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## Trophic interactions in open systems: Effects of predators and nutrients on stream food chains

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### Abstract

Theory and empirical work on food chains has focused primarily on closed, equilibrial environments. We tested the combined effects of secondary consumers (fish) and limiting nutrients (nitrogen) on intermediate trophic levels in an open stream environment, where flow redistributes organisms and materials among patches of streambed habitat. Fish reduced the biomass of the dominant herbivore (baetid mayflies) within habitat patches both by direct predation and by causing increased emigration from the patches. The resulting decrease in herbivory caused an increase in the growth and biomass of primary producers (algae) in areas containing fish. Independent of the effect of fish, algal growth and biomass was increased by augmenting the nutrient supply to patches. Nutrient-enriched areas (with high algal biomass) also supported greater populations of herbivores because they either grew faster in these areas or emigrated less frequently from them. Controlling influences on trophic structure came from both the top and the bottom of the food chain, and these influences were not conditional upon one another. Trophic structure in this system was determined by a mix of behavioral and trophic interactions between the major taxa, most of which were specific to open systems and not predicted by conventional theory.

Ecologists have focused much attention on predicting the relative biomass of organisms at different trophic levels in systems where food webs can be represented as simple chains (McNaughton et al. 1989; Brett and Goldman 1996). A central, and controversial, issue in this literature is defining the relative effects of control from the top of the food chain by predators, and control from the bottom by nutrients, or other resources limiting primary production (Carpenter et

al. 1987; McQueen et al. 1989; Power 1992; Menge 1992; Strong 1992; Polis and Winemiller 1996). Although there is general agreement that both top-down and bottom-up forces are likely to operate in most ecosystems (Carpenter et al. 1987; McQueen et al. 1989; Power 1992; Menge 1992; Strong 1992; Polis and Winemiller 1996; Hunter et al. 1997), surprisingly few studies have tested the simultaneous influences of predators and nutrients so that the nature of their effects can be compared directly. Of the tests that have been conducted, most were done in the pelagic zone of lakes (Brett and Goldman 1997) and very few have been done in other habitats (Hartvigsen et al. 1995; Osenberg and Mittelbach 1996; Stiling and Rossi 1997).

Pelagic communities in lakes are relatively self-contained and can reasonably be considered as closed equilibrial systems at the time scales over which most food-web studies are performed (Brett and Goldman 1997). Results of empirical food-chain manipulations can thus be compared to the predictions of conventional food-chain theory that forecasts outcomes only for closed systems that have reached a stable equilibrium ( Hairston et al. 1960; Fretwell 1977; Oksanen

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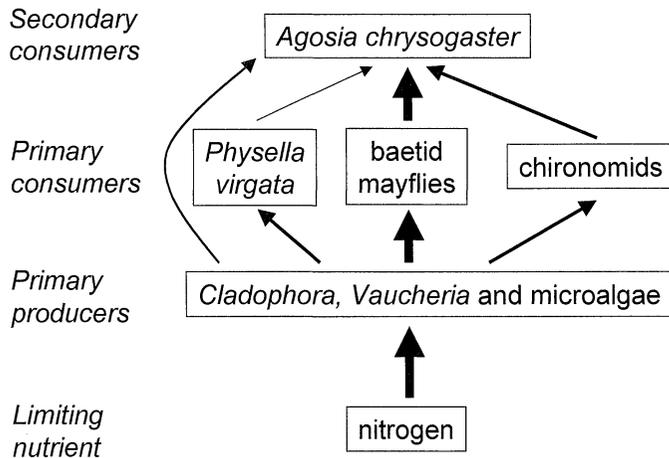


Fig. 1. Dominant taxa in run habitats in Sycamore Creek during spring and early summer. Various predatory invertebrates were also present, but their combined biomass never exceeded 14.9% of the biomass of *Agosia* during the study. Many other herbivorous invertebrates and other primary producers were also present, but all were also relatively rare. None of these taxa were affected by the experimental manipulation. Baetid mayflies are *Fallceon quilleri* (94% by mass) and *Callibaetis montanus* (6% by mass), both of which responded in the same way to the experimental treatments. Arrows indicate consumption of one taxon by another (or uptake by primary producers, in the case of nutrients). Wider arrows denote interactions that were quantitatively more important during our study than those represented by narrower ones.

et al. 1981). Many ecological communities are, however, open and/or nonequilibrium (Pickett and White 1985; DeAngelis and Waterhouse 1987), and there is growing evidence that local food webs are strongly influenced by the exchange of materials and organisms with adjacent habitats (Bustamante et al. 1995; Polis and Hurd 1996; Menge et al. 1997a). Recent theoretical analyses predict that the effects of consumers and resources on food chains in open systems may differ from those in closed systems (Nisbet et al. 1997), but there is very little empirical information that can be used to test those predictions. Here we present one of the first studies testing the combined effects of predators and nutrients on community organization in an open system.

