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Top-down and bottom-up effects of a processing detritivore

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Abstract. Detritus processing, the breaking down of organic matter into smaller particles, is an essential operation in aquatic systems because it provides resources to filter feeders and accelerates nutrient release by microorganisms. Detrital foodweb dynamics are influenced by both consumption (top-down) and production (bottom-up) effects. We tested the effects of predators and detritivores on the abundance of microorganisms in an inquiline community in pitcher plants. We manipulated densities of mosquitoes (top predator) and midges (processing detritivore) in a factorial press experiment and measured the response (density) of bacteria, protozoa, and rotifer populations over several generations. We hypothesized that: 1) midges would have a positive effect on microorganisms by increasing nutrient availability (bottom-up effects), 2) mosquitoes would depress microorganism populations through consumption (top-down effects), 3) top-down and bottom-up effects would operate independently, and 4) would attenuate with trophic position. Mosquitoes (predators) had a negative effect on all measured populations. Midges (processing detritivores) had a positive effect on bacteria, but a negative effect on rotifers and some protozoan taxa. The increase in bacterial density probably was the result of nutrient enrichment from detritus processing, whereas the decrease in rotifers seems to have been the result of consumption by midges. Our study shows that the role of processing detritivores is complex and can enhance both bottom-up and top-down effects. Specifically, omnivory can complicate simple top-down and bottom-up predictions. Although they accelerate decomposition by microorganisms and, thereby, can increase resource availability, processing detritivores can also be important consumers in detrital food webs.

Key words: detritus processing, food webs, top-down vs bottom-up, detritivores, microorganisms, *Metriocnemus knabi*, pitcher plant, *Sarracenia purpurea*, *Wyeomyia smithii*, incidental predation, inquilines.

Foodweb dynamics can be influenced by top-down (consumers) and bottom-up (resource availability) effects, and deciphering the relative importance of these effects is a major research challenge for community ecologists (Osenberg and Mittelbach 1996, Hunter 2001). Detritus is an important resource pool that can affect foodweb structure and dynamics (Wallace et al. 1999). Most of primary production is

not consumed by grazers but enters the detrital food web (Wetzel and Ward 1992). Therefore, detritus processing is a vital pathway for reincorporation of C into consumer food webs (Wetzel 1995). The supply of detritus often determines bottom-up effects (Wallace et al. 1999), but detritus processing rate also can be an important driver of bottom-up effects (Paradise 1999).

The importance of detritus processing to community structure has been demonstrated in a variety of aquatic systems (Heard 1994b). Detritus processing is especially important for organic matter dynamics in forested headwater streams that depend on allochthonous input (Cummins and Klug 1979, Mulholland et al. 1985), but it also has been demonstrated in container habitats, such as tree holes (Daugherty and Juliano 2002) and pitcher plants (Heard 1994a).

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Particle size reduction is necessary because most large particles cannot be used by filter-feeding microorganisms (Wallace and Merritt 1980). For example, shredders increase the amount of leaf material available to collector species (Short and Maslin 1977) and even increase collector growth rates in streams (Cummins et al. 1973). In addition, detritivores increase nutrient (N and dissolved organic C) availability to primary producers and microorganisms (Crowl et al. 2001). Foodweb dynamics can be strongly affected by the presence of even a single detritivore species because processing detritivores accelerate decomposition by comminuting detritus (Mulholland et al. 1985, Larned et al. 2003). Processing detritivores also can bring about top-down effects as omnivorous consumers of other detritivores (Usio 2000).

Top-down and bottom-up effects on detritus-based communities have been examined in streams (Rosemond et al. 2001), tree holes (Kaufman et al. 2002), and pitcher plants (Kneitel and Miller 2002, Gray et al. 2006, Hoekman 2007). Leaves are the primary detrital input to streams and tree holes (but see Yee et al. 2007), but animal carcasses are the primary allochthonous input in pitcher plants.

The dominant detritivore found in the aquatic inquiline community in purple pitcher plants (*Sarracenia purpurea* L.) is the pitcher plant midge (*Metriocnemus knabi* Coq.). The presence of the pitcher plant midge increases release of soluble N (Bradshaw 1983) and accelerates the conversion of coarse detritus to fine detritus, initiating a processing chain that benefits bacteria and ultimately the top-predator pitcher plant mosquito (*Wyeomyia smithii* Coq.) (Heard 1994a). Mosquito growth increases with midge density but midge growth is unaffected by mosquito density, and Heard (1994a) termed this interaction a "processing chain commensalism." However, he did not address how the midge affected other members of the food web or how its detritus processing role might influence top-down or bottom-up effects in the rest of the inquiline community.

