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Top-down and Bottom-up Regulation in a Detritus-based Aquatic Food Web: A Repeated Field Experiment Using the Pitcher Plant (*Sarracenia purpurea*) Inquiline Community

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ABSTRACT.—The aquatic food web found within the leaves of the purple pitcher plant (*Sarracenia purpurea*) is useful for studying top-down and bottom-up effects. The food web has an omnivorous top-predator and is fueled by invertebrates drowned in the pitfall trap of the pitcher plant. Modeled on a previous experiment for the purpose of comparison, I conducted a 3×3 factorial press experiment over 4 wk, using 45 pitcher leaves in a bog in Michigan. Treatments included 3 levels (none, low and high) of both resource input and top-predator density. Both top-down and bottom-up treatments had significant effects on populations within the inquiline food web. Rotifer, mite, protozoan and bacterial density and protozoa richness increased when resources were added. Top-predator density negatively affected rotifer, protozoa and bacteria density. These findings suggest that in this food web bottom-up forces predominate, but top-down forces are also important. A similar study conducted in Florida is used to make a latitudinal comparison of food web regulation and temperature is hypothesized to be responsible for observed differences between the inquiline food webs.

INTRODUCTION

Ecologists have often attempted to determine how consumption (*i.e.*, top-down) and production (*i.e.*, bottom-up) effects regulate populations in communities (Hunter and Price, 1992; Polis *et al.*, 1996). Bottom-up regulation occurs through resource availability at the base of the food web, such that increased productivity at lower trophic levels may result in increased biomass at higher trophic levels (Elton, 1927; Lindeman, 1942; Persson *et al.*, 2001). This may include nutrient inputs to primary producers in an autotrophic-based system or to bacteria in a decomposer loop. Top-down regulation occurs when predator populations limit prey populations, which may reduce the effect of prey populations on their resources, a trophic cascade (Pace *et al.*, 1999). The relative importance of these forces and how their strength may vary in different systems is not well known (Strong, 1992; Shurin *et al.*, 2002). Bottom-up proponents have argued that populations are limited primarily by nutrients and that this resource shortage is the major force structuring communities (White, 1978; Polis and Strong, 1996), whereas top-down proponents have argued that predators are the main determinants of food web dynamics (Hairston *et al.*, 1960; Hairston, 1993).

It is broadly recognized that top-down and bottom-up effects are not mutually exclusive, but that these forces in combination determine food web structure and dynamics (Power, 1992; Denno *et al.*, 2003; Nyström *et al.*, 2003). Examining the relative importance of top-down and bottom-up forces requires a factorial design where both factors are manipulated. Such experiments have been conducted in pitcher plant food webs in Florida (Kneitel and Miller, 2002; Miller *et al.*, 2002). A next step is to understand if the patterns of top-down and bottom-up effects observed in one location can be generalized, especially as patterns of productivity and predation change across gradients. In this study, I investigate top-down and bottom-up effects in pitcher-plant inquiline food webs from different latitudes using a combination of experimentation and comparison with a previous study.

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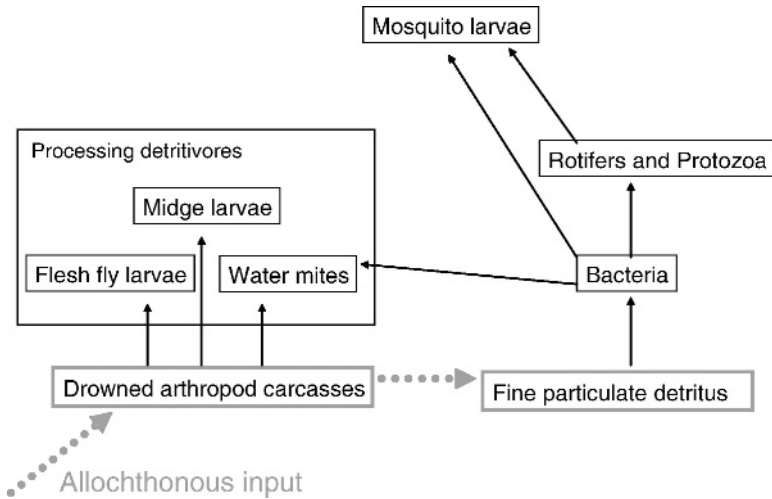