Our study was completed in Sycamore Creek, a perennial desert stream in central Arizona. Like most streams, Sycamore Creek consists of a loosely alternating sequence of habitat patches (mostly gravelly runs and pools with sandy sediments [Grimm and Fisher 1989]) among which organisms are continually redistributed by stream flow. The stream is scoured by winter spates and summer flash floods (Boulton et al. 1992) and also dries to become spatially intermittent in late summer (Stanley et al. 1997). Recovery from these disturbances is rapid because primary (Grimm and Fisher 1989) and secondary (Jackson and Fisher 1986) production rates are high, and the fauna is dominated by species with short life spans and good recolonizing ability (Gray 1981; Gray and Fisher 1981). The pattern of succession following disturbance is quite variable and depends on season, nutrient levels, and the nature of disturbance (Grimm and Fisher 1989; Boulton et al. 1992). As a result of the linkages

among neighboring habitat patches and frequent disturbances to the system, the streambed community in Sycamore Creek is open and unlikely to reach equilibrium. We simultaneously manipulated top predators and limiting nutrients (Grimm and Fisher 1986) within patches of the major habitat type (gravelly runs). Our aim was to test their relative effects on intermediate trophic levels and to identify mechanisms for effects that are specific to open systems.

### Experimental design

Our study was done in spring and early summer (27 May–13 July 1991), and we summarize the trophic relationships of the dominant biota present at this time in Fig. 1 (Boulton et al. 1992; Peterson 1996). The density of long fin dace (*Agosia chrysogaster*), the dominant predatory fish (present and absent), and the supply of nitrogen (ambient and augmented) were manipulated in a factorial design, with six replicates of each of the four treatment combinations. The replicate patches of habitat were rectangular enclosures (5 m long  $\times$  0.4 m wide) that were set into the streambed 2 weeks before the start of the experiment. The enclosures had walls on their sides and ends but were open on the top and bottom. The enclosure walls extended 30 cm above the surface of the water and 10 cm into the streambed. The sidewalls that ran parallel to the flow were made of solid plastic, whereas the upstream and downstream ends were made of Vexar (3-mm plastic mesh) to allow natural flux of organisms and materials. The mesh was cleaned two to three times each day during the experiment to prevent clogging with debris. Mean water depth in the enclosures was 12 cm, and the mean flow rate through them was  $0.13 \text{ m s}^{-1}$ .

To establish the treatments, *Agosia* were stocked in the predators-present enclosures at a density of five per  $\text{m}^2$ . Electrofishing surveys indicated that this density was slightly below the ambient density in the stream at the beginning of the experiment ( $5.9 \text{ per m}^2$ ). Nitrogen levels in the nutrient-addition enclosures were augmented by setting up a continuous drip feed of nitrate in solution (as  $\text{NaNO}_3$ ) from reservoirs on the stream bank. To assess the effectiveness of the nutrient addition, we took four water samples from each enclosure for nitrate analysis on day 29 of the experiment. We used established methods for taking water samples and determining the concentration of dissolved nitrate in the stream (Wood et al. 1967; Grimm 1987). Nitrate concentrations were raised from a mean of  $0.09 \text{ mg liter}^{-1}$  ( $\pm 0.05 \text{ mg liter}^{-1}$  standard error [SE]) in the ambient enclosures to  $0.76 \text{ mg liter}^{-1}$  ( $\pm 0.1 \text{ mg liter}^{-1}$  SE) where nutrients were added.

### Effects of predators and nutrients on herbivores

To assess the effects of the treatments on the biomass of herbivores we took two cores (area =  $78.5 \text{ cm}^2$ , depth = 5 cm) of sediment per enclosure on each of three dates. Invertebrates in the cores were counted using a dissecting microscope, after sieving one core through a 0.125-mm screen (to count all taxa) and the second core through a 2.8-mm screen (to get more accurate counts for large, rare taxa). Subsamples of each taxon were measured (body length), and

Table 1. Results of repeated-measures MANOVA testing for effects of the treatments on the benthic biomass of herbivores and algae. Significant *F*-values are indicated as follows: \**P* < 0.05, †*P* < 0.01, ‡*P* < 0.001.

Treatment	df	<i>F</i> -value and significance			
		Baetids	Chironomids	Snails	Algae (Chl <i>a</i> )
Fish	1, 12	17.8‡	4.21	0.27	11.5†
NO <sub>3</sub>	1, 12	5.91*	0.4	5.88*	11.1†
Fish × NO <sub>3</sub>	1, 12	0.16	1.86	0.1	1.48
Time	2, 11	142.3‡	80.0‡	35.3‡	97.5‡
Time × fish	2, 11	14.5‡	5.88*	0.03	5.25*
Time × NO <sub>3</sub>	2, 11	1.19	6.46*	2.99	3.28
Time × fish × NO <sub>3</sub>	2, 11	0.22	1.12	0.16	3.03

the biomass in each enclosure was estimated using length-weight regressions. Treatment effects were tested using repeated-measures analyses of variance (ANOVA). We used the multivariate approach (MANOVA) to repeated measures, because it makes less restrictive assumptions about the data than univariate approaches (Johnson and Wichern 1998). Inspection of normal probability plots and cell means and variances was used to check assumptions of normality and homoscedasticity. Data were occasionally log transformed in order to better meet those assumptions. We were primarily interested in the occurrence of treatment effects, not their precise temporal development during the experiment. For this reason, when effects of nutrients or predators occurred at some times but not others (as indicated by significant interactions with sampling date in the MANOVA) we conducted univariate ANOVA tests on separate dates simply to get a rough idea of when during the experiment effects occurred. In some cases, we pooled nonsignificant interaction terms (which explained <5% of variance and for which *P* > 0.25) in order to allow more powerful tests for main effects of fish and nutrients (Winer et al. 1991).

