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# Mechanical abrasion and organic matter processing in an Iowa stream

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## Abstract

Rates of organic matter processing are key parameters for studies of stream ecosystem function and stream community ecology. Most studies of organic matter processing in streams use leaves in leafpacks or litterbags, which are immobilized and partly shielded from contact with stones in transport and in the stream bottom. As a result, these studies may underestimate the contribution of mechanical abrasion to overall processing rate (of coarse organic detritus to fine particles). We compared leaf processing rates in litter bags with and without stones (5 cm crushed limestone ballast) in Big Mill Creek, eastern Iowa. In two of three experiments, processing was significantly more advanced in bags with stones than in bags without stones: the fraction of leaf mass reduced to small fragments (1.4–9.5 mm) was 45% and 93% higher in bags with stones. In a fourth experiment, we compared the effects of stones and shredders (*Gammarus pseudolimnaeus*, at near-natural densities) on fragmentation of leaves in litterbags. This experiment indicated that mechanical and biological agents of processing are roughly equally important in Big Mill Creek. Our results indicate that mechanical abrasion can be an important contributor to organic matter processing in streams. If so, it may be an important source of the finer particles used by collectors. Litterbag and leafpack experiments may underestimate total processing rates and overestimate the relative importance of processing by microbes and invertebrates.

## Introduction

The processing of organic matter (especially dead leaves) from large to smaller particles has been a central concern for ecologists working in lotic systems. In particular, the roles and relative importances of shredder activity, microbial action, and other processes in organic matter processing have received considerable attention. Causes of organic matter processing (and spatial and temporal patterns in processing) have been an integral part of conceptual models of lotic ecosystem function (Minshall et al., 1985), and have been the subject of many empirical studies (reviews: Webster & Benfield, 1986; Boulton & Boon, 1991; Wallace & Webster, 1996). While it is widely recognized that organic material may be processed in part via mechanical abrasion (e.g. Benfield et al., 1977; Webster & Waide, 1982; Chauvet et al., 1993), surprisingly little is known about the role of mechanical abrasion in organic matter processing or its importance relative to other processing agents. No study to our knowledge has manipulated exposure to abrasion directly and independently of other factors.

Our study of abrasion was motivated by interest in how it might influence particle availability for collectors (Heard & Richardson, 1995). In particular, the importance of shredder-generated particles for collector populations (Heard & Richardson, 1995) must depend on rates of shredder-independent processing as well as shredder-dependent processing (Heard, 1994, 1995), and mechanical abrasion may be an important agent of shredder-independent processing. We suspected that mechanical abrasion was more important than conventional litterbag and leafpack experiments might

indicate (see 'Discussion') and that the relative importance of other processing agents might therefore have been overestimated.

We manipulated exposure to mechanical abrasion of leaves placed in a small midwestern stream (Big Mill Creek, eastern Iowa) and tested for effects on fragmentation of leaf material. Our experiments allowed us to separate differences in exposure to abrasion from other, potentially confounding factors that plague comparisons between reaches or between streams. Our results suggest a substantial and potentially important role for mechanical abrasion in organic material processing in streams.

## Methods

We studied mechanical abrasion in Big Mill Creek, in Jackson County, Iowa, U.S.A. (42° 17′ N, 90° 32′ W). Big Mill is a second-order stream with baseflow approximately 50 L/s, limestone pebble/cobble substrate and well-developed riffle-pool structure. We conducted three replicate abrasion experiments ('stone-only experiments', in autumn, 1996 (4 November–2 December), winter 1997 (8 February–8 March), and spring 1997 (17 April–15 May). Except as noted, all procedures were identical for the three experiments. We compared mechanical abrasion to biological processing (by shredders) in a fourth experiment ('shredder-stone experiment'), conducted in spring 1998 (1 April–7 May).

### *Experiments measuring mechanical abrasion (stone-only experiments)*

In our three abrasion experiments, we measured fragmentation of white oak (*Quercus alba* L.) and sugar maple (*Acer saccharum* Marsh) leaves held in litterbags with and without stones, and with lesser or greater mobility in the stream. We assume that contact by leaves with stones in litterbags is analogous to contact with stones on the stream bottom or in transport (bedload). We collected leaves after leaf-fall in 1996 and stored them at −20 °C until needed. Before placing leaves into litterbags, we dried them (48 h, 55 °C), recorded their dry mass to the nearest 10 mg, and then rehydrated them so they would be less fragile during transport to the field. We dried leaves to allow accurate measurement of percent fragmentation. Drying leaves may influence their susceptibility to both leaching (Taylor & Bärlocher, 1996) and abrasion, but any artifacts introduced by drying do not affect the interpretation of our experiment because we were interested only in differences among treatments.