FIG. 1.—The purple pitcher plant inquiline food web. Solid arrows designate feeding relationships. Dotted arrows designate basal resource pathways

THE PITCHER PLANT AND ITS INQUILINE COMMUNITY

The purple pitcher plant (*Sarracenia purpurea*) has modified leaves arranged in a rosette that both attract invertebrates and entrap them in its rainwater filled cavity. It grows in ombrotrophic bogs and other wetlands with low nutrient soils. A simple aquatic community coexists symbiotically with the plant in a food web fueled by dead invertebrates drowned in the pitfall trap (Fig. 1, Miller and Kneitel, 2005). The food web is composed of bacteria, protozoa, a bdelloid rotifer (*Habrotrocha rosa*), water mites and three larval dipterans. The dipterans are the pitcher plant mosquito (*Wyeomyia smithii*), the pitcher plant midge (*Metricnemus knabi*) and the pitcher plant flesh fly (*Fletcherimyia fletcheri*). All three dipterans are obligate symbionts of the pitcher plant inquiline habitat and are univoltine at northern latitudes (Hardwick and Giberson, 1996). The midge, flesh fly larvae and mites feed directly on insect carcasses, comminuting them and accelerating their digestion by bacteria (Heard, 1994; Ellison *et al.*, 2003). Bacteria consume suspended particles in the water and are consumed by a diverse group of bacterivorous protists and rotifers. Mosquito larvae are omnivorous top predators, feeding on small rotifers, protozoa and bacteria.

THE PITCHER PLANT INQUILINE COMMUNITY AS A MODEL SYSTEM

There are several advantages to utilizing the inquiline community in the northern pitcher plant as a model food web for research (Ellison *et al.*, 2003; Miller and Kneitel, 2005). The system is small, relatively simple, easily manipulated and replicable (each leaf). Larval insect movement between pitchers is minimal, therefore each leaf is a naturally isolated experimental unit (Heard, 1994). Simple aquatic food webs have been proposed as model systems for studying food webs (Morin and Lawler, 1996; Spencer and Warren, 1996; Peacor and Werner, 1997) and this simple aquatic system is particularly useful because it is a naturally occurring community.

The pitcher plant inquiline food web is well suited to experiments manipulating top-down and bottom-up forces. Instead of primary productivity driving the system, productivity of the food web, (*i.e.*, the rate at which it incorporates carbon and other nutrients), is fueled by

bacterial production based on allochthonous input (arthropod carcasses that drown in the pitcher) (Cameron *et al.*, 1977; Cochran-Stafira and von Ende, 1998), which is under extrinsic control (*sensu* Persson *et al.*, 1996). Therefore, bottom-up processes can be manipulated by varying allochthonous inputs (arthropod bodies) and top-down processes can be varied by manipulating top consumer (mosquito larvae) density. The plant itself does not respond (*e.g.*, by growing more or larger leaves) to resource addition within one growing season (Chapin and Pastor, 1995; Wakefield *et al.*, 2005).

The trophic dynamics of pitcher plant inquiline food web have been well studied in Florida (Kneitel and Miller, 2002; Miller *et al.*, 2002; Kneitel and Miller, 2003). Though the food web is well conserved across the wide geographical range of the plant, from Florida up the Atlantic coast and across most of Canada (Buckley *et al.*, 2003), pitcher plant food webs at northern latitudes experience cooler temperatures, longer summer day length and a different regional species pool of protozoa and bacteria. These environmental differences may have consequences for trophic dynamics. For example, warmer temperatures may result in increased feeding activity. The goal of this study is to compare top-down and bottom-up forces between model food webs in different environments.

MATERIALS AND METHODS

STUDY SITE

The manipulated pitcher plants occur at the University of Notre Dame Environmental Research Center (UNDERC, 46' 13" N by 89' 32" W) in Michigan's Upper Peninsula. I conducted the study in a *Sphagnum*-dominated ombrotrophic bog with scattered tamarack (*Larix laricina*) and black spruce (*Picea mariana*) trees. Common shrubs and forbs include cottongrass (*Eriophorum* spp.), white beaksedge (*Rhynchospora alba*), leatherleaf (*Chamaedaphne calyculata*) and bog Labrador tea (*Ledum groenlandicum*). Carnivorous plants present are the purple pitcher plant and the roundleaf sundew (*Drosera rotundifolia*).