The three dominant herbivores in the system were each affected differently by the treatments (Table 1, Fig. 2). Baetid mayflies were by far the most abundant herbivore present (Fig. 2) and comprised 73% of the benthic community by mass at the end of the experiment. The benthic biomass of baetids was both reduced in the presence of fish and increased by nutrient supplementation (Table 1, Fig. 2). Repeated-measures MANOVA indicated that these effects were not conditional on each other, in that the influence of fish did not depend on nutrient levels and vice versa (tests for interactions were nonsignificant, see Table 1). The reduction in baetid biomass by fish was, however, not consistent throughout the experiment, as indicated by a significant fish × time interaction term in the MANOVA (Table 1). Analyses of the data for each date separately showed that the interaction occurred because baetid biomass was lower in the presence of fish on days 33 ( $F_{1,12} = 26.0, P < 0.0004$ ) and 46 ( $F_{1,12} = 21.9, P < 0.0004$ ) of the experiment, but there was no detectable effect earlier in the experiment (day 16:  $F_{1,18} = 0.81, P > 0.05$ ) (Fig. 2).

Herbivorous chironomid midge larvae were the second most abundant herbivores, comprising 5% by mass of the

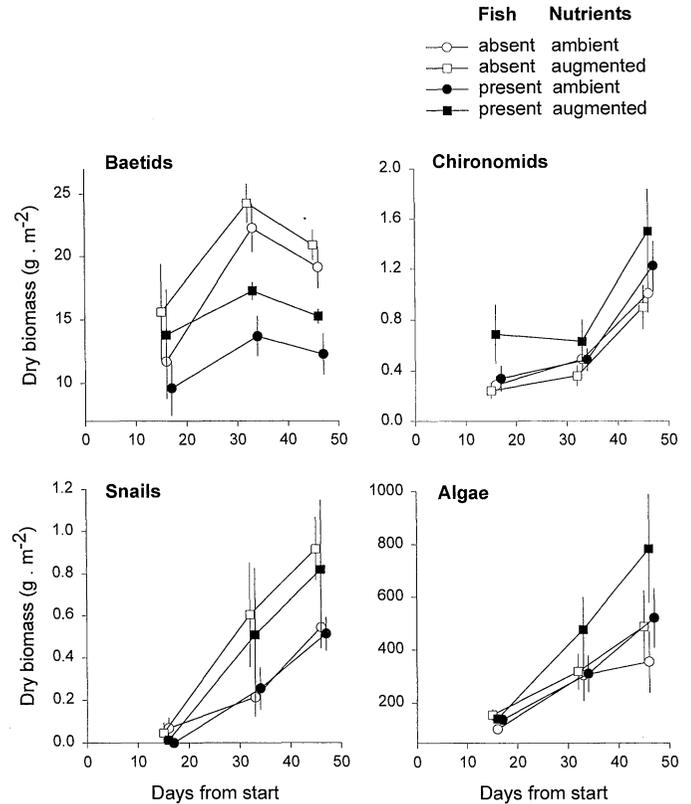


Fig. 2. Effects of predatory fish and nutrient addition on the mean biomass ( $\pm$  standard errors) of dominant taxa in Sycamore Creek.

community on day 46 of the experiment. Effects of the treatments on chironomid populations were relatively modest (Table 1, Fig. 2). Chironomid biomass was slightly elevated in enclosures containing fish (Fig. 2), but this enhancement was not detectable on all sample dates (Table 1). Separate analyses of the data at different points during the experiment revealed statistically significant increases in chironomid biomass caused by fish early (day 16:  $F_{1,14} = 4.92, P < 0.05$ ) and late in the experiment (day 46:  $F_{1,18} = 4.97, P < 0.05$ ) but not in the middle (day 33:  $F_{1,18} = 2.39, P > 0.05$ ). Statistical analyses also indicated a possible influence of supplemental nutrients on chironomid biomass, based on a significant NO<sub>3</sub> × time interaction in the MANOVA (Table 1). Analyses on individual dates were, however, all nonsignificant ( $F_{1,18} < 1.84, P > 0.05$ ), leading us to conclude that any effect was minor (Fig. 2). The third major herbivore (3% by mass on day 46), a grazing snail (*Physella virgata*), showed a substantial increase in abundance in response to nutrient supplementation but was unaffected by the predator manipulation (Table 1, Fig. 2).

#### Effects of predators and nutrients on primary producers

Algal biomass was estimated by measuring the chlorophyll *a* (Chl *a*) content of three replicate cores (area = 26 cm<sup>2</sup>, depth = 2 cm) per enclosure. Samples were taken on

three dates using established sampling methods and analytical procedures (Tett et al. 1977; Grimm 1987). The biomass of primary producers was increased in the presence of fish and was also increased by nutrient augmentation, though the effect of fish was not consistent across all sampling dates (Table 1, Fig. 2). The effect of fish on algal biomass followed a similar temporal pattern to the effect on baetids, in that it was statistically significant only late in the experiment (ANOVA on day 16:  $F_{1,12} = 0.56$ ,  $P > 0.05$ ; ANOVA on day 33,  $F_{1,12} = 3.26$ ,  $P > 0.05$ ; ANOVA on day 46,  $F_{1,12} = 8.45$ ,  $P < 0.05$ ). Repeated-measures MANOVA also indicated that the effects of fish and nutrients were not conditional upon one another, because tests for interactions were nonsignificant (Table 1).

