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Source: *Journal of the North American Benthological Society*, Mar., 1991, Vol. 10, No. 1 (Mar., 1991), pp. 42-56

Published by: The University of Chicago Press on behalf of the Society for Freshwater Science

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Effects of detritus loading and fish predation on leafpack breakdown and benthic macroinvertebrates in a woodland stream

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Abstract. To test the roles of coarse particulate organic matter (CPOM) loading and fish predation on benthic community structure and leafpack breakdown, CPOM and fish density were manipulated in a stream. Mt. Sinai Creek, a 3rd-order stream in Piedmont North Carolina, USA, was divided into twelve 30-m² segments with 0.5-m high weirs. CPOM was loaded and maintained at 0.01 ambient, ambient and 4× ambient levels for 19 mo. Fish were excluded from half the segments and maintained at natural densities in the others, in a fully cross-classified design.

Neither CPOM loading nor fish predation had significant effects on leafpack breakdown and macrobenthic species richness or diversity in leafpack and sediment samples on all dates. The total abundance of invertebrates was reduced by fish in sediment samples but not in leafpacks. Almost all species were not significantly affected by the CPOM or fish treatments. Only two taxa responded to each treatment in sediments throughout the study, and none responded in leafpacks, i.e., less than 5% of the taxa tested. Interactions between fish and CPOM were rarely significant.

This work shows that CPOM loading and fish predation, and their interactions, were not major forces in determining the diversity, richness, or litter breakdown rates of this lotic community. The absence of a fish effect on the animals in leafpacks suggests that leafpacks function as a refuge from fish predation for macrobenthic invertebrates. The effect of fish predation on total individuals but not on populations in sediments suggests that fish feeding has a significant impact on the benthos, but that natural variability in population sizes can obscure this effect.

Key words: fish, predation, CPOM loading, benthos, benthic invertebrates, detritus, leaf litter, colonization, aquatic insects, breakdown, lotic, stream.

The question of what determines macrobenthic community structure is still unresolved in stream ecology. Detritus has been implicated as an important factor in several studies on macroinvertebrate microdistribution in streams. The experiment described here attempted to establish whether or not total coarse particulate organic matter (CPOM) availability is exerting "bottom-up" control (sensu Carpenter et al. 1985) of lotic community structure and dynamics.

Rabeni and Minshall (1977) showed that fine particulate organic matter (FPOM) accounted for a significant portion of the variance in insect distributions between sediments. Peckarsky (1980) showed that only shredders responded to whole leaf (CPOM) additions to sediments. Culp et al. (1983) showed that the presence of fine (230–850 µm) and medium (850–2000 µm) detritus particles was a key determinant of the abundance of several detritivores. In addition, the effects of detritus on the local distribution and abundance of macrobenthos on stream sediments have been examined with loose leaves

(Egglishaw 1964, Peckarsky 1980) and leafpacks (Reice 1980, 1981). However, the effect of the total amount of detritus in stream reaches on the benthos has never been experimentally tested. My experiment tested the response of the benthic macroinvertebrate community to three levels of total detritus loads.

"Top-down" control of stream benthic community structure by fish predation apparently has rarely been demonstrated. Reice and Edwards (1986), Culp (1986), Reice (1983), and Allan (1982) all manipulated fish, although on different scales. The abundance of the overwhelming majority of individual taxa was unaffected by fish presence or absence. Reice (1983) and Reice and Edwards (1986) worked on the small scale of <0.1 m². Allan (1982) removed trout from a 1220-m long stream section and compared the result with similarly sized control reaches upstream and downstream. In contrast, a strong effect of fish predation in stream pools was demonstrated by Power et al. (1985). Gilliam et al. (1989) increased creek chub (*Semotilus atromaculatus*) densities in small, iso-

lated stream channel pools and found a 90% reduction in the invertebrate community within one month relative to fishless controls. In this experiment I tested the effects of the presence or absence of a mixed fish assemblage on the macrobenthic community at an intermediate scale (30-m² reaches).

Responses of leafpack breakdown to the fish and detritus manipulations were also monitored. Leafpack decomposition is determined by leaf type and particle size of underlying sediments (Petersen and Cummins 1974, Boling et al. 1975, Reice 1978, and Cummins et al. 1989). Sediment size is important to the control of decomposition rates (Reice 1974, 1977, 1980). Experimental disturbances of sediments did not affect the breakdown rate of leafpacks (Reice 1984, 1985). Direct disturbance of leafpacks also had no effect on mass losses from the leafpacks (unpublished data).

If detritus is a limiting resource, I hypothesized that leafpack breakdown rate would be a function of the total detritus available. This would demonstrate bottom-up control of an ecosystem process. If surrounding detrital biomass were reduced then the breakdown rate of the test leafpacks would increase relative to leafpacks in stream reaches with normal or increased detritus loads because detritivores should become concentrated in test leafpacks, accelerating mass losses. Conversely, if CPOM were superabundant then the rate of leafpack breakdown would decrease relative to normal loading because the shredders would be spread among the superabundant resources. There should also be changes in the benthos such as higher densities in the sediments of high detritus treatments (due to enhanced stocks of FPOM), but lower concentrations of detritivores (especially shredders) in leafpacks (dilution effect). I also tested whether the presence or absence of fish has an effect on the breakdown rate (top-down control). Obendorfer et al. (1984) showed that predators *Megarcys signata* (Plecoptera) and *Rhyacophila* sp. (Trichoptera) reduced the breakdown rate of leafpacks, principally through consumption of the dominant shredder *Zapada cinctipes*, a nemourid stonefly. I predicted that fish predation would reduce litter decomposition rates by consuming detritivores.

The overall goal of this research was to test the relative effects of fish predation and detritus

loading and their interactions on lotic macrobenthic community structure and function. By simultaneously manipulating CPOM load with fish density this project tested the effects of detritus loads on fish predation. That is, are the effects of fish on the benthos in an open, litter-free streambed different from those when heavy detritus loads offer abundant cover?

Study Site

The experiment was conducted in Mount Sinai Creek, a small 3rd-order tributary of New Hope Creek in the Duke Forest, Orange County, North Carolina. The stream averages 3 m in width and 0.1–0.3 m in depth during normal base flow. It flows continuously, being fed by both springs and runoff. During the experiment, current velocity was between 6 and 12 cm/s except during spates when flow exceeded 1 m/s. Spates occurred 12–15 times a year, and there were three out-of-bank floods (7 August 1978, 25 January, and 6 June 1979). The headwaters of Mt. Sinai Creek flow through mixed hardwood forest and pasture. In the experimental area the stream is lined with dense riparian forest including American Beech (*Fagus grandifolia*), Dogwood (*Cornus florida*), Sycamore (*Platanus occidentalis*), White and Southern Red Oak (*Quercus alba* and *Q. falcata*). The banks are steep, and incised to 1.2 m below the surrounding forest floor. Dissolved oxygen remained at or above saturation levels throughout the study in both summer (>8 ppm) and winter (≥12 ppm). Summer high temperatures reached a maximum of 21.5°C; winter lows fell to 1°C in January 1979. The substrate is >70% cobbles with sand and gravel patches and a few boulders.