EXPERIMENTAL MANIPULATIONS

Using the simple food web found within the purple pitcher plant, I conducted a 3×3 factorial press experiment. I initiated the experiment by collecting 800 mL of inquiline fluid from approximately 75 pitchers on 13 Jul., 2003, after most pitcher plant mosquito adults had laid their eggs and the new generation of larvae was beginning to grow. I removed dipteran larvae, homogenized fluid by pooling and filtered (using a 1-mm mesh folded $8 \times$) the fluid to remove debris and arthropod carcasses. The 3×3 factorial design included three levels of resource input (0, 2 and 10 insect carcasses) and three predator levels (0, 3 and 20 mosquito larvae). I selected treatment levels to mimic the range of combinations of resources (arthropod carcasses: mean = 2.7 SD = 3.6 N = 100) and predators (mosquito larvae: mean = 7.3 SD = 9.5 N = 100) naturally occurring in the field based on on-site surveys. I replicated each of the nine treatments five times ($n = 45$). In a homogenous open area of the bog, I chose 45 newly opened pitchers (<2 wk old) of approximately the same size from among the 75 emptied pitchers, rinsed them with sterile water and stocked them with 15 mL of filtered fluid. Pitchers were assigned to one of each of the nine treatments in five blocks: mosquito larvae and insect carcasses were then added as appropriate. I covered the pitchers with 1-mm tulle mesh to prevent additional prey entry or mosquito colonization. Mosquito larvae used for stocking were those removed from inquiline fluid collected that day, whereas insect carcasses (large adult mosquitoes, *Aedes* spp.) were collected a few days earlier from a New Jersey mosquito trap and frozen until stocking. I excluded midge and flesh fly larvae from the experiment for consistency with Kneitel and Miller's methods (2002).

I sampled the pitchers twice a week for 3 wk, and once during the 4th week, for a total of seven sampling sessions. Sampling included gently mixing the community and temporarily removing all the pitcher contents. I counted mosquito larvae and insect carcasses and adjusted their densities as necessary. I added larvae to replace those lost to mortality and removed new eggs or young larvae that were previously undetected. I added additional prey carcasses after the prey body segments had broken apart and, on a few occasions, removed drowned ants that had entered the pitcher. Previously added decomposing prey were not removed, in keeping with Kneitel and Miller's methods (2002). All adjustments to treatment levels were recorded. Small samples (<300 μL) of inquiline fluid were taken for protozoa and bacteria analysis.

I enumerated protozoa, rotifers and mites using Palmer counting cells and a compound microscope ($\times 100$). From each pitcher sample, I pipetted 100 μL onto the slide, and recorded the density and richness of protozoa, as well as the density of rotifers and mites. I counted one slide per pitcher and identified protozoa to genus (Patterson, 1996). Protozoan density is a problematic measure to compare protozoa communities found in different treatments because the protozoa present range in size over an order of magnitude. To remedy this problem, I calculated biovolume (μm^3) based on the dimensions (mean of samples from this study, $n = 15$) and density of each genus.

To estimate bacterial density, I treated a 25 μL sample from each pitcher with formaldehyde, stained it with acridine orange and strained it through a Nuclepore filter with 0.2 μm pore size. I put these filters onto slides and counted the bacteria using a Whipple grid on an epifluorescence microscope (Hobbie *et al.*, 1977; Pace, 1992).

STATISTICAL ANALYSIS

I tested the effect of resources and predators on average mite and rotifer density over the sampling sessions with two-way ANOVA and Tukey post hoc tests on each factor. I used repeated measures ANOVA to test for the effect of resources and predators on bacterial and protozoan abundance and protozoa species richness over time. Mite and rotifer density was too low (too many zero counts) to conduct repeated measures ANOVA, so average mite and rotifer density in each pitcher was calculated and log transformed to meet test assumptions for a conventional ANOVA. The effects of blocking were not significant ($P > 0.30$), so data were pooled between blocks. I used SYSTAT 10 for all tests (SYSTAT, 2000).