*Table 1.* Final sample sizes (number of litterbags), for the three stone-only experiments, by abrasion treatment

| Experiment | No rocks | | Rocks | |
|---|---|---|---|---|
| | Attached | Tethered | Attached | Tethered |
| Autumn 1996 | 9 | 10 | 9 | 8 |
| Winter 1997 | 6 | 9 | 3 | 5 |
| Spring 1997 | 10 | 9 | 10 | 10 |

We made litterbags (20×25 cm) from fiberglass window screen (1.4 mm mesh). We used fine mesh bags so that leaf fragments would be retained for analysis (the fine mesh also excluded most shredders). The two walls of each bag were held about 4 cm apart by a loop of stiff wire sewn to the outside of the bag; separating the walls allowed more natural movement of the bag's contents. Each litterbag contained either 4 g dry mass of a 1:1 mixture of oak and maple leaves (autumn 1996), or 3 g dry mass maple leaves (winter and spring, 1997).

We used 4 experimental treatments in a 2×2 factorial design. Half the litterbags contained leaves plus stones (5–6 pieces of 5 cm crushed-limestone ballast), while half contained only leaves. The stones we used were in an intermediate and abundant size class for natural substrate at our site, and resembled natural substrate in being little smoothed by erosion. All bags were attached to anchor bricks, but half were fastened tightly to the upper surfaces of bricks using plastic cable ties, while half were tethered to bricks by 45 cm chains of three looped cable ties. We intended tethered bags to move more freely in the current, allowing more movement of the contents. We began with 10 bags per treatment (40 total) for each experiment, but in each experiment some bags were excluded from the final analysis (Table 1). In autumn 1996, we excluded 4 bags due to mislabelling (final $n$=36). In winter 1997, 17 bags were lost (and all bags tumbled and transported) in a violent freshet (final $n$=23). In spring 1997, we excluded 1 damaged bag (final $n$=39).

We placed litterbags in riffles in blocks of 4 (one bag from each treatment), so we could detect and statistically remove differences in leaf processing arising from within-stream heterogeneity in factors such as current velocity, turbulence, substratum, and sediment accumulation. Neighboring blocks were at least 10 m

apart. We dug the bricks into the substrate so that the litterbags were approximately even with the stream bottom. We left the bags in the stream for 28 days, and then collected and preserved the bags with their contents in 70% ethanol (to preserve invertebrates) for return to the laboratory.

In the lab we opened each bag and sorted remaining leaf material into two size classes: fragments 1.4–9.5 mm, and fragments $>$9.5 mm (the lower limit of 1.4 mm was imposed by the mesh size of the litterbags). The 9.5 mm division was arbitrary, but provided a convenient indicator of particle size reduction. We gently cleaned leaf fragments of adhering sediments under running water, and determined dry masses for small and large fragments from each litterbag. We also calculated the fraction of the original leaf mass lost from each bag [(original mass – large fragments – small fragments)/original mass]. Finally, we identified invertebrates which had colonized the litterbags, assigned them to functional feeding groups using keys in Merritt & Cummins (1996), and measured total dry mass of shredders for each litterbag.

*Experiment comparing mechanical abrasion and biological processing (shredder-stone experiment)*

We compared the magnitudes of mechanical abrasion and biological processing with an experiment manipulating both shredders and stones. This shredder-stone experiment used 4 treatments in a $2\times2$ factorial design: half the litterbags had stones as described above, and half contained shredders (50 amphipods, *Gammarus pseudolimnaeus*). *G. pseudolimnaeus* is a dominant shredder in Big Mill Creek. Individuals used for this experiment were collected in a nearby stream (Spring Branch, Delaware County, Iowa) and held in cooled stream water for about 24 h before being added to the litterbags. There was no tethering treatment in this experiment. Each litterbag contained 3 g dry mass maple (*Acer saccharum*) leaves. There were initially 10 litterbags per treatment, but one bag was damaged and excluded from analysis (final $n$=39). In this experiment, we preserved litterbags after collection by freezing rather than in ethanol. In all other details this experiment was identical to the stone-only experiments.