Our objective was to examine the effects of a processing detritivore, the pitcher plant midge, on top-down and bottom-up effects in the pitcher plant inquiline community and to use this model system to better elucidate the role of processing detritivores in freshwater detritus-based communities. We manipulated the presence/absence of larvae of the pitcher plant midge (processing detritivore, bottom-up treatment) and mosquito (top predator, top-down treatment) in a 2×2 factorial design and measured their effects on population densities of bacteria, protozoa, and rotifers. We hypothesized that: 1) by comminuting arthropod carcasses, midges would increase nutrient availability

by size fractionation or by releasing dissolved organic matter (DOM), resulting in higher microorganism densities; 2) mosquitoes, the top predator of the system, would depress microorganism populations; 3) on the basis of previous experiments (Hoekman 2007, DH, unpublished data), the effects of mosquitoes and midges would be largely independent (no interaction); and 4) the effects of mosquitoes and midges would attenuate (i.e., lose strength with each trophic transfer; McQueen et al. 1986) with trophic distance. We tested these hypotheses about the counteracting effects of top-down and bottom-up forces in a field experiment.

Methods

Model system

The purple pitcher plant grows in low-nutrient wetlands across eastern North America. It has modified leaves (pitchers) arranged in a rosette that attract invertebrates (mainly ants) and entrap them in a rainwater-filled cavity, which also provides a habitat for a diverse aquatic fauna of inquilines (Miller and Kneitel 2005). This aquatic community is composed of bacteria, bacterivorous protozoa and rotifers, and larvae of the pitcher plant mosquito and the pitcher plant midge (hereafter mosquito and midge). The midge feeds primarily on drowned insect carcasses, speeding their decomposition and increasing surface area for bacterial growth through organic particle size reductions (Heard 1994a). A diverse group of protozoa and a bdelloid rotifer (*Habrotrocha rosa* Donner) comprise the intermediate trophic level and are consumed by the mosquito, an omnivorous top predator (Addicott 1974). This model system is well suited for foodweb research because it is small, relatively simple, easy to manipulate, and occurs in a circumscribed and replicated habitat (each pitcher) (Miller and Kneitel 2005).

Study site

We conducted our study in a *Sphagnum*-dominated ombrotrophic bog at the University of Notre Dame Environmental Research Center in Michigan's upper peninsula, USA (lat 46°N, long 89°W). In May 2005, when we did the experiment, average temperature was 10.6°C (range, -3 to 26) and mean daily precipitation was 1.5 mm (≤ 3 consecutive days without rain). At this latitude, mosquito and midge larvae are univoltine and are in their 3rd or 4th instar in the spring, but do not pupate until midsummer.

Experimental design

We used a fully crossed 2×2 factorial design with repeated measures for protozoa; bacteria and rotifers

were treated as a regular 2×2 design ($n = 15$). The treatment levels were predators (0, 15 mosquito larvae/pitcher) and processing detritivores (0, 16 midge larvae/pitcher). The levels reflect controls and common densities found in field surveys done the week before the experiment (mean ± 1 SE: mosquito 10.5 ± 1.3 , midge 13.9 ± 1.7 , $n = 66$). In late May, we selected 60 healthy undamaged pitchers on separate plants in one bog. We collected the inquiline fluid from the pitchers and rinsed them with deionized H₂O. In the laboratory, we removed the mosquito and midge larvae, filtered out debris, and pooled the fluid to homogenize the microorganisms. Using mosquito and midge larvae and pooled fluid collected that day, we filled 50-mL plastic centrifuge tubes with 15 mL of pitcher fluid (the approximate volume per leaf found in the field), and the treatment levels of dipterans. We added a small amount (<20 mg) of ant bodies to the mixture to ensure adequate C for processing. We transported these tubes to the bog and stocked our previously marked and rinsed experimental pitchers. We covered the pitchers with 1-mm tulle mesh to prevent prey entry or dipteran colonization.