RESULTS

One pitcher was found to be damaged on the second day of the experiment and the treatment was consequently restocked in another leaf. No other pitchers were lost or damaged during the experiment. The volume of water in all the pitchers increased over the course of the experiment due to occasional rain.

BOTTOM-UP EFFECTS

The addition of insect carcasses significantly increased the density of all measured inquiline populations ($P < 0.05$). Both mite and rotifer density increased with resource addition (Fig. 2A, B, Table 1), and rotifer population density was significantly different among all three resource levels (Tukey test $P < 0.05$). Protozoan biovolume increased with resource addition (Fig. 2C, Table 1). Bacterial density increased with resource addition (Fig. 2D, Table 1). In addition to the increased density of consumer populations, protozoa species richness also increased with resource addition (Fig. 3, Table 1).

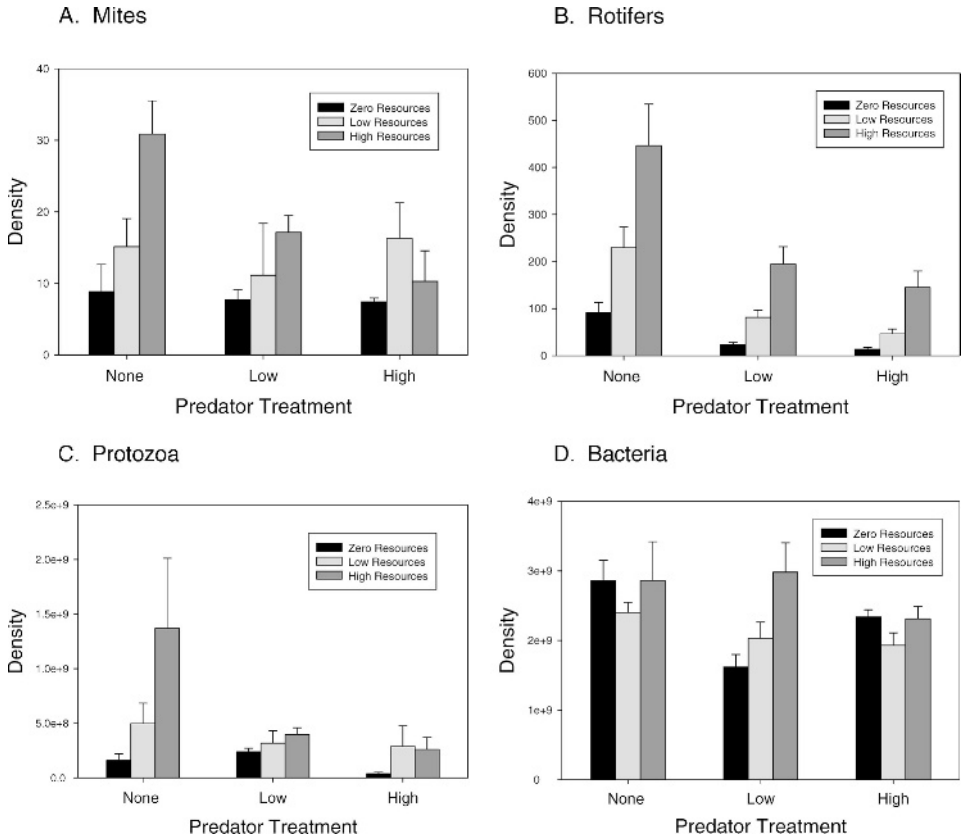


FIG. 2.—Mean density (\pm SE) over time for each measured inquiline population in the nine treatments. A: Mite density (per mL). B: Rotifer density (per mL). C: Protozoa biovolume (μm^3 per mL). D: Bacteria density (cells per mL)

TOP-DOWN EFFECTS

The presence of predacious mosquito larvae reduced the density of their prey populations. Rotifer density decreased markedly in mosquito treatments (Fig. 2, Table 1). The absence of mosquito larvae in zero predator treatments resulted in a significant increase in rotifer density (Tukey test $P < 0.001$). Protozoan biovolume and bacterial density both decreased with mosquitoes present (Fig. 2C, D, Table 1). Protozoan richness was also reduced by mosquito density (Fig. 3, Table 1).