We also made visual estimates of the percent cover of the macroscopic primary producers present in each enclosure on days 15, 32, and 44 of the experiment. *Cladophora glomerata* was the dominant macroalga present and occurred in the enclosures throughout the experiment. In contrast, *Vaucheria* sp. was observed only on the first two sampling dates. In the later stages of the experiment, macrophytes and macroscopic cyanobacteria (*Nostoc* sp.) colonized the enclosures at low levels. None of these primary producers differed in percent cover among treatments (repeated-measures MANOVA,  $P$  always  $> 0.05$ ) except that, by day 44, aquatic macrophytes were more abundant in enclosures with added nitrate (mean cover =  $1.65\% \pm 1.1\%$  SE) than in enclosures with natural nitrate levels (mean cover =  $0.0\% \pm 0.0\%$  SE) (ANOVA,  $F_{1,18} = 16.6$ ,  $P < 0.01$ ). The lack of treatment effects on the other dominant macroalgae, despite the strong effects on Chl *a* levels, may be because percent cover estimates are poor indicators of biomass. We did observe, for example, that the *Cladophora* in the enclosures with ambient nutrient levels was beginning to senesce toward the end of the experiment, while the *Cladophora* in the enclosures receiving supplemental nitrate continued to appear healthy. Another possibility is that predators and nutrients might have exerted their effects primarily on microalgae (mainly diatoms) that occur as films on the gravel and later also as epiphytes on the macroscopic algae. Unfortunately, our samples of microalgae were lost, so we were not able to examine the microalgal community directly.

### Mechanisms for effects of predator and nutrients

Following any manipulation of an intact community, it is always difficult to pinpoint the causes of changes in the abundance of a given species. There are usually many possible direct and indirect interactions that can produce similar net effects on the abundance of a focal species (e.g., Adler and Morris 1994; Billick and Case 1994; Wootton 1994). We attempted to gain insight into the possible mechanisms for the treatment effects by measuring some of the processes directly affecting the biomass of herbivores and algae in the enclosures, namely the rates of predation on herbivores and the rates of dispersal into and out of the enclosures. We note, though, that there were other processes that we did not account for. Populations of algae and all three herbivores were growing rapidly for most of the experiment and have gen-

eration times substantially shorter than the duration of the experiment (Gray 1981). They were thus undoubtedly experiencing major gains from reproduction that we did not measure and experiencing losses to mortality factors other than predation and to emergence into flying adults for baetids and chironomids.

We estimated the predation rates of *Agosia* in the enclosures by analyzing the stomach contents of 33 *Agosia* collected from the enclosures. These fish were replaced with *Agosia* captured from the stream to maintain the predation treatment at a constant level. We collected *Agosia* from several enclosures at various times during the study in an opportunistic, haphazard manner so the estimates of predation rate are rough approximations. Baetids and chironomids comprised 41% and 4% by mass of the stomach contents of the sampled *Agosia*, but we found very few snails in the stomachs of the fish (0.01% by mass). The mass of baetids and chironomids consumed per *Agosia* in 24 h was estimated using a simple model (Elliott and Persson 1978) that uses the dry mass of prey in the foregut (calculated using the 33 *Agosia* sampled from the enclosures) and the gut evacuation rate (from a previous study [Grimm 1988]). The 24-h consumption rate was multiplied by the number of fish in each enclosure and divided by the benthic biomass at different times during the experiment to calculate the percentage of the benthic population consumed in 24 h.

Many stream invertebrates redistribute themselves by departing the sediments to drift short distances downstream in the water column (Bird and Hynes 1981; Bergey and Ward 1989), and benthic algae can also be transported among sites in this manner (Stevenson and Peterson 1991; Peterson 1996). Previous studies indicate that drifting accounts for most movement among habitat patches by baetids and chironomids (Bird and Hynes 1981; Bergey and Ward 1989). We therefore quantified the rate at which baetids and chironomids drifted into and out of the enclosures by placing drift nets (mesh size = 0.125 mm, square mouth =  $0.2 \times 0.2$  m, length = 1 m) to intercept the flow at their upstream or downstream end. Drift out of the enclosures was sampled on three dates, whereas drift into the enclosures was sampled only once (on day 32). We sampled for 2 h during the day and 2 h after dark on each date. Assuming that these 2-h samples were representative of daytime and nighttime drift rates respectively, we extrapolated from the daytime sample to estimate the number of invertebrates collected over the entire day and made a similar extrapolation from the nighttime sample. The sum of the daytime and nighttime estimates provided a measure of the 24-h drift rate. This 24-h rate was divided by the benthic biomass at the time to estimate the percentage of the population migrating per 24 h. When testing for treatment effects on drift emigration, we analyzed each date separately because logistical constraints limited us to sampling only 18 of the 24 enclosures on two of the three sampling dates.