Eight width measures were taken in each 10-m segment to map the stream (Fig. 1). The stream was divided into 12 experimental segments with low weirs. Each segment contained 30 m² of water surface at low flow at the start of the experiment in June 1978 and averaged 10 m long × 3 m wide. In narrower segments length was increased so the total area remained constant.

The weirs were 0.5 m tall and framed in 3.8 × 3.8-cm pine lumber with vertical supports every 0.5 m. They were covered with 63.5-mm mesh hardware cloth on the upstream face of the weir and reinforced with 30-mm thick pine

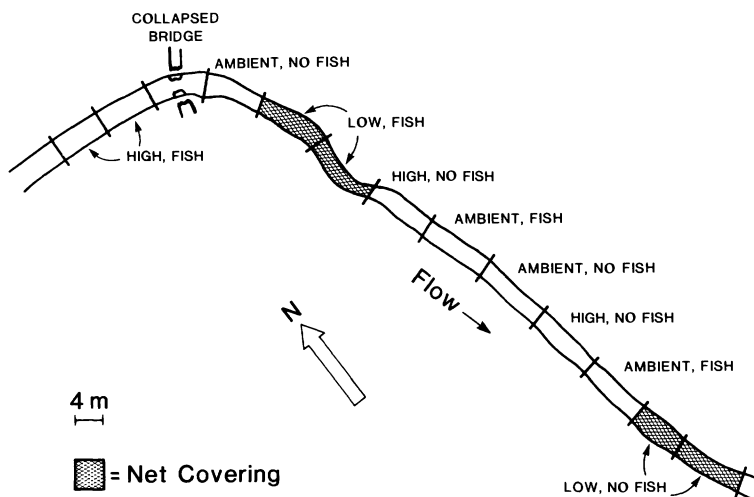


FIG. 1. Order of treatments in Mt. Sinai Creek, Orange Co., North Carolina, 200 m south of Mt. Sinai Church Road. CPOM levels are HIGH, AMBIENT, and LOW.

lath at the corners. Weirs were built 1 m wider than the channel; slots were cut into the bank, the weirs set in the slots, and the ends pounded into the ground. In the stream bed, rocks were cleared from the path of the weir and the weir was hammered down until it rested on the bottom. The side post slots were then refilled with dirt and packed down. The bottom of the weirs had 1 m of nylon mosquito netting (0.8-mm opening) along the entire width. This flap was drawn upstream and covered with rocks in order to prevent washout of the bottom and movement of fish under the weir. Deposition of sand and silt occurred on the upstream face of the weir, and completed the seal at the weir bottom.

This design permitted the weirs to last for >19 mo. The low height of the weirs was necessitated by the force of the creek during spates. Earlier 1-m tall weirs were destroyed in the first spate. The low (0.5 m) weir design withstood all spates and floods (except one on 25 January 1979, when two weirs were partially washed out). During periods of high discharge water flowed over the weirs. Sampling was adjusted to account for flood disruption.

Methods

Fish predation

Treatments were randomly assigned to the 12 segments; the array is shown in Figure 1. The adjacent location of the pairs of low detritus by

fish treatments resulted from the random assignment of treatments to segments. To manipulate the level of fish predation, all fish were electroshocked and removed from all 12 segments. The procedure was to shock each segment beginning at the downstream end. Two successive passes with a Smith-Root Model VII electrofisher were conducted in each segment, with one additional shocking run 1.5 h later. The mean (± 1 SE) number of fish per segment was 4.08 ± 1.00 . Of the 49 fish caught in the segments, 37 were *Semotilus atromaculatus* (creek chub) and 12 were *Clinostomus funduloides* Girard (rosyside dace). Three *Semotilus* and one *Clinostomus* (ranging from 7–10 cm long; anterior to notch in caudal fin) were added to each of the FISH segments approximating the natural density, species composition, and size range of fish in Mt. Sinai Creek. Observation of the NO FISH segments revealed that no fish had evaded the electrofisher.

When the weirs were submerged during high water (>50 cm deep) fish could pass between segments. After each episode of high water, fish were removed from the six NO FISH segments and replaced in the FISH segments. The maintenance of the fish manipulations is shown in Table 1. The disturbance to the sediments caused by shocking the NO FISH segments was mimicked by walking in the FISH segments for the same amount of time and in the same pattern. Several episodes of high water did not result

TABLE 1. Number of fish stocked initially, on 9 June 1978, and during the course of the experiment.

	1978				1979									
	Jun 9	Jul 20	Dec 27	Mar 2	Mar 23	Mar 28	Apr 6	May 16	May 28	Jun 8	Jun 18	Oct 8	Nov 16	Nov 29
<i>Semotilus atromaculatus</i>	3	1	2	6	4	1	3	5	2	9	6	3	3	2
<i>Clinostomus funduloides</i>	1													

in fish movements. On four dates the number of fish restocked exceeded the initial density, with a peak of nine *Semotilus atromaculatus* per FISH segment on 8 June 1979. This represents immigration into the study segments during floods. My object was to maintain normal fish populations in the FISH segments, simulating natural month-to-month variation in fish density.

High water created a problem for the timing of sampling, since fish were aperiodically washed into the NO FISH segments. To provide equal potential for a fish effect on the benthic macroinvertebrates in any sample, sampling periods were adjusted to account for floods. The basic sampling interval was every 28 days. If the segments were flooded during an interval, then the sampling date was delayed by double the number of days that water was over the weirs. As a result, 13 samples were taken in 19 months.

CPOM loading

Three levels of CPOM were randomly assigned to segments (LOW, AMBIENT, and HIGH = $0.01x$, x , and $4x$ g), where x = the mean ambient dry mass of leaves in the unmanipulated segments. The treatments were set up as follows. All visible detritus (down to 25×25 mm) was hand-picked and removed from the LOW segments. Any remaining CPOM was assumed to be no more than 0.01 ambient. Leaves were washed in the creek to dislodge invertebrates, drained of excess water and then weighed to determine mean wet weight. Subsamples were dried (48 h at 50°C), and reweighed to establish a wet to dry mass conversion (2:1). The mean dry mass removed from the LOW segments was an estimate of x , the ambient detritus load. The amount removed on each date is shown in Table 2. Detritus was removed from the LOW segments as needed. To prevent new leaves from

falling in, nets with 4×4 cm mesh were suspended over the LOW stream segments and staked to the bank. Dry leaves were periodically removed from the nets, beginning 16 August 1978. Except for periods of high leaf fall (November of each year), the leaves trapped in the nets did not significantly reduce the incident light to the stream. For example, when filamentous algae appeared in March their abundance was roughly equal in all segments (personal observation).

TABLE 2. Biomass of leaves removed from LOW experimental segments and added to HIGH segments. Values are mean (± 1 SE) per segment on specific dates and totals for annual periods.