*Natural leafpacks*

We compared shredder masses from our litterbags with shredder masses from 25 natural leafpacks collected in Big Mill Creek between October 1996 and February 1997. These leafpacks were collected intact, preserved in 70% ethanol, and processed as described for litterbags. We calculated means and upper 95% quantiles for shredder densities (shredder mass per leaf mass); we used quantiles rather than standard deviations because shredder mass distributions were severely non-normal.

*Statistical analysis*

There were no significant block effects in any experiment (‘blocks’ being the 10 locations in the stream where we installed sets of 4 litterbags); therefore, in further analyses we ignored blocking. In stone-only experiments, we compared mean shredder colonization among treaments using analysis of variance (ANOVA), and then compared total mass loss and production of small fragments (as fractions of original dry mass) among treatments using analyses of covariance (ANCOVAs). The covariate was shredder dry mass, included to test for within-treatment effects of shredder colonization on processing rates. For the shredder-stone experiment, we compared mass loss and production of small fragments among treatments using ANOVA; we did not use shredder mass as a covariate because variation in shredder mass within treatments was small compared to the difference between shredder and no-shredder treatments.

For each analysis, we began by testing a statistical model including all main effects and all possible interactions among them. Because no interactions were significant in any experiment, we pooled interactions with the error terms and repeated the analyses using only the main effects. We estimated effect sizes for each experimental factor as the difference in means between levels of that factor. For the shredder mass covariate in stone-only experiments, we estimated an effect size as the predicted difference (from the ANCOVA regression) between a litterbag with no shredders and one with the mean shredder density (mg per g leaves, dry mass) from our natural leaf pack data.

We conducted all analyses with SAS (version 6.04; SAS Institute Inc., Cary, NC) using type III sums of squares.

## Results

*Mass loss*

Mass loss from the litterbags averaged 22% (fall 1996, winter 1997)–36% (spring 1998). The only significant treatment effect on total mass loss (out of 8 tests

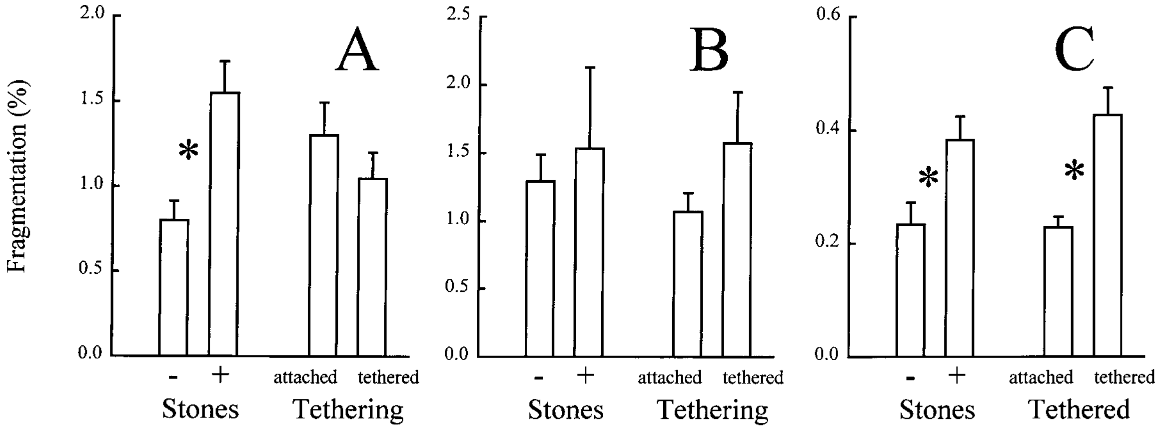


*Figure 1.* Leaf fragmentation in the stone-only experiments. 'Fragmentation' is dry mass of leaf fragments 1–9.5 mm, as a percentage of the original dry mass. Error bars are ±1 SE; asterisks indicate significant ($P$<0.05) differences among treatments. See Table 2 for statistical details. (A) Autumn 1996 experiment. (B) Winter 1997 experiment. (C) Spring 1997 experiment (note different scale).

