The effect of shredder community composition on the production and quality of fine particulate organic matter

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Abstract. Decomposition of senesced primary production starts processing chains in aquatic systems. Shredding macroinvertebrates convert coarse particulate organic matter (CPOM) to fine particulate organic matter (FPOM) that supports 2 other feeding groups, collecting and filtering macroinvertebrates. This linkage is often invoked by aquatic ecologists, but the effect of detritivore assemblage composition on production of FPOM is relatively understudied. I manipulated detritivore assemblage composition (*Limnephilus* sp., *Caecidotea* sp., and *Hyalella azteca*) in aquatic mesocosms stocked with green speckled alder leaves (*Alnus incana rugosa*). I measured production rate, size distribution, and stoichiometry of FPOM produced through time. Detritivore species richness had a positive effect on FPOM production resulting from inclusion of the functionally dominant shredder, *Limnephilus* sp., in mixed-species treatments (e.g., sampling effect). Mixed-species treatments had significantly faster particle production than predicted from single-species treatments. The significant increases in particle production in mixed-species treatments could have resulted from release of *Limnephilus* sp. from intraspecific competition, facilitation between shredders, or both processes. FPOM size distribution and C:N varied significantly among treatments and was affected by species interactions in mixed-species treatments. The presence of *Limnephilus* sp. significantly skewed the FPOM size distribution and increased the mass of particles >250 μm by ~60%. These results suggest that the specific shredding insects in an assemblage could strongly affect production of FPOM and the size distribution and stoichiometry of FPOM produced by the benthos of a stream.

Key words: leaf decomposition, particle production, FPOM, shredder, processing chain ecology, biodiversity.

Decomposition of plant litter is a central component of ecosystem functioning in terrestrial and aquatic food webs (Gessner et al. 2010). Transformation of plant litterfall into its constituent parts is greatly affected by the detritivore community (Heemsbergen et al. 2004, Srivastava et al. 2009). Human stressors on ecosystems and climate change have the potential to alter carbon and nutrient cycles across systems by modifying detritivore diversity (Wardle 2002, Bardgett 2005, Gessner et al. 2010). Therefore, the effect of detritivore diversity on decomposition must be fully understood by ecologists. Forested-stream food webs are particularly dependent on leaf fall from the riparian zone and are excellent model systems for studying decomposition (Webster and Benfield 1986, Benson and Pearson 1993, Wallace et al. 1997, Mathuriau and Chauvet 2002).

Aquatic decomposition begins when bacteria and fungi colonize leaves (coarse particulate organic matter [CPOM]: >1 mm) that fall into the water (Webster and Benfield 1986). Mechanical fragmentation by flow (Anderson and Sedell 1979, Roeding and Smock 1989) and feeding by macroinvertebrates (shredders) transform the conditioned CPOM into fine particulate organic matter (FPOM: <1 mm) (Wotton 1990, Wotton and Malmqvist 2001, Joyce et al. 2007). FPOM accumulates on the benthos and is easily mobilized and exported downstream during high flow because of its small size (Wotton 1990, Thomas et al. 2001, Benda et al. 2004, Joyce and Wotton 2008).

The feeding action of shredders may be responsible for as much as 50 to 74% of decomposition rates and, therefore, a similar percentage of FPOM produced by the benthos (Cuffney et al. 1990). FPOM produced in-stream by shredders is an important resource for secondary consumers (Cummins 1973, Short and Maslin 1977) and is nutritionally superior to FPOM from terrestrial sources (Ward and Cummins 1979, Shepard and Minshall 1981). The linkage between the

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shredders and secondary consumers in streams forms a detrital processing chain (Cummins 1973, Heard and Richardson 1995). Secondary consumers, filter feeders, and collectors that are supported by FPOM, in turn, support higher trophic levels, such as predatory invertebrates and insectivorous fishes (Shepard and Minshall 1984a, b).