We were unable to measure microalgal drift but did quantify the loss rate of macroalgae from the enclosures. Macroalgal loss rates were estimated by measuring the dry weight of algae that accumulated on the mesh forming the downstream wall of the enclosure during 24 h. Collections of drifting algae were made on eight dates that were grouped



Table 3. Results of ANOVAs testing for treatment effects on immigration into the enclosures by baetids and chironomids. Significant *F*-values are indicated as follows: \**P* < 0.05.

Taxon	Treatment	Drift immigration (g 24 h <sup>-1</sup> )		Per-capita drift immigration (% 24 h <sup>-1</sup> )	
		df	<i>F</i>	df	<i>F</i>
Baetids	Fish	1, 12	0.3	1, 12	7.82*
	NO <sub>3</sub>	1, 12	0.5	1, 12	4.12
	Fish × NO <sub>3</sub>	1, 12	0.98	1, 12	1.47
Chironomids	Fish	1, 12	2.53	1, 12	0.59
	NO <sub>3</sub>	1, 12	1.04	1, 12	0.03
	Fish × NO <sub>3</sub>	1, 12	0.1	1, 12	0.25

into three intervals corresponding to the three dates on which benthic algae were sampled. For each time interval, we then divided the mean mass of drift algae collected per 24 h by the benthic biomass to give the percentage of algae drifting in 24 h. To make this calculation, we converted Chl *a* measurements of benthic algae to dry biomass, assuming that algae is 0.3% chlorophyll (Reinertson et al. 1990).

Our estimates of predation rates indicate that baetid mayflies, were being consumed by *Agosia* at modest rates

throughout the experiment (Table 2). Absolute rates of drift immigration, measured on day 32, were similar into all of the enclosures (Table 2) and did not differ significantly among the treatments (Table 3). Per-capita immigration on this date was, however, higher into enclosures with fish than into predator-free enclosures (Tables 2, 3). It is unlikely that baetids alter their drifting behavior in response to conditions downstream of them. Instead, this relationship is almost certainly a simple numerical consequence of the fact that densities of baetids were reduced in the presence of fish, causing immigration to be higher on a per-capita basis. This sort of density dependence in immigration can have a strong regulatory effect on local density (Hughes 1990). Models of predator-prey interactions in patchy open systems indicate that, when dispersal rates are high, immigration can swamp local effects of predators on prey abundance (Cooper et al. 1990; Sih and Wooster 1994; Englund and Olsson 1996; Englund 1997). The models suggest that immigration rates of baetids were not high enough to have this effect (Sih and Wooster 1994; Englund 1997), and clearly, it did not occur in our experiment. Importantly, baetids also increased their rate of drift emigration in response to *Agosia* (Table 4). This type of behavioral adjustment to predators will increase the net reduction in local prey abundance caused by predators (Forrester 1994; Sih and Wooster 1994; Englund 1997). The extent to which baetids increased their per-capita rate of drift emigration in the presence of fish (3.3% on day 16, 6.2% on day 33, and 1.4% on day 46) was roughly equal to the rate at which baetids were being consumed by fish (4.6% on

Table 4. Results of analyses testing for effects of the treatments on rates of per-capita emigration by drifting from the enclosures. For baetids, we present the results of ANOVA testing for effects of predators and nutrients and ANCOVA that also includes tests for a relationship between drift rates and the biomass of algae in enclosures. The ANCOVA for baetids on day 15 is presented after the removal of nonsignificant interaction terms (*P* > 0.25) (Winer et al. 1991). Significant *F*-values are indicated as follows: \**P* < 0.05, †*P* < 0.01, ‡*P* < 0.001.

Taxon	Treatment	Day 15		Day 28		Day 44	
		df	<i>F</i>	df	<i>F</i>	df	<i>F</i>
Baetids—ANOVA	Fish	1, 9	33.1‡	1, 8	22.8‡	1, 12	6.93*
	NO <sub>3</sub>	1, 9	38.0‡	1, 8	3.96	1, 12	7.58*
	Fish × NO <sub>3</sub>	1, 9	17.5†	1, 8	0.61	1, 12	0.05
Baetids—ANCOVA	Fish	1, 12	6.21*	1, 8	6.95*	1, 16	34.9‡
	NO <sub>3</sub>	1, 12	0.86	1, 8	0.47	1, 16	2.35
	Algae	1, 12	20.7‡	1, 8	11.7†	1, 16	9.90†
	Fish × NO <sub>3</sub>	—	—	1, 8	6.97*	1, 16	4.45
	Fish × algae	—	—	1, 8	0.97	1, 16	21.2‡
	NO <sub>3</sub> × algae	—	—	1, 8	0.24	1, 16	0.38
	Fish × NO <sub>3</sub> × algae	—	—	1, 8	5.27*	1, 16	9.23†
Chironomids—ANOVA	Fish	1, 11	0.04	1, 11	0.94	1, 18	7.81*
	NO <sub>3</sub>	1, 11	0.35	1, 11	1.59	1, 18	0.02
	Fish × NO <sub>3</sub>	1, 11	1.99	1, 11	0.97	1, 18	0.18
Macroalgae—ANOVA	Fish	1, 12	1.47	1, 12	0.07	1, 12	3.59
	NO <sub>3</sub>	1, 12	0.53	1, 12	1.06	1, 12	8.35*
	Fish × NO <sub>3</sub>	1, 12	0.7	1, 12	0.09	1, 12	0.94

Table 5. The relative strength of top-down and bottom-up effects on the benthic biomass of baetids and algae. Displayed are the changes in biomass from the natural condition (fish present, ambient nutrients) due to removing limitation from the top of the food chain (fish absent, ambient nutrients), removing limitation from the bottom (fish present, augmented nutrients), and removing both limits (fish absent, augmented nutrients).