We sampled each pitcher 3 times over a 2-wk period (on days 4, 9, and 13). Because of the short generation times of the microorganisms, this sampling regime allowed ample time for the community to respond to the treatments. Sampling involved gently but thoroughly mixing the community and temporarily pipetting out the pitcher contents. We counted mosquito and midge larvae and adjusted their densities when necessary to maintain the treatments. Small samples (<300 μ L) of well-mixed (homogenous) inquiline fluid were taken for microorganism analysis, and this fluid was not replaced.

We enumerated protozoa and rotifers using Palmer counting cells and a compound microscope (100 \times). From each sample, we pipetted 100 μ L onto a slide and recorded the density of rotifers and protozoa. We identified protozoa to genus (Patterson 1996). Because protozoa taxa vary enormously in size, we calculated the biovolume (μm^3) of all protozoa in each sample on the basis of the density, dimensions, and morphology of each genus present and used this measure of protozoan density as a dependent variable for statistical analyses (Wetzel and Likens 1991).

To estimate bacterial density, we treated a 35- μ L subsample with formaldehyde, stained it with acridine orange, and strained it through a Nuclepore filter (0.2- μm pore size). We counted the stained bacteria on an epifluorescence microscope (Hobbie et al. 1977, Pace 1993). We enumerated bacteria only during the 2nd sampling session. Previous experiments have

shown that bacterial density responds very quickly to treatments and holds relatively constant throughout the duration of a press experiment (Hoekman 2007, DH, unpublished data). Therefore, we believe the bacteria sample collected on this sampling date was representative of the responses of bacterial populations to the treatments.

Statistical analysis

We used 2-way analysis of variance (ANOVA) to evaluate the effects of mosquitoes and midges and their interaction on the density of rotifers and bacteria. We used repeated-measures multivariate analysis of variance (MANOVA) to evaluate the effect of mosquitoes and midges on protozoan biovolume over time. We used post hoc *t*-tests to evaluate the effect of midges on the density of a few common protozoa taxa individually, on the basis of the values for each pitcher averaged over 3 sampling sessions. We $\ln(x)$ -transformed all dependent variables to better meet test assumptions.

We were unable to normalize residuals for the rotifer data for use in a repeated-measures MANOVA because of sparse data (too many 0s), so we averaged values from the 3 sampling sessions to form 1 dependent variable, which we tested with a conventional 2-way ANOVA. We tested each sampling session individually to check for inconsistency between sampling sessions; results did not differ across time or from the average and are not presented.

We also evaluated the response of bacterial populations with a 2-way ANOVA. We evaluated bacterial density only on day 9 of the experiment. Therefore, to compare bacteria results with other response variables, we tested protozoa and rotifer data from the same sample session alone. We found results similar to those with all 3 sampling sessions together.

We used a conservative Bonferroni correction to control type I error ($\alpha = 0.05/3 = 0.017 \approx 0.02$) because we measured 3 populations (dependent variables) from the same community. We used log-response ratios (after Hedges et al. 1999) to measure the magnitude of top-down effects of mosquitoes on lower trophic levels. We used SYSTAT 10 for all tests (SYSTAT; SPSS, Chicago, Illinois).

Results

Protozoa

Time did not influence the strength of the main effects or their interaction (all within-subjects tests: $p > 0.05$, time \times mosquito interaction: $p = 0.27$, time \times mosquito \times midge interaction: $p = 0.10$). After

controlling for type I error, the interaction between mosquitoes and midges was marginally significant ($F_{1,56} = 4.3$, $p = 0.04$; Fig. 1A). Mosquitoes exerted the dominant effect on protozoan biovolume, and the effect of midges depended on mosquitoes. Mosquitoes had a negative effect on average protozoan biovolume ($p < 0.001$, 93% reduction; Table 1, Fig. 1A). When mosquitoes were absent, midges reduced protozoan biovolume ($p = 0.005$, 77% reduction), but mosquitoes overrode the midge effect when present ($p = 0.16$).

Rotifers

The mosquito \times midge interaction was not significant for rotifers ($F_{1,56} = 1.0$, $p = 0.33$). Main-effects tests showed that mosquitoes had a highly significant ($F_{1,56} = 13.9$, $p < 0.001$) negative effect on average rotifer density (83% reduction). Midges also had a marginally significant (overall midge effect, $F_{1,56} = 4.7$, $p = 0.03$) negative effect on rotifers (66% reduction; Table 1, Fig. 1B).