Shredder species richness tends to have a positive effect on leaf mass loss during decomposition (Jonsson et al. 2001, Ruesink and Srivastava 2001, Giller et al. 2004, McKie et al. 2008). In species-rich assemblages, inclusion of functionally dominant species (e.g., sampling effect), facilitation, and complementarity between shredders often act as mechanisms to increase leaf mass loss rates (Jonsson et al. 2001, Ruesink and Srivastava 2001, McKie et al. 2008). In some cases, interspecific competition can decrease decomposition rates at higher diversity levels (Creed et al. 2009). Despite the well documented effects of shredder assemblage composition on leaf mass loss (Jonsson et al. 2001, Ruesink and Srivastava 2001, Giller et al. 2004, McKie et al. 2008, Creed et al. 2009), surprisingly few studies have been published on the effect of shredder assemblage composition on FPOM production (but see Wotton and Malmqvist 2001, Joyce and Wotton 2008).

Quantity, C:N, and size distribution of FPOM are all important for filter-feeding invertebrates, and these factors could be affected by shredder assemblage composition. Quantity of FPOM produced affects food availability for consumers, and leaf mass loss studies clearly show that FPOM quantity can be affected by species composition. C:N of FPOM is an indicator of food quality to filtering and collector-gathering insects (Heard and Richardson 1995). C:N of FPOM produced via egestion of fecal material varies across species because of species-specific differences in assimilation efficiencies (Wotton 1990, Wotton and Malmqvist 2001). Therefore, assemblage composition could affect C:N of FPOM. Species in the filtering and collector-gatherer functional feeding groups have different preferences for particle size (Wotton 1990, Shepard and Minshall 1984a, b). Particle size of FPOM produced by different shredders varies because the diameter of the anus varies among species (Wotton 1990, Wotton and Malmqvist 2001).

In benthic assemblages, interspecific interactions might affect the stoichiometry (here defined as C:N) and size distribution of FPOM. In such cases, total FPOM production may differ from production predicted on the basis of the contributions of each species in mixed assemblages. For instance, facilitation may increase the feeding rates of some but not all taxa, or a dominant detritivore may boost total FPOM production while decreasing the feeding rates of the other species present. Such dynamics would result in FPOM size distributions and stoichiometry in mixed-species assemblages that are not related to FPOM production rates.

I investigated how shredder diversity affects the production and characteristics of FPOM in mesocosms. I manipulated the richness of detritivore assemblages similar to those found in low-gradient streams in the Upper Peninsula, Michigan (USA). During the course of the experiment, I measured the production and physical characteristics of FPOM through time. I predicted that increasing shredder species richness would: 1) increase FPOM production rates above the mean of single-species treatments (overyielding) because increasing shredder species richness typically has a positive effect on leaf breakdown, and FPOM production rates should mirror CPOM breakdown rates (Webster and Benfield 1986, Heard and Richardson 1995); 2) result in uniform FPOM size distributions (i.e., a more even FPOM pool) because the FPOM distribution will be a mix of FPOM produced by different shredders; and 3) result in FPOM with a C:N matching the mean of single-species treatments.

Methods

Study site

I conducted my study at the University of Notre Dame Environmental Research Center (UNDERC) on the border of northern Wisconsin and the Upper Peninsula of Michigan (lat 46°13′N, long 89°32′W). UNDERC is in northern mesic hardwood forest mixed with lakes, bogs, and streams. In 2007, I surveyed 9 streams to assess the composition of the benthic macroinvertebrate assemblages (CJP, unpublished data). The surveyed streams are low-gradient systems with riparian vegetation dominated by alder thickets (*Alnus incana rugosa*). *Hyalella azteca*, *Limnephilus* sp., and *Caecidotea* sp. were the most common and numerically dominant shredders in the streams, so I chose them as study species. Several morphospecies of *Limnephilus* sp. occur in the region, but the ones I used were easily identified by their unique case morphology and the others are rare. I assumed that I used one species, but it is possible that the *Limnephilus* used consisted of 2 or more cryptic taxa. *Hyalella azteca* was present in 55% of the streams, *Caecidotea* sp. was present in 22% of the streams, and *Limnephilus* sp. was present in 55% of the streams. Each species coexisted with the other species and reached numerical dominance among shredders in at least one stream.