*Table 2.* Results of ANCOVAs for production of small leaf fragments (fraction of starting leaf dry mass): stone-only experiments

| Experiment | Source | Effect[a] | df | MS[b] | *P* |
|---|---|---|---|---|---|
| Autumn 1996 | Stones | +93% | 1 | 5800 | **0.002** |
| | Tethering | −22% | 1 | 738 | 0.24 |
| | Shredders | −8% | 1 | 1170 | 0.14 |
| | Error | | 32 | 506 | – |
| Winter 1997 | Stones | +19% | 1 | 327 | 0.63 |
| | Tethering | +47% | 1 | 1800 | 0.26 |
| | Shredders | +13% | 1 | 1040 | 0.39 |
| | Error | | 19 | 1340 | – |
| Spring 1997 | Stones | +45% | 1 | 97 | **0.045** |
| | Tethering | +87% | 1 | 345 | **0.0004** |
| | Shredder | +41% | 1 | 18 | 0.38 |
| | Error | | 35 | 22 | – |

[a]'+' denotes an effect in the predicted direction: more fragments with stones, in tethered bags, or with more shredders. Effect size for 'stones' is the difference between treatments as a percentage of the control value; for 'tethering', the difference between treatments as a percentage of attached value. For shredders (the covariate), effect size is the difference between predicted fragmentation with zero shredders and with mean shredder densities from natural leaf packs (Table 4), as a percentage of the average value for the experiment.
[b]Entry is mean square$\times 10^7$.

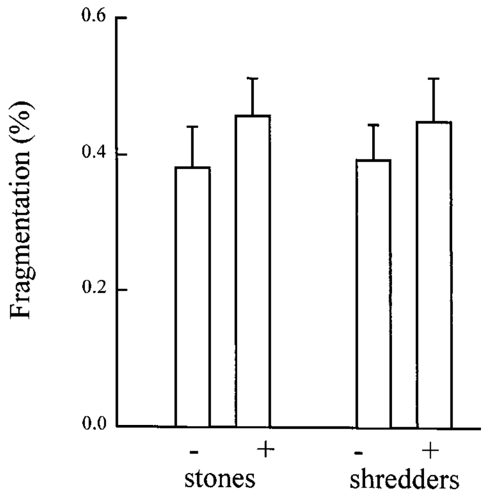


*Figure 2.* Leaf fragmentation in the shredder-stone experiment. 'Fragmentation' is dry mass of leaf fragments 1–9.5 mm, as a percentage of the original dry mass. Error bars are ±1 SE; there are no significant differences among treatments. See Table 3 for statistical details.

in total) was a shredder effect in the shredder-stone experiment ($P$=0.004).

*Fragmentation*

We detected significant treatment effects on fragmentation in two of the three stone-only experiments (Table 2): a significant stone effect in autumn 1996 (Figure 1A), and significant stone and tethering effects in spring 1997 (Figure 1C). There were no significant effects in winter 1997 (Figure 1B), although both stone and tethering effects were in the direction expected (Table 2). Litterbags with stones had much more fragment production than those without (Figure 1): 93% more in fall 1996, 19% more in winter 1997, and 45% more in spring 1997. In spring 1997,

*Table 3.* Results of ANOVA for production of small leaf fragments (fraction of starting leaf dry mass): shredder-stone experiment

| Source | Effect[a] | df | MS[b] | *P* |
|---|---|---|---|---|
| Stones | +20% | 1 | 54.9 | 0.36 |
| Shredders | +14% | 1 | 28.3 | 0.51 |
| Error | | 36 | 64.5 | |

[a] '+' denotes an effect in the predicted direction: more fragments with stones or with shredders. Effect sizes are differences between treatments as percentages of the control values.
[b] Entry is mean square $\times 10^7$.

*Table 4.* Colonization of litterbags and natural leaf packs by shredders[a] (mg per g leaves, dry mass)

| Experiment | Mean shredder mass | 95% quantile |
|---|---|---|
| **Stone-only experiments** | | |
| Autumn 1996 | 11.4 | 41.8 |
| Winter 1997 | 17.2 | 46.7 |
| Spring 1997 | 3.7 | 11.9 |
| **Shredder-stone experiment** | | |
| No-shredder treatment | 3.9 | 12.1 |
| Shredder treatment[b] | 65.9 | 84.6 |
| **Natural leaf packs** | 55.1 | 189 |

[a]Common shredder taxa included *Gammarus* (Amphipoda), *Caecidotea* (Isopoda), *Amphinemura* (Plecoptera: Nemouridae), *Allocapnia* (Plecoptera: Capniidae) and *Lepidostoma* (Trichoptera: Lepidostomidae).
[b]Shredders from experimental introduction of *Gammarus pseudolimnaeus*, not natural colonization.

tethered litterbags had 87% more fragment production than attached litterbags.

In the shredder-stone experiment, neither shredder nor stone treatment had a significant effect on fragmentation (Table 3). However, the trends were in the expected direction for both treatments: more fragmentation in treatments with stones (20% more) and treatments with shredders (14% more).