Bacteria

The mosquito \times midge interaction was not significant for bacteria ($F_{1,56} = 1.5$, $p = 0.22$). Main-effects tests showed that mosquitoes had a significant ($F_{1,56} = 6.6$, $p = 0.01$) negative effect on average bacterial density (54% decrease). In contrast, midges had a significant ($F_{1,56} = 7.0$, $p = 0.01$) positive effect on bacterial density (111% increase; Table 1, Fig. 1C).

Discussion

In our study, the effect of midges varied from positive to negative, depending on microorganism taxon, whereas top-down effects of mosquitoes significantly depressed microorganism populations. Both mosquitoes and midges were omnivorous.

Midges have variable effects on microorganism taxa

Midges had a positive effect on bacterial density (Table 1, Fig. 1C), a result that supports hypothesis 1. We expected bacterial density to increase as a result of detritus processing by midges because the comminution of large particles increases surface area for bacterial growth and might release nutrients and DOM (Bradshaw 1983, Crowl et al. 2001). We did not measure nutrient availability directly, but the increase in bacterial density in the presence of detritus processing is consistent with this mechanism and complements previous observational (Trzcinski et al. 2005b) and experimental (Heard 1994a) studies of this community. Furthermore, Bradshaw (1983) demonstrated that pitcher plant midges increase soluble N