Taxon	Treatment	Effect on benthic biomass (% difference)		
		Day 16	Day 33	Day 46
Baetids	Limitation by fish removed	21.9	62.2	55.2
	Limitation by nutrients removed	43.6	25.8	24.0
	Both limits removed	62.3	76.7	69.7
Algae (Chl <i>a</i> )	Limitation by fish removed	-25.6	-1.9	-32.0
	Limitation by nutrients removed	2.4	53.7	50.6
	Both limits removed	13.0	2.6	-6.4

day 16, 2.2% on day 33, and 1.2% on day 46). This suggests that the predator-induced increase in emigration displayed by baetids contributed substantially to the reduction of baetid biomass in enclosures containing fish. Adjustments in drift emigration are also likely to have contributed to the increased abundance of baetids in nutrient-supplemented areas. The mayflies drifted at lower rates from these enclosures (Tables 2, 5) that would cause them to accumulate there. We suspected that this adjustment in drift behavior was actually a response to higher algal abundance in nutrient-supplemented enclosures. To test for this, we performed analyses of covariance (ANCOVA) testing for a relationship between baetid emigration and algal biomass (a covariate), in addition to any effects of predators and nutrients (categorical factors). On all three dates, there was an overall negative relationship between baetid drift rates and algal biomass (Table 4, Fig. 3), and there were no significant effects of nutrient augmentation once the relationship with algal biomass was accounted for. These results support our contention that baetids were responding to levels of algal food in the enclosures. The ANCOVA also confirmed that baetids generally emigrated at higher rates from enclosures occupied by fish, independent of the level of algal food (Table 4, Fig. 3). On the second and third sampling dates, the analyses also detected three-way interactions between the influences of fish, nutrients, and algal biomass (Table 4). We suggest that these interactions do not alter the general conclusions that we have made about baetid drift responses and believe that they arose because, on both dates, one of the treatments displayed a relationship with algal biomass that differed in slope from the slopes of the other three relationships (Fig. 3).

The per-capita rate at which macroalgae drifted out of enclosures was generally quite similar among treatments (Table 2), and there were no detectable effects of predators or nutrients (Table 4). The net growth rate of algae in the enclosures, calculated assuming a linear increase in biomass over time between the first and last sampling dates (see Fig. 2), was greater than the rate of loss by drifting on the first two sample dates and roughly equal to the drift rate on the final date (Table 2). The fact that the rate of accumulation of algal biomass in the enclosures was always at least as high as the turnover from drifting precluded a swamping

effect of immigration (*sensu* Cooper et al. 1990) and suggests that the effects of predators and nutrients on algal biomass were primarily the result of interactions occurring largely within the enclosures. Increased algal biomass in the presence of fish thus occurred because fish reduced the biomass of the dominant herbivore (baetids) that in turn allowed increased algal growth. Similarly, nutrient augmentation increased algal biomass simply by causing higher algal growth rates in the enclosures to which nitrate was added.

Mechanisms for some of the effects of predators and nutrients on chironomids and snails are more difficult to pinpoint. Drift-immigration rates of chironomids were unrelated to the experimental treatments when measured on both an absolute and per-capita basis (Tables 2, 3). Chironomids also showed little tendency to adjust their drift-emigration rate in response to conditions in the enclosures. The only statistically significant response revealed by ANOVA was a slight decrease in drift emigration from enclosures containing fish that was observed on the last sampling date (Tables 2, 5; Fig. 3). Chironomids were consumed by *Agosia* during the experiment at rates slightly higher than those estimated for baetids (Table 2), whereas rates of drift migration were slightly lower overall than those displayed by baetids (Table 2, Fig. 3). If predation by fish and migration by drifting were the only two processes influencing chironomid abundance, simple models for predator impacts in open systems predict that fish predation would significantly reduce the density of chironomids in enclosures (Englund 1997). The fact that the biomass of chironomids was actually slightly higher in enclosures with fish than in fishless enclosures cannot thus be explained in these terms. One alternative explanation is that local population growth of chironomids increased in enclosures occupied by fish because of the elevated algal biomass in these enclosures. In other words, although chironomids were too rare to have impacted algal biomass themselves, they may have benefited from the increase in algal resources generated by the trophic cascade involving fish and baetids.