A combined test (Fisher's method; Manly 1985) of the overall effect of stones across our four experiments was highly significant ($\chi^2_{(8)}$=21.6, $P<0.0057$).

### *Shredder colonization*

In the stone-only experiments, shredder colonization never differed among treatments (all ANOVA $P>0.39$). Within treatments, shredder dry mass had no significant effect on fragment production in any experiment (Table 2). Shredder colonization was low (Table 4): all mean shredder dry masses were less than 20 mg per g leaves, and the 95% quantiles for all three experiments were lower than the mean shredder density in natural leafpacks.

In the shredder-stone treatments, shredder colonization and mortality of introduced shredders generated little variation in shredder dry mass among litterbags within our shredder treatments: only 15% of the variance in shredder dry mass occured within treatments (with mortality accounting for most of this variation).

## Discussion

While many studies have examined mass loss from litterbags or leafpacks (Boulton & Boon, 1991), few (if any) have examined the fragmentation of leaf material. We measured both, but we were most interested in our fragmentation data. Although we measured quite large particles (1.4–9.5 mm), we make the reasonable assumption that fragmentation to particles in this size class is a good proxy for fragmentation to finer particles. Direct measurement of finer particles would require litterbags with such a fine mesh as to nearly eliminate water flow through the bags and severely reduce fragmentation rates.

### *Mass loss*

Total mass loss is the variable most often measured in studies of organic matter processing in streams (Boulton & Boon, 1991). Overall processing rates in our experiment, as measured by total mass loss, were similar to those reported from comparable experiments (e.g. McArthur & Barnes, 1988; Hill & Perotte, 1995; Rowe et al., 1996). Measurements of mass loss, however, unavoidably confound three different processes: leaching, chemical decomposition, and fragmentation to particles small enough to escape from litterbags (Boulton & Boon, 1991). Mass loss over the course of our experiments was probably dominated by leaching, which can remove up to 35% of leaf mass in a few days (Taylor & Bärlocher, 1996); and leaching (even of intact, unabraded leaves) would have been completed long before the end of our 28-day experiments. We therefore expected differences in mass loss among treatments to be small, and our power to detect small effects was low (for a 10%

change in mass loss, power ≈14%, 13%, and 25% in our three stone-only experiments; Cohen, 1988). The rarity of treatment effects on mass loss is therefore unsurprising. Because we were interested primarily in fragmentation, not losses due to leaching, we did not further interpret our mass loss data.

*Fragmentation by mechanical abrasion*

We detected significant effects of both stone and tethering treatments on fragmentation (Table 2). Our overall fragmentation rates would seem low if compared to published processing rates. However, we stress that those processing rates are normally calculated from total mass loss (Boulton & Boon, 1991), not fragmentation; calculated in this way, our processing rates are not low (see 'Discussion' – '*Mass loss*'). Fragmentation rates should generally be much smaller than rates based on mass loss.

Our fragmentation rate data indicate a potentially important role for mechanical abrasion in the processing of organic matter in streams. The overall effect of stones on fragmentation across our four experiments was highly significant ($P<0.0057$). Considered individually, two of our four experiments (Tables 2 and 3) showed significant stone effects (autumn 1996 and spring 1997). Of the remaining two experiments, one (winter 1997) was affected by a major freshet (discharge at the nearest gaged stream, 80 km NW, peaked at about 25 times baseflow). The lack of any significant treatment effects in this experiment is unsurprising, because nearly half of our litterbags were lost in this freshet (Table 1), and the remainder were tumbled with substrate cobbles and boulders (so even bags without stones experienced strong mechanical abrasion).

For several reasons, we expect that even the strong treatment effects we saw (up to 93% more fragmentation in bags with stones) underestimate abrasion effects on leaves free in the stream. First, in our litterbags, stones remained at the downstream ends of the bags; our methods could not reproduce the tumbling of stones in transport along the streambed. Second, our experiment simulated abrasion from pebble/cobble sized stones in transport or on the streambed, but did not measure scouring by finer sediments in suspension. Finally, abrasion may be most effective at producing particles from leaves well macerated by microbial action (Ward, 1984; Ward, et al., 1994), but at the end of our experiments maceration was not far advanced. Because it is underestimated, the importance of abrasion in our results is especially compelling.