None of the interactions between top-down and bottom-up effects were statistically significant ($P > 0.05$ Table 1). However, for mites and protozoa, the effects of increasing predators were mostly clearly seen at higher resource levels (Fig. 2A, C).

DISCUSSION

Both top-down and bottom-up forces had significant effects on populations within the food web. Bottom-up theory predicts that greater nutrient availability will support larger consumer populations and resource availability did have a marked positive effect on all

TABLE 1.—Statistical summary of ANOVA results showing the effects of predators and resources on inquiline population density and species richness

Dependent variable	Source	df	F	P
Mite Density (log transformed)	Predator	2	1.471	p = 0.24
	Resource	2	3.568	p = 0.04
	Predator × Resource	4	2.147	p = 0.09
	Error	36		
Rotifer Density (log transformed)	Predator	2	55.866	p < 0.001
	Resource	2	33.908	p < 0.001
	Predator × Resource	4	0.566	p = 0.69
	Error	36		
Protozoa Biovolume	Predator	2	3.287	p = 0.05
	Resource	2	3.731	p = 0.03
	Predator × Resource	4	1.785	p = 0.15
	Error	36		
Bacteria Density	Predator	2	3.799	p = 0.03
	Resource	2	4.115	p = 0.03
	Predator × Resource	4	1.575	p = 0.20
	Error	36		
Protozoa Richness	Predator	2	13.580	p < 0.001
	Resource	2	14.022	p < 0.001
	Predator × Resource	4	0.206	p = 0.93
	Error	36		

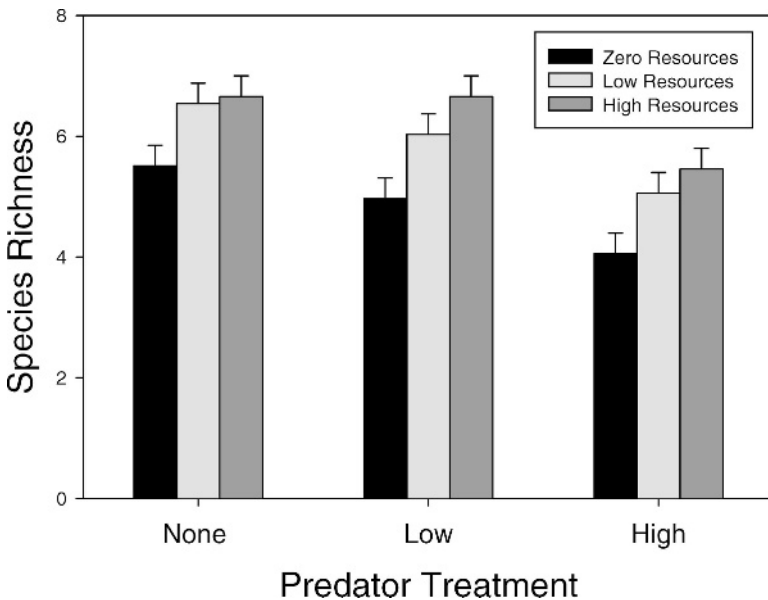


FIG. 3.—Mean protozoa species richness (\pm SE) over time in the 9 treatments. Units are number of protozoa species found per 0.1 mL.

measured consumer populations (Fig. 2, Table 1). Bottom-up effects were transmitted by bacteria up the food web to higher consumers, suggesting that the whole community is resource limited, which is consistent with expectations for a detritus based allochthonous system (*i.e.*, a donor system, *sensu* Pimm, 1982), where consumers do not influence the rate of energy entering the system. The richness of the protozoa community also increased with the addition of insect carcasses (Fig. 3). Enriched pitchers, with high bacterial productivity, supported rare protozoa that are generally unable to persist in lower resource environments.