*Physella* was rarely observed to disperse by drifting but shows very rapid growth and reproduction. We therefore assume it increased in biomass in nutrient-supplemented enclosures due to rapid local population growth. We consider it most likely that this response occurred because nutrient-

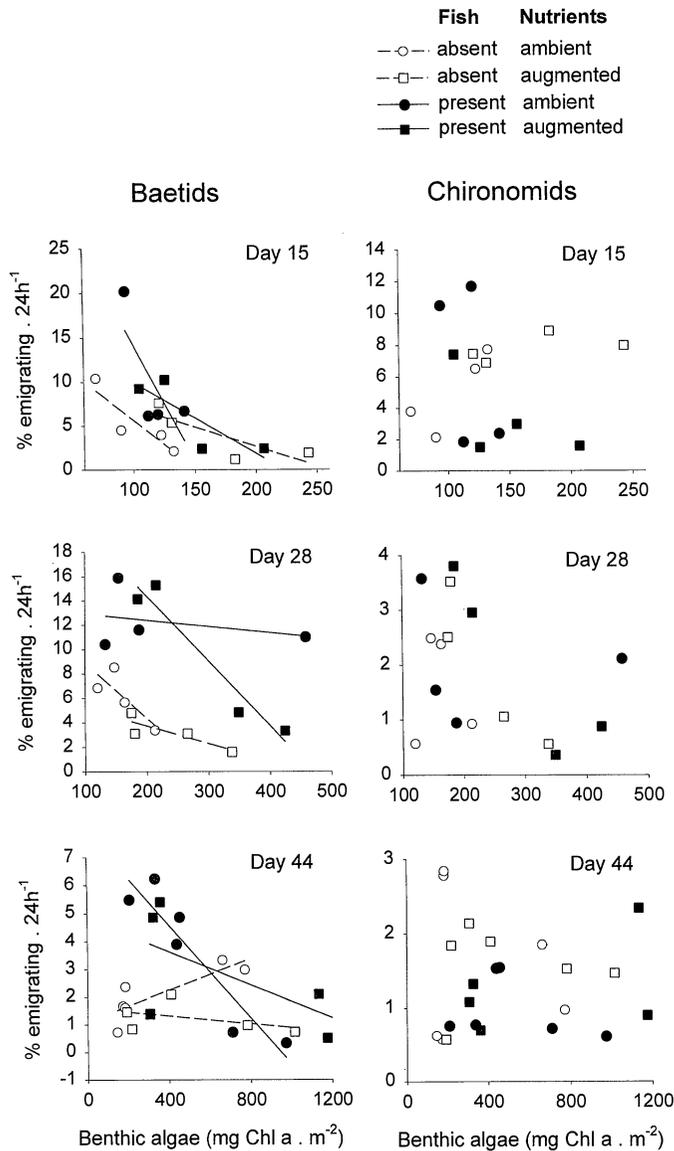


Fig. 3. The relationship between per-capita emigration by drifting of two herbivores and the benthic biomass of algae. Relationships are displayed under different combinations of predator presence and nutrient supply. Linear regressions for each treatment combination are shown for baetids.

supplemented sites supported algal food in greater quantity and/or of better quality than sites with ambient nutrient levels. If this explanation is correct, we might have expected a corresponding increase in snail biomass in enclosures with fish, due to the greater supply of algal food they supported. Increasing the likelihood of such a response is the fact that *Physella* was rarely consumed by *Agosia* during the experiment and so suffered negligible mortality from predation. No increase in snail biomass was, however, observed in the presence of fish. One possible explanation is that *Physella* are known to lower their grazing rate considerably in response to the mere presence of fish in their vicinity (McCollum et al. 1998). If the *Physella* in Sycamore Creek showed this behavioral response to the presence of *Agosia*,

it may have counteracted any benefits of an enhanced food supply.

Conclusions

We conclude from our experiment that biomass at intermediate trophic levels in this stream is controlled by effects propagating both from the top and bottom of the food chain. A simple estimate of the relative magnitude of these effects can be made by comparing the proportional change in mean biomass from the natural condition (predators present, ambient nutrients) due to removing control from above (predators absent, ambient nutrients), removing limitation from below (predators present, nutrients augmented), and removing both limits (predators absent, augmented nutrients) (Table 5). Some workers have suggested that bottom-up control via nutrient limitation should be greater at the base of the food chain, and top-down control by predators should have greater influence on consumers nearer the top of the food chain (McQueen et al. 1986; McQueen 1990). Three-level food chains in the pelagic zone of lakes have been shown to respond consistently in this manner. A meta-analysis of several cross-factored fish and nutrient manipulations in freshwater lakes indicates that fish have greater effects on zooplankton than on phytoplankton, whereas the converse is true for the effect of nutrients (Brett and Goldman 1997). This prediction was generally supported by our results because the increase in algal biomass in response to nutrient addition was greater than the increase in baetid biomass from the middle of the experiment onward (Table 5). Furthermore, the effect of predatory fish was damped at lower trophic levels because the reduction in baetid biomass on the latter two sampling dates was considerably greater than the increase in algal biomass (Table 5). We are cautious of interpreting these patterns too strongly, however, because the relative magnitude of consumer and resource control did not conform to these predictions early in the experiment (Table 5), and the open setting of our study means that there is unlikely to be an internally generated equilibrium to which the food chain will stabilize.