The significant effect of tethering treatment in one of our experiments (spring 1997; more abrasion in the tethered bags) has two potentially important implications. First, it suggests that the importance of mechanical fragmentation in natural litter processing will depend on current velocity, turbulence, and substrate (see also Chauvet et al., 1993). Second, it underscores our contention that standard litterbag techniques, while valuable, are likely to seriously underestimate the importance of mechanical abrasion.

Most previous studies of organic matter processing have estimated processing rates or constructed processing budgets while disregarding or minimizing the contribution of mechanical fragmentation (e.g. McDiffett, 1970; Cummins et al., 1973; Petersen & Cummins, 1974; Wallace et al., 1982; Barnes et al., 1986; McArthur & Barnes, 1988; Petersen et al., 1989; Cuffney et al., 1990; Newman, 1990; Baldy et al., 1995; Rowe et al., 1996), and may therefore have underestimated natural processing rates. A few studies (McDiffett, 1970; Cummins et al., 1973) have examined processing in laboratory settings without natural flow or substrate to cause abrasion. Most other studies have used either leafpacks or litterbags to retain the organic matter being studied, and these techniques reduce or eliminate mechanical abrasion because they restrict access by abrading particles. Reduced mechanical abrasion has even been cited as an advantage of the litterbag technique (Anderson & Sedell, 1979), and may account in part for faster processing of unconfined leaves versus leaves confined in litterbags (Cummins et al., 1980; Benfield et al., 1991; D'Angelo & Webster, 1992). Our design, too, certainly reduced contact with natural bedload and suspended particles, which is why we focus on differences among abrasion treatments and do not interpret our absolute rate estimates.

Two studies have explicitly considered mechanical abrasion. Chauvet et al. (1993) invoked abrasion to explain differences in processing rates between a high-gradient stream and a lowland river, but in contrast Reice (1977) found no among-reach effect of current velocity on processing (implying little effect of mechanical abrasion). In both studies, however, differences in abrasion were (unavoidably) confounded with other differences among reaches or streams. Replicated and controlled experiments such as ours are necessary for unequivocal attribution of differences in processing to differences in exposure to abrasion.

*Relative importance of mechanical and biological fragmentation*

The importance of mechanical abrasion in our results contrasts with claims that organic matter processing in streams is primarily due to biotic agents, principally shredders (Reice, 1977; Cummins et al., 1980). We have two kinds of evidence suggesting that the role of mechanical abrasion may equal or exceed the role of shredders in driving fragmentation.

First, in our stone-only experiments, some shredders did colonize the litterbags (Table 4). Shredder colonization was low, as only very small invertebrates could enter through the 1.4 mm mesh, and therefore the absence of significant shredder effects in ANCOVA (Table 2) is unsurprising. Nevertheless, we could use our shredder colonization data to obtain a crude prediction of the effect on fragmentation of shredders at natural densities (see 'Methods' – '*Statistical analysis*'). These effect sizes (Table 2) should be interpreted with caution, as they extrapolate well beyond the data on which they are based, but in two of the three experiments they are similar to (but somewhat smaller than) the effect sizes from the stone treatment.

Second, our shredder-stone experiment was explicitly designed to compare mechanical and biological effects on fragmentation. In this experiment, the shredder effect size was calculated based on the actual shredder density (slightly greater than the average density from natural leaf packs; Table 4). As with the stone-only estimates, the shredder effect was comparable to (but a bit less than) the stone effect.

Together, these two lines of evidence suggest that in Big Mill Creek, the contribution of mechanical abrasion to organic matter processing is not less than the contribution of shredders. In fact, since our methods likely underestimate the effect of abrasion (see 'Discussion' – '*Fragmentation by mechanical abrasion*'), mechanical abrasion may be considerably more important than shredders as an agent of organic matter processing. We caution, however, that neither of these comparisons involves truly natural processing. Simultaneously assessing the roles of shredders, mechanical abrasion, and other factors in determining processing rates presents a substantial methodological challenge, because it is impossible to exert experimental control over mechanical abrasion while keeping treatments entirely realistic. In particular, leaf litter must be confined if its fate is to be known; but confining litter reduces its exposure to natural abrasion and prevents access by shredders. We took a litterbag approach to allow fully controlled and replicated experiments, accepting as an inevitable cost that our treatments simulate natural processing but do not exactly duplicate it.

Without accounting for mechanical abrasion, we can neither understand overall organic matter dynamics in streams nor measure the importance of any one agent of processing against overall processing rates. Our results are an important first step toward a fuller understanding of mechanical abrasion as an agent of organic matter processing in streams.

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