levels in other aquatic systems (Osenberg and Mittlebach 1996). This trend probably reflects greater turnover in bacteria that resulted from increased consump-

tion rates as the abundance of the middle trophic level increased.

Protozoan species richness increased with resource addition (Fig. 3). Many explanations have been advanced for the positive relationship between productivity and diversity (e.g., Begon et al. 1990, Rosenzweig and Abramsky 1993, Abrams 1995). The most likely explanation in our system is that increasing resources reduced extinctions of rare species by increasing their abundance levels in the pitcher plant system. Most of the rare species were detected in higher resource treatments.

Top-down theory, in which predation regulates species abundances, predicts negative effects on adjacent trophic levels and positive effects on nonadjacent trophic levels below the top predator (trophic cascades or indirect effects; Hairston et al. 1960, Oksanen et al. 1981, Carpenter et al. 1985, Persson 1999; however see Sinclair et al. 2000). *Wyeomyia smithii*, an omnivorous filter feeder in this inquiline community (Fig. 1; Addicott 1974, Istock et al. 1975), is thought to consume bacterivores (rotifers and protozoa) as well as the bacteria themselves. However, rotifers were the only species at the second trophic level that was negatively affected by predation (Fig. 2b). Previously, Bledzki and Ellison (1998) found a similar negative relationship between *W. smithii* and *H. rosa*. The generation time for rotifers are longer (0.4–1.3 d; Bledzki and Ellison 1998) than protozoans (0.1–0.5 d; Pianka 2000), which may have rendered rotifers more vulnerable to predation effects.

Protozoans, which are at the same trophic level as rotifers, were unaffected by predation. One explanation for this result is that protozoan species may have been more resistant to predation. Species within a trophic

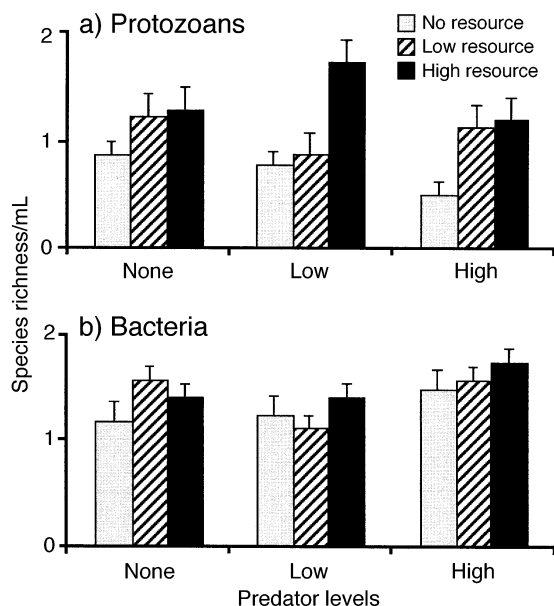


FIG. 3. Mean richness (adjusted by rarefaction) over time (+1 SD) for (a) protozoa and (b) bacteria in each of the nine treatments.

level can differ in their vulnerability to predators (Leibold 1989), which can decrease the importance of predation through a compensatory increase in the abundance of less vulnerable species (Leibold et al. 1997, Bohannan and Lenski 1999, 2000). Predator resistance may occur as the result of a refugia (size or spatial) or growth rates that exceed predator consumption rates. Heterogeneity in response to increased predator density was also found among individual protozoan species: *Colpidium* was positively affected by resources, and *Bodo* abundance had a unimodal relationship with predation. It is likely that different types of resistance occur among the protozoans. Another explanation for a lack of protozoan response to predation is that increased bacteria abundance levels resulting from the trophic cascade provided added resources for protozoan growth to match consumption rates. Another alternative explanation for the lack of response by protozoans is prey switching by the top predator (Murdoch 1969). It is not known whether *W. smithii* targets particular species during feeding.

The presence of mosquito larvae did have positive indirect effects on bacterial richness and marginal effects on abundance, by way of the *W. smithii*–rotifer–bacteria pathway (Figs. 2, 3). Our findings corroborated Cochran-Stafira and von Ende's (1998) detection of indirect effects on bacterial abundance, which may have resulted from predation or release of nutrients. An alternative explanation is that the presence of the top predator could have affected the basal trophic level by releasing nutrients into the system (Vanni and Layne 1997, Vanni et al. 1997, Cochran-Stafira and von Ende 1998). Two conclusions arise from this result: (1) trophic cascades are strong in this system but primarily affect diversity, and (2) omnivory is not strong enough to overcome the trophic cascade in this system, as bacteria abundance and richness did not decrease with increased predator densities. However, it remains unclear the degree to which bacteria sustain *W. smithii*.