Specific date	Leaves removed (g) ^a from LOW segments	Leaves added (g) ^b to HIGH segments
1978		
9 June	2105 \pm 706	6316
16 Aug	163 \pm 39	490
16 Oct	877 \pm 111	2630
7–16 Nov	20,761 \pm 6713	62,280
1979		
11 Jul	562 \pm 87	1686
5 Oct	2775 \pm 1491	8325
16–26 Oct	5760 \pm 962	17,280
19–20 Nov	18,358 \pm 2239	55,076
Annual per segment		
1978	23,906	71,716
1979	26,893	82,362
Annual per m ²		
1978	796.9	3187.4
1979	896.4	3660.8

^a Dry mass.

^b There are no error terms for leaf additions to high segments since the leaves were weighed and then the measured amount was added to each HIGH segment.

To establish the HIGH treatments, wet CPOM collected from the LOW segments was divided into equal lots and added to the HIGH segments. Leaves collected from the nets were distributed similarly. The sum of 0.5 times the wet leaves (to convert to dry weight) plus the air-dried mass of net caught leaves was the ambient detritus load, \times g. The HIGH treatments were raised to a total of $4\times$ g of detritus by adding air-dried leaves of the same species as the riparian forest (*Fagus grandifolia*, *Platanus occidentalis*, *Quercus alba*, *Q. falcata* and *Cornus florida*) which were collected from the forest and from interior lawns of the University of North Carolina. In autumn, nearly all leaves falling into the LOW segments were trapped on the nets. Eight times during the experiment (Table 2), the detritus manipulation was updated. Since only conspicuous detritus (CPOM) was manipulated, fine particulate organic matter (FPOM) detritus levels in all treatments were assumed to be initially equal.

Sampling methods: sediments

Open-topped 63-mm mesh hardware-cloth baskets filled with natural cobbles from the creek were the sampling units. Forty-eight large baskets ($25 \times 25 \times 10$) were embedded (flush) in each segment in June 1978, totaling 3 m^2 or 10% of the surface area of each segment. From July to October 1978, two baskets were removed per segment on each sampling date. In December 1978 I removed the remaining large baskets and put 36 small baskets ($20 \times 20 \times 10 \text{ cm}$) in each segment. Beginning in January 1979 I took three of the smaller baskets from each segment monthly, thus increasing the number of estimates of the benthic populations by 50%.

A wood-framed wire mesh sample receiver lined with 0.8-mm mosquito netting was held just downstream of the sample basket and the basket was lifted $\sim 5 \text{ cm}$ off the bottom and directly into the sample receiver. The contents of the basket sample and the net box liner were transported back to the laboratory within 2 h and washed the same day through a $250\text{-}\mu\text{m}$ sieve (see Reice [1980] for methods). Collected animals were preserved in 70% ethyl alcohol, stained red with Bieberich Scarlet and Eosin B (1 g:1 g:100 ml water), sorted by eye, and keyed to the lowest taxonomic level possible. On five sample dates, random subsamples of all Chi-

ronomidae from all segments were keyed to genus. Subsample size was a function of the total number of Chironomidae per sample. We keyed all individuals if $N \leq 25$ and a decreasing proportion as N increased.

Sampling methods: leafpacks

Mixed-species leafpacks were used to study litter decomposition. One gram each of *Quercus alba* and *Platanus occidentalis* were combined with 3 g of *Cornus florida* into 5-g leafpacks. The oak and sycamore were the outer layers and the dogwood was nested inside. The initial ash free dry mass (AFDM) of a sample of these leafpacks was $4.508 \pm 0.040 \text{ g}$ ($\bar{x} \pm \text{SE}$, $n = 6$). Leafpacks were moistened and held together with Buttoneer plastic staples (Dennison Manufacturing Co. Framingham, Massachusetts). A length of 20-lb-test nylon monofilament line was sewn through each leafpack and tied to a concrete reinforcing rod (driven into the sediment) with 1 m free play in the line; leafpacks lay flat on the streambed.

Three leafpacks per segment were inserted on each sampling day and removed on the next sampling date. Each leafpack was sampled by cutting the nylon lines, then slipped into a zippered plastic bag, and transported to the laboratory. They were frozen for up to 2 wk. The animals were washed off gently into a $250 \mu\text{m}$ sieve, picked, preserved, and keyed as in the sediment samples. The leaves were dried at 50°C for 48 h, weighed, and then coarsely ground. A subsample of $\sim 0.25 \text{ g}$ was ashed at 550°C for 4 h and the AFDM was computed.

Statistical analysis

The entire experiment was conducted in one stream, with repeated sampling in each segment through time. Treatment effects were evaluated using a split-plot repeated measures ANOVA (PC-SAS 1989, General Linear Models), which counteracts the problem of nonindependence of successive samples. Seasonal fluctuations in detritus loads, fish activity, and benthic population dynamics require this approach, since the treatment and interaction effects may vary through time with cumulative effects in each segment. To dissect the specific effects of CPOM and predation in each time interval, each date was also analyzed separately

(S. H. Hurlbert, San Diego State University, personal communication) although this approach has limited power.

This design was restricted by two aspects of pseudoreplication (see Hurlbert [1984] and note that sampling was completed in 1979). First, the experiment was restricted to one stream, so my conclusions must be limited to Mt. Sinai Creek, North Carolina. Second, the “replicate” sediment samples from each segment are not true replicates, they are just multiple estimates of a single mean. The segment means are the true replicates, hence, the mean of all samples from a given segment was computed and is the datum entered into the analysis of variance. The ANOVA for the sediment and leafpack samples is a split-plot design, with two replicates (i.e., segments) per treatment combination. This design assigns most of the degrees of freedom to the within segment variation (i.e., the repeated measure through time). The three-way interaction is part of the error term. The ANOVA table is:

TREATMENT	df
FISH	1
CPOM	2
FISH × CPOM	2
TIME	12
TIME × FISH	12
TIME × CPOM	24
ERROR	102
TOTAL	155

To dissect the effects of CPOM and FISH predation on each date, a two-way ANOVA (FISH vs. CPOM) was run for each date separately. The ANOVA table for these analyses is:

TREATMENT	df
FISH	1
CPOM	2
FISH × CPOM	2
ERROR	6
TOTAL	11

Leafpack AFDM samples on each date were independent of each other, so AFDM was analyzed in a three-way factorial ANOVA, with TIME as the third factor. The animals from leafpacks as well as from sediments were analyzed with repeated measure as above, since the pool of colonizing organisms was dependent on the cumulative effects of the treatments through

time. Separate date analyses were conducted as above for sediment samples.