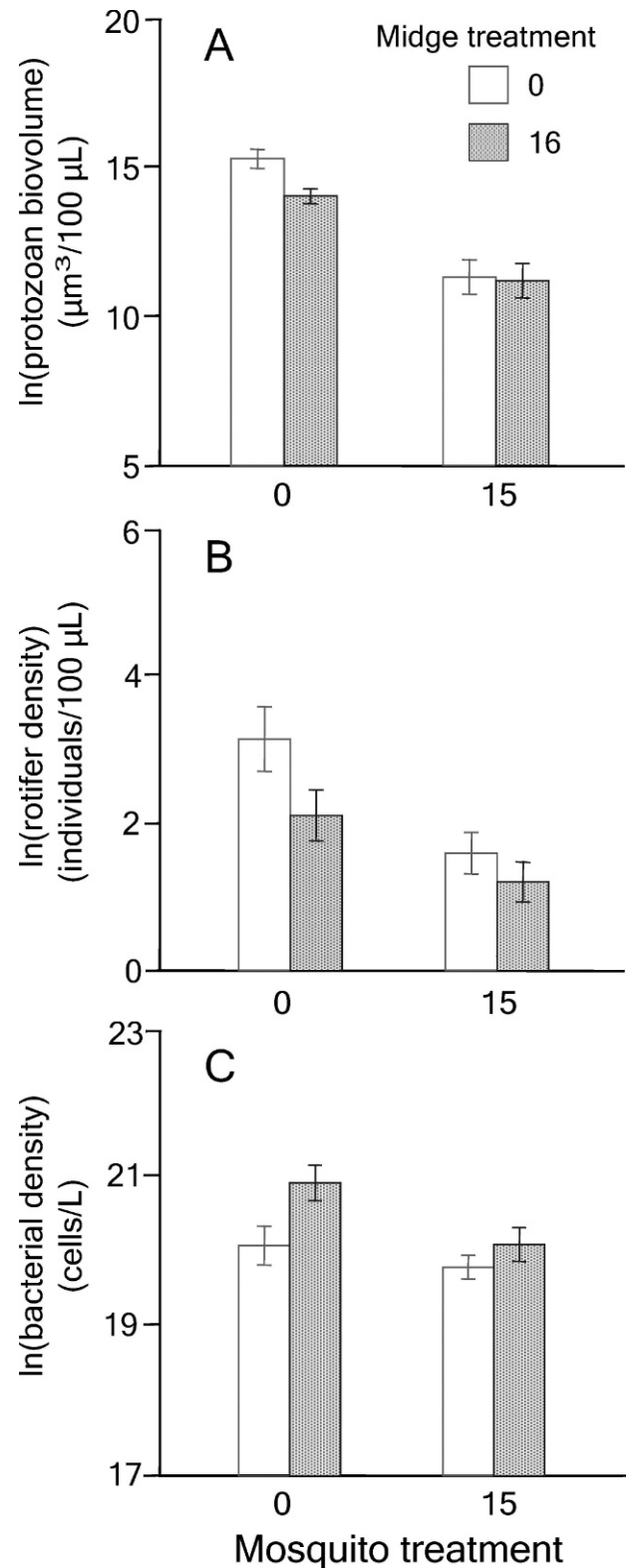


FIG. 1. The effects of midges (0, 16 individuals/pitcher) and mosquitoes (0, 15 individuals/pitcher) on mean (± 1 SE) protozoan biovolume (A), rotifer density (B), and bacterial density (C) in the freshwater environment found in the leaves of the purple pitcher plant (*Sarracenia purpurea*).

TABLE 1. Results of a 2-way repeated-measures multivariate analysis of variance (RM-MANOVA) on protozoan biovolume, and 2-way ANOVA on rotifer and bacterial density. All within-subject effects of the RM-MANOVA and interactions with time were nonsignificant ($p > 0.05$). All dependent variables were $\ln(x)$ transformed.

Population	Source	df	Mean square	F-ratio	p
Protozoa	Midge	1,56	25.0	2.0	0.16
	Mosquito	1,56	570.1	46.6	<0.001
	Midge \times mosquito	1,56	52.3	4.3	0.04
Rotifers	Midge	1,48	7.0	4.7	0.03
	Mosquito	1,48	20.8	13.9	<0.001
	Midge \times mosquito	1,48	1.4	1.0	0.33
Bacteria	Midge	1,48	4.6	7.0	0.01
	Mosquito	1,48	4.4	6.6	0.01
	Midge \times mosquito	1,48	1.0	1.5	0.22

concentrations. Trzcinski et al. (2005b) found a correlation between midge abundance and bacterial density in a survey of pitcher plant communities, and our study demonstrated this bottom-up effect of detritus processing in a field experiment.

Bacterial density also might increase in the presence of midges because of a rotifer-mediated trophic cascade. Rotifer density was reduced in the presence of midges (Fig. 1B), and rotifers consume bacteria. Therefore, the indirect effect of midges on bacteria also might have contributed to the pattern of increased bacterial density in midge treatments. Trophic cascades have been observed in the pitcher plant food web. Bacterial abundance increases when rotifer density is reduced by predators (Kneitel and Miller 2002), but this result appears to be context dependent (Hoekman 2007).

Our results suggest that midges are omnivorous and feed on rotifers and some protozoa while processing detritus. The net effect of midges on protozoan and rotifer populations (most notably rotifers) was negative (Fig. 1A, B), but we expected midges to enhance protozoan and rotifer populations indirectly by promoting bacterial growth. The simplest explanation for the negative effect of midges on rotifers is predation by midges. Paradise and Dunson (1997) suggested that midge larvae in tree holes might be facultative predators. In our samples, rotifers were observed feeding predominantly while attached to detritus. During live counts, we often observed that rotifers were congregated on particulate detritus, a common posture from which a rotifer can filter feed with its foot attached to a substrate. Midges forage in and feed on detritus, and they might consume rotifers coincidentally on a regular basis, thereby decreasing rotifer population density. Trzcinski et al. (2005a) also found a negative ($p = 0.06$) effect of midges on rotifer density in a survey of pitcher plant inquiline communities in Newfoundland.

In contrast to rotifers, most protozoa are distributed throughout the water column and are not congregated where midges are feeding, so we did not expect a negative effect on their populations. However, incidental predation also might affect protozoa, although we did not detect an effect of midges on this diverse group as a whole (Table 1). Some protozoan taxa we encountered are closely associated with detritus (e.g., *Colpoda*), whereas others forage on suspended bacteria in open water (e.g., *Cyclidium*). Post hoc t -tests confirmed that midges have a marginally significant negative effect on detritus-associated *Colpoda* ($p = 0.06$; Fig. 2A), but have no effect on open-water taxa, such as *Cyclidium* ($p = 0.36$) (Fig. 2B) and *Chrysonomas* ($p = 0.21$; Fig. 2C). Therefore, even though midges might consume some protozoa with detritus, other taxa are invulnerable to such predation because of their microhabitat preferences. Microhabitat preference also affects susceptibility to predation in tree-hole detritivore communities. Paradise and Dunson (1997) found that the density of large ciliates (*Colpoda* is a genus of large ciliates) was lower in all insect (consumer) treatments and speculated that being located on leaves or sediment predisposed these ciliates to consumption by aquatic insects. Kaufman et al. (1999) found that the effects of larval mosquitoes on bacterial density depended on the location of the bacteria; bacterial density decreased on leaf surfaces but increased in the water column.