Scavenging mites may contribute to the observed strong bottom-up effects. I suspected that the detritus processing action of mites may have amplified the community-wide response to resource addition. Because mite density was not controlled, it may have initiated a positive feedback on resource levels because insect carcasses were replaced after they had broken into segments. By actively breaking down carcasses, mites may have increased the rate of experimental carcass addition (by increasing the replacement rate) and detrital surface area. This activity may increase the density of bacteria that feed on suspended detritus and consequently the other bacterivores in the food web and, thereby, accelerate the community-wide effects of resource addition. Similar effects have been suggested for other processing detritivores in this system (Heard, 1994). However, this hypothesis was tested by a regression of mite density on insect carcass addition and mite density was only weakly related to resource input (regression of mites on prey added; $P = 0.10$, $R^2 = 0.06$). Since mite density only explains 6% of the variation in prey addition, the potential for a positive feedback of mite density on resource addition is not a likely explanation for the observed strong bottom-up effects. Additionally, mosquito larvae treatment had no effect on number of prey added (ANOVA: $df = 2$, $MS = 61.42$, $F = 0.81$, $P = 0.45$).

While resource addition increased the density of all measured consumer populations, mosquito density concurrently had a negative effect on their prey, especially rotifers and protozoa. Top-down theory predicts that increasing predator density will result in decreased prey populations and an increase in prey resources, in this case bacteria (a trophic cascade). However, in the case of top-predator omnivory, a trophic cascade is not expected (Diehl and Feissel, 2000), and in this experiment it was not observed. In fact, mosquitoes decreased bacterial density. The direct effect of the omnivorous top-predator consuming bacteria may have masked any trophic cascade in this food web. Although bacteria did not respond positively to mosquito density (*i.e.*, no trophic cascade), the negative response of bacteria to the mosquito treatment was weaker than the intermediate trophic level response (especially rotifers, *see* Table 1). The response of bacteria to mosquitoes may have been mitigated by the reduced densities of bacterivorous rotifers and protozoa in mosquito treatments. Alternatively, the absence of a trophic cascade may simply be explained by the predominance of bottom-up effects in this system. However, strong bottom-up effects do not preclude the importance of top-down effects. The whole community is ultimately resource limited, though mosquitoes do act as a regulating factor for several populations within the food web.

In a recent paper, Worm *et al.* (2002) argue that the effects of consumers and nutrients on diversity consistently interact. This relationship is predicted by multivariate models, demonstrated by their experimental results, and confirmed by a number of other experiments in aquatic communities (Worm *et al.*, 2002). In contrast, top-down and bottom-up treatments did not significantly interact in this experiment (Table 1, protozoan richness $P = 0.93$). This may be due to the range of resource treatments imposed and specifically the relationship between diversity and productivity in that range. The multivariate models referred to by Worm *et al.* (2002) (*e.g.*, Kondoh, 2001) are based on a unimodal relationship

between diversity and productivity. However, in this experiment, higher productivity resulted in a monotonic increase in protozoan species richness (Fig. 3), perhaps reducing the potential for a consumer–nutrient interaction.

At the conclusion of the experiment, protozoan richness was about 3× higher in zero-mosquito than high-mosquito treatments (Fig. 3). (Buckley *et al.*, 2003) suggest that protozoa and bacteria are the primary trophic groups driving richness patterns in purple pitcher plants. Higher diversity of the inquiline community at northern latitudes is hypothesized to be due to lower top predator (mosquito larvae) densities (Buckley *et al.*, 2003). These results confirm that protozoan richness does increase with decreasing densities of mosquito larvae at a northern site (latitude 46°).

LATITUDINAL COMPARISON

In a similar experiment using the same model system (same dipterans, rotifer and protozoa) but conducted in Florida, (Kneitel and Miller 2002) also found top-down and bottom-up effects to influence the density and diversity of pitcher plant inquilines. Using three levels of resource and mosquito density in a factorial design, they found that adding resources positively affected bacteria, protozoa, rotifer and mite populations, whereas mosquito predation negatively affected rotifer populations. There are two major differences between the experiment conducted in Florida and that presented here from Michigan. First, Kneitel and Miller found no effect of mosquitoes (predator treatment) on protozoa (however, *see* Kneitel and Miller, 2003). Second, they observed a trophic cascade of mosquitoes on bacteria. Bacterial abundance ($P = 0.06$) and richness ($P = 0.02$) were found to increase with mosquito density (a trophic cascade), whereas rotifer density decreased ($P < 0.001$) and protozoan density was unaffected ($P = 0.67$). They concluded that mosquito larvae omnivory on bacteria was not strong enough to affect a trophic cascade mediated by rotifers in their experiment.