Statistics were calculated for population sizes of each of the common taxa (as defined by Reice 1980). A taxon was considered common if one of the following criteria was met on a given day: 1) the mean number of individuals over all replicates was >1 (widely distributed); 2) ten individuals were found in any one sample (locally abundant); 3) the taxon was present in at least 25% of the samples (i.e., occurred frequently). Community variables were total numbers of individuals (N); species richness (S, total number of species); and H' = species diversity, where

$$H' = - \sum p_i \ln p_i$$

and

$$p_i = \frac{\text{number of individuals in species } i}{N}$$

To homogenize the variances, all animal numbers were transformed by the natural log of $N + 1$. The transformation was successful and analyses were performed on the $\ln(N + 1)$ transformed data. The results are reported as means ± standard errors of the untransformed data in order to simplify numerical comparisons. The total number of samples analyzed was 420 sediment baskets over a period of 19 months, with over 42,600 individuals identified, as well as 439 leafpacks (29 were lost).

Results

Effects of detritus load

Leafpack samples: breakdown.—AFDM loss did not differ significantly among CPOM manipulations (Fig. 2a). The mean AFDM remaining in HIGH segments (2.275 ± 0.227 g, $\bar{x} \pm \text{SE}$) was slightly greater than the AFDM in AMBIENT and LOW detritus segments (2.025 ± 0.188 g and 2.090 ± 0.179 g respectively). AFDM data points were in a tight cluster for all three treatments until March 1979, after which they showed an assortment of monthly patterns (Fig. 2a). Every treatment had the highest AFDM remaining on at least one of the last eight sample dates. However, leafpacks in LOW CPOM segments never showed significantly greater AFDM loss than AMBIENT or HIGH treatments. One significant finding was that AFDM remaining

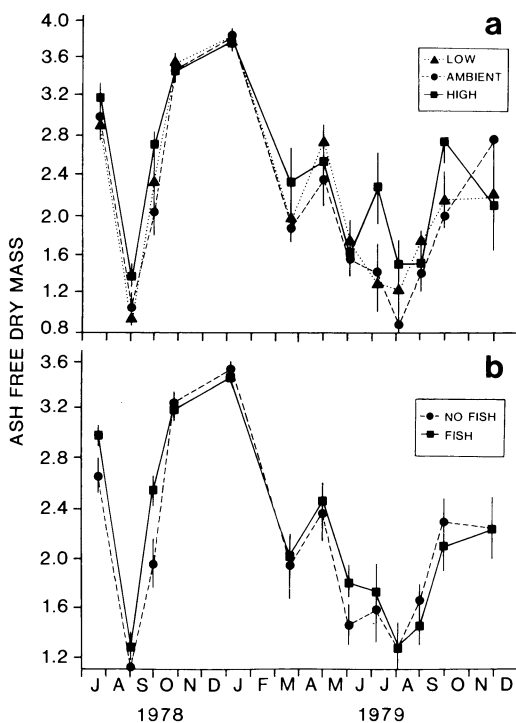


FIG. 2. Mean (± 1 SE) Ash free dry mass (AFDM) remaining in leafpacks in Mt. Sinai Creek. (a) CPOM treatment effects (b) FISH treatment effects.

was inversely related to the stream temperature (simple linear regression analysis, $p < 0.05$).

Leafpack samples: community patterns.—Community variables, including macrobenthos diversity, richness, and total numbers in leafpacks did not respond to the 400-fold range of detritus loads (Fig. 3). All CPOM treatments had the highest N, S, and H' per leafpack on at least one date, but these differences were not significant.

Leafpack samples: population abundances.—In leafpacks, invertebrate population responses to the CPOM treatment were universally insignificant for the entire study. The typical response is illustrated by the leaf-shredding stonefly *Allocapnia* sp. (Fig. 4a). Low and high abundances of *Allocapnia* in leafpacks were found in every CPOM treatment. Although *Allocapnia* feeds only on CPOM and is typically found in leafpacks (Reice 1980), it did not respond to the level of CPOM. Only five (2.2%) of 229 taxon \times date combinations showed significant effects of the CPOM treatment. This is

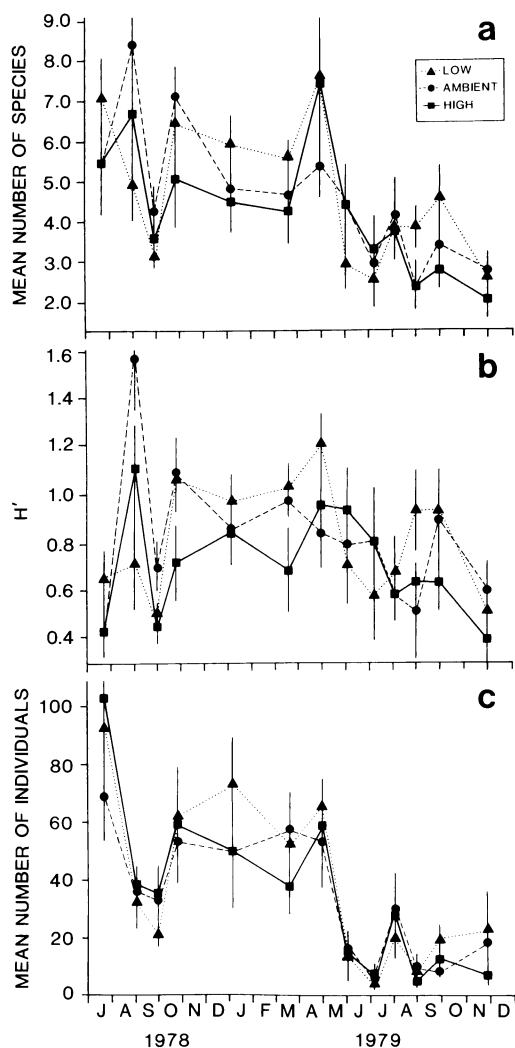


FIG. 3. Community variables at three CPOM levels in leafpacks in Mt. Sinai Creek ($\bar{x} \pm 1$ SE). (a) Species richness. (b) Species diversity (H'). (c) Mean number of individuals per leafpack.

less than the 11 which should be significant by chance alone with a 5% Type I error rate. In July 1978, the amphipod *Crangonyx gracillus* was moderately common in AMBIENT segment leafpacks, but was absent in HIGH and LOW leafpacks. In August 1978, two chironomids, *Conchapelopia* sp. and *Tanytarsus* sp. peaked in AMBIENT segment leafpacks and had lowest densities in LOW segment leafpacks. In May 1979, the water beetle *Ectopria* sp. (Eubriidae, false water pennies) was significantly affected

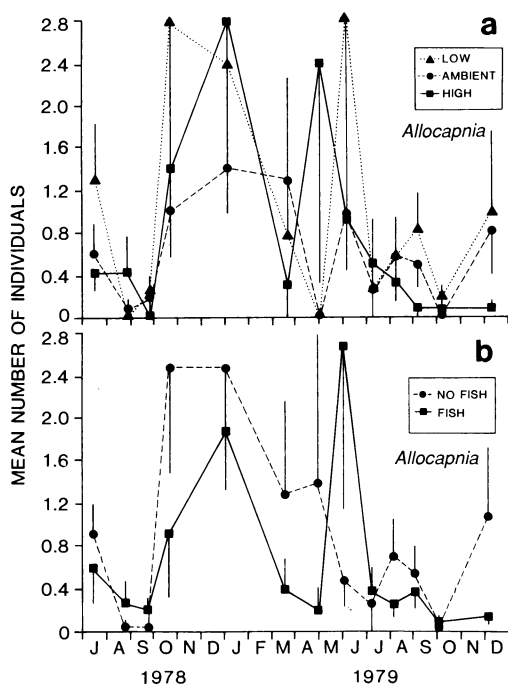


FIG. 4. Mean (± 1 SE) number per leafpack of *Allocapnia* sp., a shredder, in Mt. Sinai Creek. (a) CPOM treatment effects. (b) FISH treatment effects.

by detritus, with its lowest densities in LOW segment leafpacks. Only one taxon ever displayed the predicted increase in leafpacks in LOW CPOM segments: total oligochaetes in October 1979 ($p < 0.01$, F -test). No other leafpack colonist had different abundances in different CPOM treatments.