Mosquitoes exert strong top-down effects

In contrast to effects of midges, the effects of mosquitoes were uniformly negative; they depressed populations of protozoa, rotifers, and bacteria (Fig. 1A–C, respectively), a result that strongly supports hypothesis 2. This result is consistent with omnivory of the top predator in this food web, as shown by other studies at this site (e.g., Hoekman

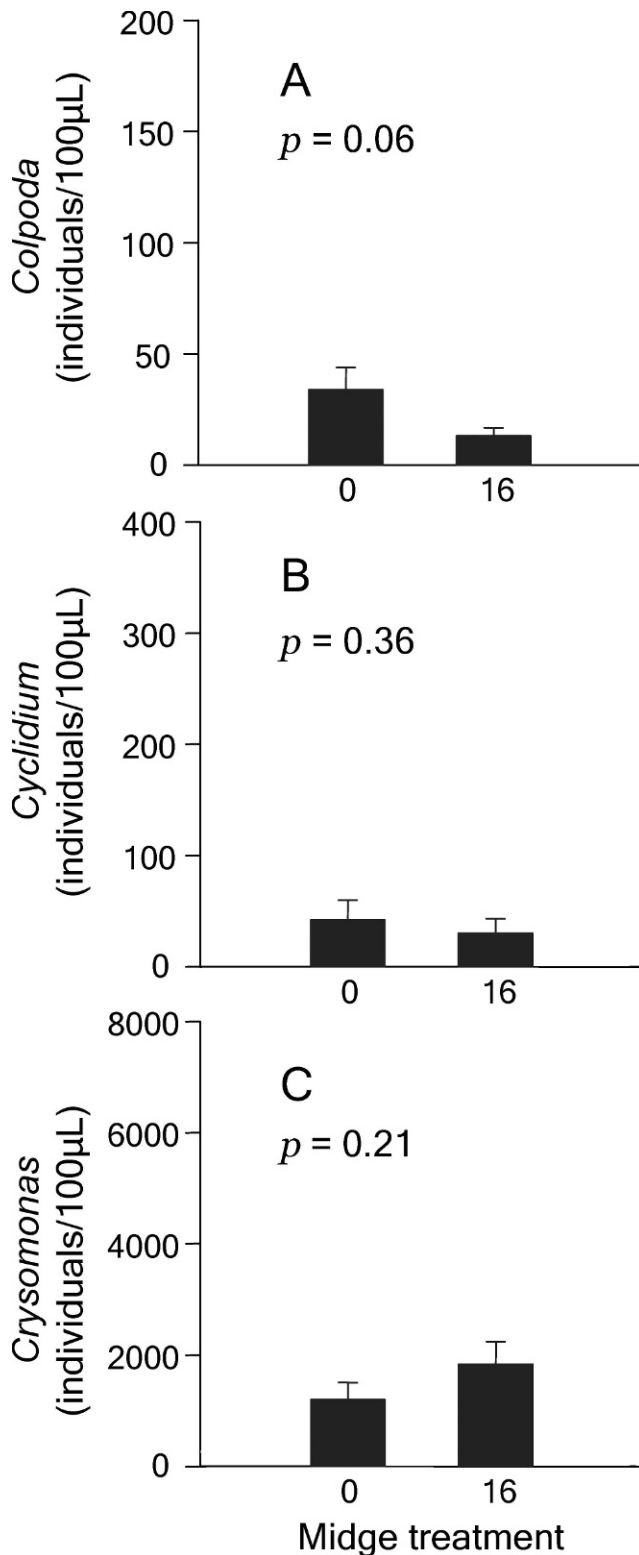


FIG. 2. The effect of midges (individuals/pitcher) on mean (± 1 SE) densities of *Colpoda* (A), a protozoan taxon closely associated with detritus, and *Cyclidium* (B) and *Chrysomonas* (C), 2 protozoan genera that feed in open water. The effect of midges was evaluated using post hoc *t*-tests (*p*-values shown on plots).