Classical models for food-chain dynamics in closed systems predict that increasing primary productivity will not cause increased biomass at all trophic levels. Instead, biomass will be increased only at the highest trophic level and at trophic levels that are even numbers of levels below the top (Fretwell 1977; Oksanen et al. 1981). Raising primary productivity in a two-level food chain (for example by nutrient addition) should thus cause increased biomass of primary consumers but no change in primary producer biomass (Oksanen et al. 1981). In contrast, food webs with three trophic levels should show increases in the biomass of primary producers, but not primary consumers, when the rate of primary production is raised. Recent theoretical studies have provided several mechanisms that might cause increases in biomass at all trophic levels when primary productivity is increased in closed systems. These include various compensatory interactions among organisms within trophic levels, omnivory by consumers, and instability of the food chain (e.g., Mittelbach et al. 1988; Leibold 1989; Strong 1992;

Abrams 1993; Abrams and Roth 1994; Oksanen et al. 1995). The many empirical studies of nutrient enrichment in lakes have produced results that conform to both patterns of biomass accrual in response to enrichment (Hansson 1992; Brett and Goldman 1997; Leibold et al. 1997). The few equivalent studies in open stream settings have also produced variable results. Wootton and Power (1993) tested the effects of increased primary productivity and the addition of a fourth trophic level to a three-level food chain in an open stream setting. Their results matched the predictions of classical food-chain theory because increasing productivity caused higher biomass only at the top trophic level and at alternative trophic levels below it. Nutrient manipulations in simpler one- or two-level food chains in streams have, though, given rise to higher biomass at both trophic levels (e.g., Hill et al. 1992; Rosemond et al. 1993). Our results also differ from the pattern predicted by classical theory because increasing primary production by nutrient addition caused marked increases in both primary producer (algae) and primary consumer (baetid) biomass. This was true whether a third trophic level (predatory fish) was present or absent.

We cannot conclusively determine the mechanism for the increase in algal and herbivore biomass that we observed in response to nutrient addition. This pattern of biomass accrual is, however, predicted by recently published models for simple food chains in open systems (Nisbet et al. 1997). Notably, the food web in Sycamore Creek was relatively simple and chain-like during our study, as is required by the models, because *Agosia* and baetids dominated the consumer trophic levels. Furthermore, the system displayed the key properties causing increased abundance of all trophic levels under these models. These properties include immigration by all trophic levels that is independent of local conditions plus emigration by herbivores that is a positive function of predator density and a negative function of producer density. The theoretical framework developed by Nisbet and coworkers (1997) thus provides a plausible explanation for the response to nutrient enrichment that we observed. Measurements of the rates at which organisms and materials are exchanged among habitat patches have rarely been incorporated in studies of food-chain dynamics. Their inclusion in future studies of trophic interactions would permit us to test whether these mechanisms are important determinants of trophic structure in open systems.

Our results suggest that adjustments of consumer dispersal rates in response to predators and resources can influence biomass at multiple trophic levels. Similar adjustments in dispersal rates by consumers have been frequently observed in streams, suggesting that their influence on food-chain dynamics may indeed be quite widespread. The type of predator-induced increase in drift dispersal shown by baetids is also shown by several other herbivorous stream invertebrates (Wooster and Sih 1995), and a similar response is displayed by marine amphipods (Ambrose 1984). Such adjustments of dispersal behavior enhance the effect of direct predation to increase the overall depletion of local prey populations caused by predators. Although we did not observe it in Sycamore Creek, some species in streams have been observed to show predator-induced reductions in dispersal rate that can cancel out or even override the depletion of local abun-

dance by direct predation (Sih and Wooster 1994; Wooster and Sih 1995). The interaction between herbivores and algae was also influenced by behavioral adjustments in dispersal rate. Baetids reduced their rate of drift from nutrient-supplemented areas that were rich in algae and thus accumulated in those areas. Insect herbivores in other streams have been found to reduce their rate of departure from patches with abundant algae (Hildebrand 1974; Kohler 1984; Hinterleitner-Anderson et al. 1992). Responses of other herbivore populations to nutrient enrichment may thus be influenced by their ability to redistribute themselves according to local algal abundance.

Theory for open systems is not yet sufficiently developed to predict the consequences for primary producers of these various changes in the behavior of consumers (Nisbet et al. 1997), but it seems likely that trophic interactions in Sycamore Creek would differ from those we reported if *Physella* or chironomids were the dominant herbivores. The apparent importance of these behaviors for trophic interactions is striking because the experiment ran longer than the generation time of all three herbivores (Gray 1981), so there was ample opportunity for population-level responses to predation. Behaviorally mediated trophic cascades have recently been reported in terrestrial habitats (Beckerman et al. 1997; Schmitz et al. 1997), and there is some evidence that they can occur in streams (Huang and Sih 1991; McIntosh and Townsend 1996). In these other studies the presence of secondary consumers resulted in increased primary producer biomass by inducing risk-based reductions in herbivore-foraging activity. Our results illustrate additional mechanisms through which behaviors can influence the dynamics of food chains that are specific to open systems. Further development of theory that can integrate demographic and behavioral processes to predict trophic structure is thus critical to understanding the dynamics of trophic interactions in open systems. Many local communities are open and are linked to neighboring communities by the exchange of materials and organisms (Bustamante et al. 1995; Bustamante and Branch 1996; Polis and Hurd 1996; Menge et al. 1997a,b), and so an enhanced understanding of these systems is an important goal for ecologists.

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