Sediment samples: community patterns.—Manipulation of CPOM level had no significant effects on macrobenthic community variables in sediment samples throughout the experiment, according to the repeated measures ANOVA (Fig. 5). Analysis of each date separately showed that on the first sample date species richness (S) and diversity (H') were significantly affected by levels of CPOM. S was highest in the HIGH treatment ($S = 23.00$) and lowest in the LOW treatment ($S = 17.44$, $p < 0.05$, Fig. 5a). H' was greater ($p < 0.05$) in the HIGH segments than in the others (Fig. 5b). In June 1979, the total number of individuals was significantly ($p < 0.05$) lower in AMBIENT segments than in HIGH or LOW CPOM segments (Fig. 5c). These were the only sample dates when these variables were signif-

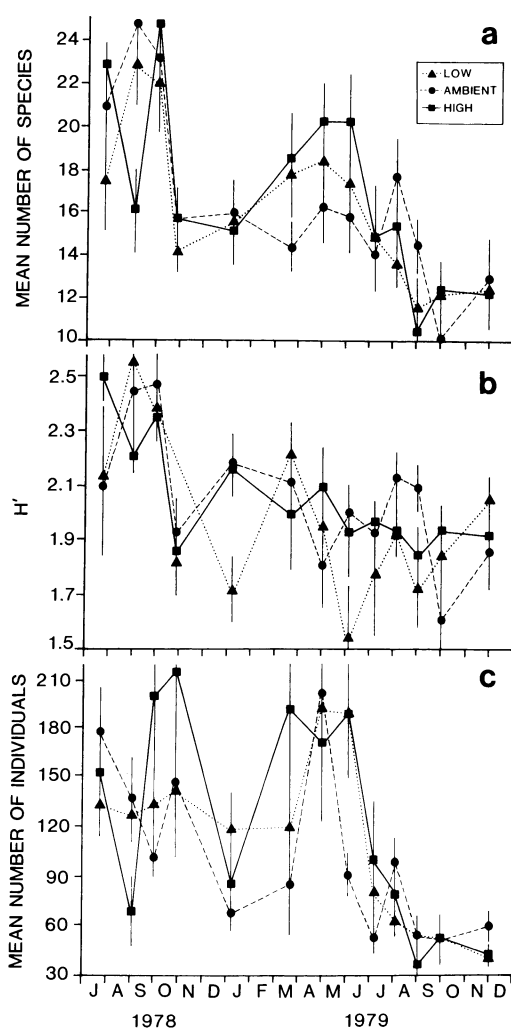


FIG. 5. Community variables at three CPOM levels in sediments in Mt. Sinai Creek ($\bar{x} \pm$ SE). (a) Species richness. (b) Species diversity (H'). (c) Number of individuals.

icantly altered as a result of manipulating detritus loads.

Sediment samples: population abundances.—As many as 39 taxa met the criterion for statistical analysis on a given day. The most common population response to the detritus (CPOM) manipulation was none at all. For most taxa on all dates, numbers of individuals were similar in each detritus treatment. This is illustrated by the large, predacious megalopteran *Sialis* sp. (Fig. 6a) and the grazing, ephemereiid mayfly *Attenella attenuata* (Fig. 6b). In the repeated mea-

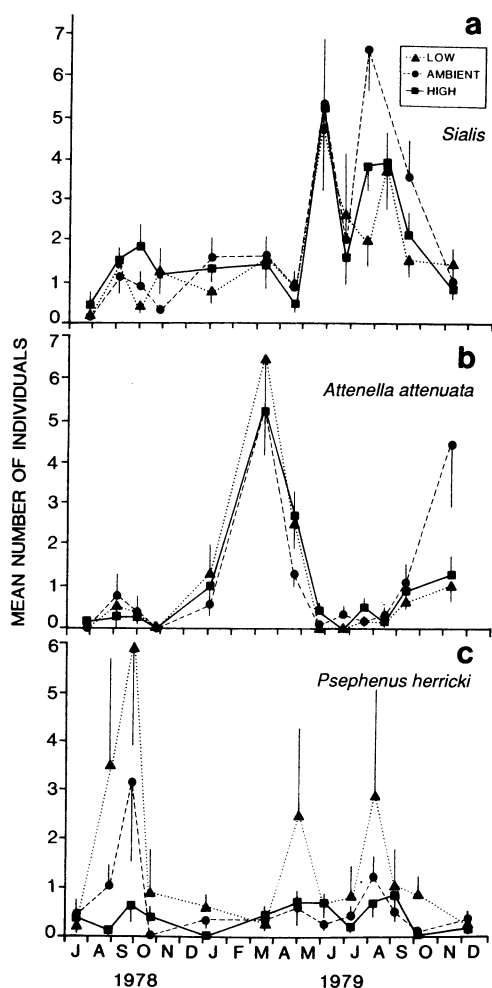


FIG. 6. Species abundances ($\bar{x} \pm 1$ SE) at three CPOM levels in sediments in Mt. Sinai Creek. (a) *Sialis* sp. (b) *Attenella attenuata* (c) *Psephenus herricki*.

tures ANOVA, only three species had significant responses to CPOM levels. These were a clam (*Sphaerium*), a water beetle (*Ectopria*), and a water penny (*Psephenus herricki*). *Ectopria* had its highest density in AMBIENT CPOM segments on 8 of 13 dates. From May until October 1979, *Sphaerium* was most abundant in LOW segments, except for June when there were no differences in its abundance among CPOM treatments. *Psephenus herricki* (Fig. 6c) was the only taxon to have routinely highest abundances (10 of 13 sample dates) in LOW segments, reflecting its need for bare rock surfaces.

Of the 406 taxon \times date combinations tested,

12 were significant, or 2.95% (Table 3). This is fewer than the 20 effects which should be significant by chance alone, with a Type I error rate of 5%. If CPOM were limiting, the expected trends were that animals would have highest densities in HIGH segments, and lowest in LOW segments. This pattern was never found. The overall response to the CPOM manipulations was very modest.