2007) and confirms strong top-down effects of the pitcher plant mosquito shown in other field (Kneitel and Miller 2002, 2003) and laboratory (Cochran-Stafira and von Ende 1998) studies. The effects of mosquitoes and midges were largely independent, a result that supports hypothesis 3, except in the case of protozoa (Table 1, Fig. 1A).

Attenuating top-down and bottom-up effects

We expected top-down effects to be stronger on bacterivorous protozoans and rotifers than on bacteria, i.e., to attenuate down the food web. In support of hypothesis 4, the mosquito effect was strongest for protozoa (-2.8) and rotifers (-1.8) and weaker for bacteria (-0.8) (effect sizes cf. Hedges et al. 1999). This result probably was a consequence of the larger body size of protozoa and rotifers. These larger prey are more readily captured by the filter-feeding mosquito than are smaller prey, and their population growth rates are slower than are bacterial growth rates (Ellison et al. 2003). Therefore, the potential for rotifer and protozoan populations to counteract the negative effect of predation via reproduction is limited relative to that of bacteria and might explain why top-down effects of an omnivorous predator attenuate down the food chain in this system. We also expected bottom-up effects to attenuate up the food chain; i.e., we expected the bottom-up effect of detritus processing to be stronger on bacteria and weaker on protozoans and rotifers that are farther removed trophically from detrital resources. The bottom-up effect of detritus processing was detected at the base of the food web, but it was not detected at higher trophic levels (protozoa and rotifers), a result that also supported hypothesis 4.

Omnivorous processing detritivores

Our study shows that processing detritivores can promote bottom-up effects as hypothesized, but that they also can exert top-down effects on other detritivores. Our results are broadly applicable to aquatic detritus-based systems. Processing detritivores accelerate decomposition and promote bottom-up effects in streams (Cummins et al. 1973, Short and Maslin 1977). In tree holes, scirtid beetles facilitate microorganisms and their consumers by processing detritus (mainly leaf litter) (Paradise and Dunson 1997, Paradise 1999, Daugherty and Juliano 2002). Processing detritivores might benefit consumers of fine particulate material via a processing chain (sensu Heard 1994b), but our study suggests that omnivory by processing detritivores might result in a net negative effect on some smaller consumers that

benefit indirectly from detritus processing but also experience direct predation pressure.

Omnivory is a common feature of detritus-based food webs and the process of decomposition (Thompson et al. 2007). For example, in stream systems, bacteria and fungi colonize leaves and begin decomposition by forming a biofilm. Conditioned leaves are selectively consumed by larger macroinvertebrates (shredders) that further enhance decomposition while feeding on the biofilm consisting of many smaller detritivores (e.g., bacteria, fungi, protozoa, rotifers, microarthropods) (Cummins and Klug 1979). In some cases, shredding macroinvertebrates are, in turn, vulnerable to predation by omnivorous crayfish that also shred leaves (Usio 2000). Thus, omnivory and the presence of top-down effects appear to be commonplace in the process of decomposition in any detritus-based food web where macrodetritivores consume microdetritivores associated with detritus. Schröter and Dekker (2005) use the term panphytophagous to refer to an organism that feeds on both detritus and microorganisms. In reality, detritus and the detritivore community are often completely intertwined, making detritivore omnivory inevitable (Maltby 1992).

Conclusion

We conclude that the effects of the top predator are uniformly strong in the pitcher plant system. In addition, the detritus processing action of the pitcher plant midge had significant bottom-up effects by increasing bacterial density, the primary resource for other consumers in the food web. Top-down effects were stronger at the top of the food web (i.e., mosquitoes had stronger effects on protozoa and rotifers than on bacteria), whereas bottom-up effects were stronger at the bottom of the food web (i.e., midges had positive effects on bacteria, but not on higher trophic levels). The role of the processing detritivore was complicated by its coincidental predation of microorganisms associated with detritus. Processing detritivores might promote bottom-up effects by increasing resource availability, but they also might contribute to top-down effects by consuming other species. The perspective gained from this model system suggests that processing detritivores maintain an omnivorous diet that complicates their ecological role.

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