The results of the present experiment differed from previous top-down studies in the same system. Addicott (1974) found reduced protozoan diversity as mosquito larva density increased, whereas Cochran-Stafira and von Ende (1998) found that adding *W. smithii* allowed four protozoan species to coexist. These previous studies examined the role of predation; our study incorporated varying levels of predator and prey densities in order to clarify the relationship between top-down and bottom-up effects in this system. Our results differed from the two previous studies in that we found no effect of predation on protozoan species richness, but there was an interaction between predation and resource addition (Table 2).

Several factors could have contributed to the differences among the studies. First, the studies had methodological differences. For example, Addicott's (1974) study used six predator densities in three nonconsecutive months. In contrast, Cochran-Stafira and von

Ende (1998) used two predator levels which were lower than ambient densities and presented results from only 72 h after experimental initiation. Our study utilized a greater range of predator levels and our sampling frequency and length was intermediate to these other two studies.

Second, diversity levels in all three studies differed significantly. Addicott's (1974) study had high natural species diversity (41 protozoan and rotifer species). He concluded that increases in diversity would occur at low mosquito densities, but that such densities rarely occurred in the field. However, Cochran-Stafira and von Ende (1998) utilized only four protozoan species and showed that *W. smithii* facilitates coexistence under very specific conditions, low predator density and over a short-time period. These studies, and ours, varied in natural protozoan diversity and *W. smithii* densities. Therefore, geographic variation in these important community components (species richness and composition) may also contribute to different results.

Third, different levels of productivity can affect trophic-level responses to predators (Oksanen et al. 1981, Leibold 1996). Addicott (1974) used ambient resource levels and found that adding resources (prey) had no significant effect, whereas Cochran-Stafira and von Ende (1998) used lower than ambient resource conditions. Our study found a strong effect of ambient resource levels and an interaction between resource addition and predation on protozoan species richness. These results indicate that the response of protozoan species richness to predation can differ at varying levels of resources.

The last difference between the studies was in how rotifers were treated. Addicott (1974) lumped rotifers with the protozoans and Cochran-Stafira and von Ende (1998) did not include rotifers in their laboratory microcosms. The presence of rotifers in our study may have minimized the effects of mosquito larvae on protozoans.

Several studies have simultaneously manipulated resource and predator levels in other types of communities (Persson et al. 1992, Wootton and Power 1993, Balciunas and Lawler 1995). They have addressed abundance and biomass at each trophic level but not the effects of top-down and bottom-up forces on diversity. Our results emphasize that top-down and bottom-up regulation can simultaneously affect both species abundances and diversity of middle trophic levels. The relative effects of added resources were less on the basal trophic level (bacteria) when compared to the middle trophic level (protozoans and rotifers). This may be an artifact of protozoan and rotifer predation simultaneously occurring on bacteria, thereby inhibiting larger increases in bacteria abundance.

Recently, omnivory has been shown to have important effects in simple protozoan communities (Morin 1999, Diehl and Feiel 2000). If omnivory was an important part of this system, bacteria abundance should

have decreased with increasing predator densities because of the simultaneous predation by mosquito larvae, protozoans, and rotifers. Our results show that the indirect effects of predation (mosquito larvae–rotifers–bacteria) were more important than omnivory itself. Bacterial species richness did increase with predator density, which we believe is most likely the result of an indirect effect acting through changes in the abundance of intermediate species.

We conclude that basal resource availability and, to a lesser extent, predation from the top trophic level have large effects on basal and intermediate trophic levels in inquiline communities. Contrary to some previous studies, however, we conclude that there is little interaction between the community effects of predators and resource availability, and that omnivory is not strong enough to prevent trophic cascades in this system. Our work emphasizes the importance of simultaneous experimental manipulations of resources and predators, and quantifying the role of species-specific, rather than whole trophic level, responses (e.g., Leibold 1996).

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