Effects of fish predation

Leafpack samples: breakdown.—There was no significant difference between AFDM losses from leafpacks in FISH and NOFISH segments (Fig. 2b) over the whole experiment. In July and September 1978 (by 2-way ANOVA) there was significantly less AFDM remaining when fish were absent than when they were present ($p < 0.05$, two-way ANOVA). From September until June 1979 the patterns of AFDM were virtually identical in FISH and NOFISH segments, and subsequently were variable.

Leafpack samples: community patterns.—There were no significant differences in S, H' or N in leafpacks from FISH and NOFISH segments over the whole experiment (Fig. 7). On 26 September 1978 significantly more total individuals were in leafpacks with FISH ($\bar{x} = 39.33$) than in NOFISH leafpacks ($\bar{x} = 20.67$, $p = 0.02$). Mass loss was not correlated with invertebrate densities.

Leafpack samples: population abundances.—Only three taxa in leafpacks (1.31%) showed a significant response to FISH treatments out of 229 taxon \times date combinations tested, compared with 5% by chance alone. On the first sample date, *Simulium* spp. were present in NOFISH segment leafpacks ($\bar{x} \pm \text{SE} = 2.50 \pm 1.68$ per leafpack) and absent in FISH leafpacks. Oligochaetes were significantly ($p < 0.01$) more common in FISH segment leafpacks in October 1979 ($\bar{x} = 3.00 \pm 1.40$) and than in NOFISH leafpacks ($\bar{x} = 0.78 \pm 0.26$). In September 1978, nearly twice the number of total chironomids were in leafpacks in FISH segments (31.66 ± 5.60) as in NOFISH segments (17.06 ± 4.63 , $p < 0.05$). No taxon was consistently correlated with high AFDM loss rates.

Sediment samples: community patterns.—The mean number of macroinvertebrates in NOFISH segments was significantly greater than in FISH segments throughout the study ($p < 0.05$, repeated measures ANOVA, Fig. 8c). This

TABLE 3. Taxa in sediments with significantly different densities in different CPOM treatments (F-test).

Date	Taxon	Mean density (no./m²)		
		LOW	AMBIENT	HIGH
1978				
18 Jul	Chironomidae*	11.22	49.55	8.75
28 Aug	Coleoptera**	14.50	0.87	0.62
	Ceratopogonidae**	4.375	1.375	0.125
26 Sep	<i>Psephenus herricki</i> **	5.875	3.125	0.625
	<i>Paraphaenocladius</i> *	18.625	8.25	3.375
23 Oct	None			
1979				
04 Jan	None			
21 Mar	Tipulidae*	9.166	4.00	9.583
	Decapoda*	0.917	0.167	2.333
02 May	Simuliidae*	1.417	4.583	0.250
05 Jun	Ceratopogonidae*	1.727	5.583	5.083
10 Jul	None			
07 Aug	None			
04 Sep	None			
04 Oct	None			
06 Dec	Tipulidae*	3.583	1.333	1.667
	<i>Sphaerium</i> sp.*	1.75	2.25	0.083
	<i>Ephemerella</i> sp.*	1.00	4.417	1.250

* $p \leq 0.05$.
** $p \leq 0.01$.

pattern was apparent on 9 of 13 sample dates. When analyzed date by date, this pattern was statistically significant on only two dates (2-way ANOVA): on 5 June 1979, nearly twice as many macroinvertebrates were in NOFISH (\bar{x} = 194) as in FISH segments (\bar{x} = 108, $p < 0.05$, Fig. 8c) and again on 7 August 1979 ($p < 0.05$). N never was significantly greater in FISH than NOFISH segments.

Fish effects on S or H' were insignificant over the entire study (repeated measures ANOVA, Figs. 8a, b). The only statistically significant effect on S (Fig. 8a) was in July 1978 when there were 22.00 species in NOFISH and 19.19 in FISH ($p < 0.05$). Diversity was never significantly different between FISH and NOFISH segments (Fig. 8b).

Sediment samples: population abundances.—Fish predation had a significant effect on only five (1.23%) of 406 taxa \times date combinations, only one quarter of the 20 significant effects predicted from a 5% Type I error rate by chance alone. Three of these five had higher abundances with fish than without them, and two were lower in the presence of fish. Figure 9 shows three contrasting species' responses to

the fish manipulation. *Acroneuria abnormis*, a large predacious stonefly, is suggestive of fish effects but none were significant. *Attenella attenuata* (mayfly, Fig. 9b) showed no effect of fish at all. *Psephenus herricki* (water penny, Fig. 9c) was more abundant without fish than with fish on 10 of 13 sample dates ($p < 0.05$). The overwhelming majority of taxa were unaffected by the presence or absence of fish in Mt. Sinai Creek.

Interactions between fish predation and CPOM loading

The interaction between fish and detritus level was rarely significant in leafpacks or sediment samples, using repeated measures ANOVA. In leafpacks, no community variables (S, N, or H') or taxon showed a significant CPOM \times FISH predation interaction. In sediments, S, N and H' did not show an effect and only three taxa showed a significant CPOM \times FISH interaction.

One pattern of interaction was found somewhat more frequently than others. *Psephenus herricki*, for example, had peak abundances in HIGH CPOM when FISH were present and in

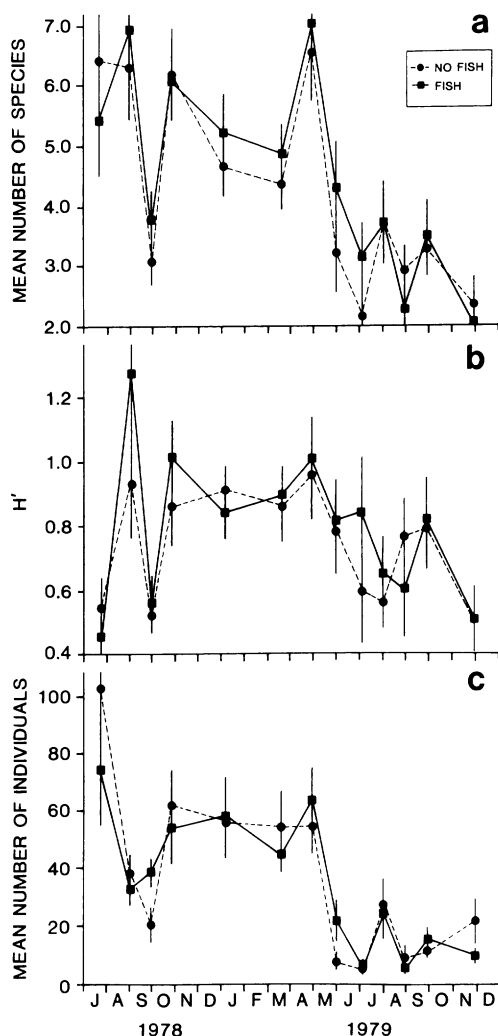


FIG. 7. Community variables ($\bar{x} \pm 1$ SE) with FISH present or absent in leafpacks in Mt. Sinai Creek. (a) Species richness. (b) Species diversity (H'). (c) Number of individuals.

LOW CPOM with NOFISH. This suggests increased risk of fish predation when detritus was reduced and a preference for LOW CPOM areas when fish were absent. Other significant interactions were idiosyncratic and were probably chance events.