Both experiments detected strong bottom-up effects and some top-down effects. Whereas top-down effects were detected in Michigan, I did not observe a trophic cascade, but Kneitel and Miller did. Generally, the presence of a trophic cascade is thought to indicate strong top-down effects. However, the specific trophic levels at which those effects are manifested may determine whether or not a trophic cascade is detected. Various characteristics of a system may obfuscate the relative importance of top-down and bottom-up effects. For example, by making food webs more reticulate, increased species richness and omnivory tend to diffuse strong trophic links (Polis and Strong, 1996). Additionally, selective feeding on a specific taxa or trophic level may influence where top-down effects occur. For example, mosquito predation does differentially affect protozoan species in this system (Addicott, 1974; Kneitel and Miller, 2003, Hoekman, pers. obs.). Due to these complicating factors, the question of whether or not a food web is controlled by top-down or bottom-up effects may not be appropriate at the whole food web level, but may have to be evaluated separately for each trophic level or even species. Indeed, theoretical and empirical studies have demonstrated that due to trophic complexity, food webs often cannot be simplified into discrete trophic levels that behave like simple food chains (Leibold, 1989; Polis and Strong, 1996).

Omnivory is an aspect of trophic complexity that appears to differ between pitcher plant inquiline food webs in these two studies. In Kneitel and Miller's study, mosquitoes appear to have fed primarily on rotifers, depressing their population and consequently increasing bacteria populations (a trophic cascade), whereas protozoa were unaffected. In contrast, mosquitoes in the current study were more omnivorous and depressed rotifer, protozoa and bacteria populations (no trophic cascade). Though their effect on rotifers was strongest,

mosquito omnivory may have prevented the occurrence of a trophic cascade. Why would mosquito larvae be more omnivorous at the northern site? One explanation is that their preferred prey, rotifers, may be less abundant at northern sites, so rotifers are quickly depleted and mosquitoes feed on other prey. Mosquito larvae have been observed to prefer rotifers over protozoa in feeding trials (J. Kneitel, pers. comm.). Rotifers may be preferable prey because they are larger than protozoa and bacteria and therefore contain more nutrients per individual eaten. However, average rotifer density (rotifers per mL) was comparable between the two experiments (141 as compared to 96 in Florida, J. Kneitel, pers. comm.). The differing effects of top-predators in these two studies is an example of the context dependent effects of consumers, a phenomenon observed in a variety of ecological systems (e.g., Menge *et al.*, 1994; Nowlin and Drenner, 2000). Identifying what biotic or abiotic conditions contribute to this context dependency will be the goal of future studies.

Temperature is a factor that may contribute to the observed differences between pitcher plant inquiline food webs in these studies and help explain apparent differences in omnivory. Average daily temperature during the experiments differed by about 10 degrees (19 C compared to 28.5 C in Florida, T. Miller, pers. comm.). In general, warmer temperatures result in faster metabolism, individual growth, population growth rate and turnover (Brown *et al.*, 2004). Due to higher mean temperature, I would expect greater bacterial productivity in Florida and faster population turnover. Faster bacteria and protozoa growth rates may explain why these populations were not significantly depleted by mosquito predation in Florida, but were in Michigan. Mosquitoes may appear to be more omnivorous in Michigan because of the slower population growth rate of protozoa and bacteria at lower temperatures. Smaller body size also results in faster metabolism and growth (Brown *et al.*, 2004). Approximate body size and generation times for pitcher plant taxa are: bacteria 1 μm , 0.014 d; protozoa 10–30 μm , 0.1–0.5 d; and rotifers >150 μm , 2 d (Ellison *et al.*, 2003; Trzcinski *et al.*, 2005). Because rotifers are much larger than bacteria or protozoa in this system, their population growth rate is slower and therefore their population may be more vulnerable to depletion by predators. However, increased temperature may also increase mosquito activity, specifically feeding (Walker, 1995), counteracting greater productivity.

Many factors may have contributed to the contrasting results of these two studies including: surrounding environment and experimental treatment differences. Though similar in design, the studies employed slightly different mosquito and insect carcass densities, based on local field densities. Clearly, top-down and bottom-up forces are important in pitcher plant food webs in both locations. Determining how the relative importance of top-down and bottom-up forces vary with location within the range of the pitcher plant and the consequences for members of the inquiline community requires further study.

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