Effects of time and its interactions with fish and CPOM

Temporal patterns were significant for nearly all community and population variables in leaf-

packs and sediment samples. The repeated measures design allocates most of the degrees of freedom to within-segment effects, i.e., to time. Consequently, these analyses are highly sensitive to temporal changes in abundance. Such changes are to be expected in the overwhelming majority of stream taxa which have annual or shorter life cycles.

Discussion

This research was designed to test the roles of two variables that are potentially important to lotic community structure, i.e., fish predation and CPOM loads. Results demonstrate that these variables are not major factors in community structure and decomposition dynamics in Mt. Sinai Creek, North Carolina.

Leafpack breakdown

The manipulation of total benthic detritus loads (0.01 normal to $4 \times$ normal) had no significant effect. The null hypothesis of no differences in animal colonization and breakdown rates of leafpacks resulting from CPOM manipulations in this stream cannot be rejected. Therefore, availability of CPOM was not a significant factor in leafpack breakdown dynamics in Mt. Sinai Creek. These results suggest that the dynamics of leafpacks in this system are largely independent of the other leaves in their surroundings and of the macroinvertebrates which colonize them. Fish predation similarly had no effect on the invertebrate community structure in leafpacks or their breakdown.

Effect of fish predation on the macroinvertebrate community

Fish predation has repeatedly been demonstrated to control benthic animal abundances and community structure in lakes and ponds (Hall et al. 1970, Werner 1977, Crowder and Cooper 1982, Gilinsky 1984). In this project I asked if fish predation was important in a woodland stream. When the project was begun this issue was very much in doubt. Caging studies in New Hope Creek (Reice 1983) suggested the lack of a fish effect. Subsequently, work by Allan (1982, 1983), Flecker and Allan (1984), Culp (1986) and myself (Reice 1983, Reice and Edwards 1986) suggested that fish effects on in-

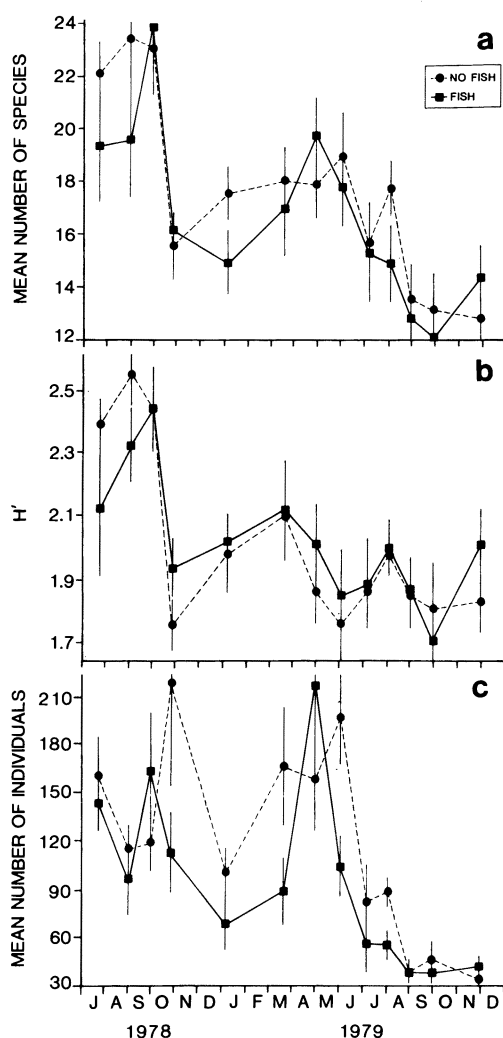


FIG. 8. Community variables ($\bar{x} \pm 1$ SE) with FISH present or absent in sediments in Mt. Sinai Creek. (a) Species richness. (b) Species diversity (H'). (c) Number of individuals.

vertebrate prey communities might be minimal in streams.

Flecker (1984) showed that while sculpins caused no statistically significant effect on total prey abundance, there was a "consistent inverse relationship between invertebrate abundance and sculpin density". Open baskets had, on average, 457.4 invertebrates per basket, while fish exclusion baskets had 1257.4 per basket. Sculpins altered the prey community by reducing the abundance of Chironomidae and *Leuctra*, a stonefly. Flecker (1984) suggested that the pre-

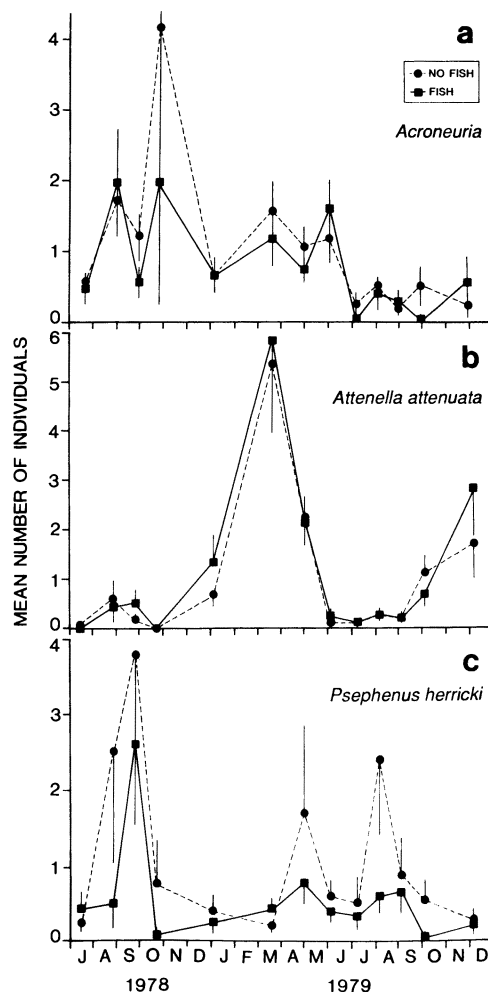


FIG. 9. Species abundances ($\bar{x} \pm 1$ SE) with FISH present or absent in sediments in Mt. Sinai Creek. (a) *Acroneuria*. (b) *Attenella attenuata*. (c) *Psephenus herricki*.

duction effect may have been heightened by warmer temperatures during the late-summer timing of the study.

Gilliam et al. (1989) manipulated *Semotilus atromaculatus* densities in a 2nd-order stream to mimic the conditions found in semi-isolated stream pools where fish congregate during summer drought. At densities of 2.88 fish/m², the fish reduced densities of the macrobenthos by up to 90% (mainly chironomids and oligochaetes). The isolated pool environment and the relatively sedentary prey made this situation comparable to dynamics of benthos in ponds. Fish densities as high as this are rarely

encountered in North Carolina Piedmont streams and then only during summer low flow. Average fish density in the 3rd-order Piedmont streams I have studied is $0.2/\text{m}^2$, about 7% of the densities employed by Gilliam et al. (1989). The experiment of Gilliam et al. (1989) may be more analogous to the "environmental crunch" of Wiens (1977). These papers were the first to show that fish have major impacts on stream macrobenthic populations. The Mt. Sinai Creek data add support to that argument in that even at the naturally low fish densities, there was a significant reduction in total invertebrates due to fish predation in sediments.

Even so, the constituent populations in Mt. Sinai Creek, species richness, and diversity did not respond to the FISH manipulation. Fish predation significantly impacted only 10 of 406 taxa \times date combinations, or 2.46% of the possible animal taxa. This value is so low that it becomes a relevant finding itself. What can explain the lack of significance of fish predation effects for macrobenthic taxa while the total community abundance is being reduced?

A reasonable hypothesis is that the relative densities of prey organisms are too great for low natural densities of fish to have an impact. Prior to the experiment the observed density of fish in Mt. Sinai Creek was 0–11 per 30 m^2 with a mean of $0.136/\text{m}^2$. The original fish treatments (see Table 1) had 4 fish/ 30 m^2 (or $0.133/\text{m}^2$). Migration during spates and floods (measured during post-flood fish redistributions) increased the density up to at least 9 fish/ 30 m^2 (or $0.3/\text{m}^2$). Benthic invertebrate densities from individual sediment samples ranged from 550/ m^2 to 17,450/ m^2 . Daily mean invertebrate densities ranged from a low of 1091/ m^2 to a high of 5335/ m^2 . The ratio of mean numbers of prey items to mean numbers of fish in this experiment ranged from 8022 to 39,228 prey per fish. If fish could eat 100 or more prey per day the effect might still be undetectable, since the percent reduction in benthic density would range from 0.255% to 1.2% per fish per day. Gut contents of *Semotilus atromaculatus* from Mt. Sinai Creek averaged 15 invertebrate prey items in autumn samples, far below the level needed to significantly reduce the density of most species (Reice, unpublished data). Such modest reductions could be obscured by drift, migration, and reproduction. Stronger fish effects should be expected in streams with higher fish densities and lower benthic prey densities.

The inherently high patchiness of stream benthic distributions (variances often exceeding means) contributes to the problems of detecting the effects of fish predation on individual taxa. More true replication is needed to increase the power of the design. This means using multiple streams or widely spaced stream segments as replicate experimental units.

Fish reduced total macroinvertebrates in sediments but not in leafpacks. This result adds support to my contention (Reice 1978, 1983) that invertebrates use leafpacks more for a refuge from predation than for food. It suggests that animals exposed on the sediments are more vulnerable to fish predation than those in leafpacks.

This research showed that fish predation (top down control) in Mt. Sinai Creek did affect total benthic densities but the effect, while significant, was modest. The effect of fish predation was not great enough to alter species richness or diversity. This suggests that while fish have the potential to limit total abundances, their predation is not a key factor in determining lotic community structure.

Effect of detritus load on the macroinvertebrate community

This paper is one of the first to analyze responses of benthic macroinvertebrates to variation in levels of allochthonous detritus (CPOM) in a woodland stream. Previous workers have manipulated ground-up leaves in sediment patches (Culp et al. 1983) or correlated benthic abundances with in situ detritus levels (Rabeni and Minshall 1977). Culp et al. (1983) showed that the presence of detrital particles (fine (FPOM) = 230–850 μm , medium (MPOM) = 850–2000 μm) was a key determinant of the abundance of several detritivores in Carnation Creek, British Columbia, Canada; they found that nine taxa (plus total individuals) were significantly more abundant when detritus particles were added. However, no differences in abundance were observed among five different sediment mixtures when detritus was held constant. Culp and Davies (1985) manipulated interstitial detritus (MPOM, and LPOM) in the sediments of Carnation Creek. Many species responded to the manipulation of alder detritus but the results were unexpected. In the low alder treatment nine taxa increased and three decreased; in the high alder treatment six taxa increased

and six decreased. Doubling the amount of alder did not produce a corresponding increase in invertebrates, but rather caused some taxa to decrease.

The remarkable finding in the Mt. Sinai Creek experiment is that a 400-fold range of CPOM had very little effect on the macrobenthos. CPOM loading had very few effects on species richness, diversity and total numbers and population sizes of individual taxa. Among the individual taxa a common pattern was for HIGH and LOW CPOM to be similar and AMBIENT different. No taxon showed increasing density with increasing detritus. In Mt. Sinai Creek, CPOM abundance did not exert bottom-up control of community structure.

Why did this detritus manipulation not have a major effect on the abundance of benthic macroinvertebrates? If CPOM was limiting, animals should have migrated from areas of low detritus to areas of high detritus, changing the relative macroinvertebrate densities in the different CPOM treatments. This did not happen. The physical design of the detritus exclusion (with weirs and nets) successfully excluded new leaves and twigs from entering the LOW CPOM segments. However, no attempt was made to measure or redistribute FPOM and MPOM, which was present in all segments. Mesh size of the weirs (6.35 mm) was large enough for FPOM and MPOM particles to pass through. The random assignment of treatments to segments resulted in the two most upstream segments having HIGH CPOM. So, small particles comminuted there could be flushed into the AMBIENT and LOW CPOM zones downstream, obscuring the effects of CPOM manipulations. To test for a longitudinal bias in animal distribution and abundance patterns, I compared the four upstream with the four midstream and four downstream segments. There was no position effect. It is very likely that unmanipulated FPOM detritus was more uniformly distributed than the manipulated CPOM. In streams of the Matamek region of northern Quebec, FPOM was far more important than CPOM as a determinant of animal distributions (Reice, unpublished data). If FPOM is more critical than CPOM to animal distributions in Mt. Sinai Creek, the lack of response by macroinvertebrates to CPOM manipulations would be explained. In any case, CPOM is not limiting in this stream.

Few of the common macroinvertebrate taxa of Mt. Sinai Creek are shredders (*Allocapnia*,

Taeniopteryx and *Tipula*) and thus only a few detritivores are likely to be affected by the manipulation of CPOM. Other taxa may be responding to algae or FPOM rather than CPOM. In any case, it is clear that macroinvertebrates did not respond to the levels of CPOM in this stream as a detritus-based bottom-up model of community structure would predict.

Although CPOM availability and fish predation were expected to have controlling effects on the abundance of lotic invertebrates, neither factor was important in this experiment. This result suggests that the relative roles of CPOM, FPOM, and primary production in lotic energetics should be thoroughly reevaluated.

Acknowledgements

This research was supported by NSF grant DEB-7680443. I want to thank Drs. Rob Creed, Philip Service and Sara Via for their technical help and enthusiasm for this project during the early stage of their careers. John Alderman and Rob Creed did most of the identifications. Alan Stiven and Val Smith offered friendship and constructive criticism on different phases of this work. Ernie Patterson provided valuable programming and data management assistance through the many analyses and reanalyses of this large dataset. Bill Baillargeon and Susan Whitfield did the graphics. Thanks also to the generations of undergraduates at Chapel Hill who picked the animals. I could never have done it without all of you.

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Received: 21 July 1989

Accepted: 19 October 1990