Shredder density varied greatly within streams. Densities were much higher in debris dams than in the streams as a whole. *Limnephilus* sp. density was 0 to 107 individuals (ind)/m² in Surber samples and as high as 800 ind/m² in concentrated pockets of debris dams. *Caecidotea* sp. density was 0 to 86 ind/m² in Surber samples and between 0 and 11,100 ind/m² in litter bags deployed in the field. *Hyalella azteca* density was 0 to 505 ind/m² in Surber samples, 0 to 2300 ind/m² in litter bags, and as high as 4000 ind/m² in debris dams. *Hyalella azteca* consistently had the highest density across sample types except in litter bags where *Caecidotea* sp. occasionally reached extremely high densities. I chose green speckled alder leaves as the allochthonous input for the experiment because it is the dominant riparian species at the surveyed streams. I ran experiments in June 2008 using the summer shredder assemblage (Maloney and Lamberti 1995).

Experimental design

The experimental treatments consisted of all possible 1-, 2-, and 3-species combinations of shredders. After the experiment, I ran a control treatment under the same conditions with no shredders to estimate FPOM production. The control was run separately because of space constraints ($n = 8$ treatments each with 4 replicates). I used a replacement design (Byrnes and Stachowicz 2009) and held shredder biomass approximately constant (~154 mg ash-free dry mass [AFDM], average mass calculated from 100 ind/species) across treatments and allowed species-specific relative density to vary (25 amphipods to 1 caddisfly to 4 isopods). Shredder masses were: *H. azteca* = 2.89 ± 0.0615 mg, *Limnephilus* sp. = 79.39 ± 4.092 mg, and *Caecidotea* sp. = 40.043 ± 3.829 mg. Densities for each species in treatments were: *Limnephilus* sp. = 40 to 80 ind/m², *Caecidotea* sp. = 160 to 320 ind/m², and *H. azteca* = 1000 to 2000 ind/m². These densities were comparable to densities observed in debris dams in the field.

I collected shredders in May 2008. *Caecidotea* sp. and *H. azteca* were from Brown Creek (lat 46°20′N, long 89°50′W), and 4th and 5th instars of *Limnephilus* sp. were from Plum Creek (lat 46°22′N, long 89°50′W). I inspected *Limnephilus* sp. to ensure they all had the same case morphology and were of the same species. I kept shredders in separate containers (by species) in aerated, filtered stream water and provided them with leaf litter as food until the experiment began. I moved them to containers with no leaves 24 h before the start of the experiment to void their guts.

I ran the experiment in mesocosms aerated by air stones and held in an environmental chamber at 15°C on a 14:10-h light:dark cycle. Mesocosms consisted of plastic containers with the bottoms replaced by plastic funnels attached with nontoxic aquarium glue. At the bottom of the funnel, I attached 10 cm of 2.54-cm-diameter tubing sealed with a valve that could be opened and closed. I replaced the plastic floor of the container with a 500-µm-mesh floor that allowed particles to fall through to the funnel and tube. This arrangement prevented reingestion of particles by the organisms and allowed easy particle collection.

At the start of the experiment, I added 0.3 ± 0.01 g of leaves that had been dried at 60°C for 48 h to each mesocosm and filled the mesocosms with 500 mL of filtered (125-µm mesh) stream water. The filter removed invertebrates but allowed microorganisms to pass through. I left the mesocosms undisturbed for 5 d to allow microbial colonization and then drained the mesocosms to remove leachate (Swan and Palmer 2006). I added fresh, filtered stream water and invertebrates to each mesocosm using a randomized design.

Every 4 d for 24 d ($n = 6$ time periods), I opened the valve in each mesocosm and drained all of the water and particles into a container. I then closed the valve, added fresh, filtered stream water to each mesocosm, and noted and replaced dead invertebrates. I separated particles into 3 size classes by wet sieving (500 to 250 µm, 251 to 125 µm, and 126 to 63 µm), dried the particles at 60°C for 48 h, and weighed them. I saved the dried particles for elemental analysis of C and N content on a Costech Elemental Analyzer (Costech Instruments, Valencia, California). I did not run elemental analysis on control samples because there was too little material (<0.5 mg).

Statistical analysis

I checked data for normality with Lilliefors tests and examined residual plots to check for equal variance. Data transformations, where necessary, are detailed below. I estimated particle production rates by calculating a unitless coefficient (r) that reflected the change in particle mass produced over time in the logarithmic model:

$$M_t = r\ln(t) - b$$

where M_t is the mass of particles produced up to time t, and b is a fitted constant. I estimated coefficients with the *glm* function in R (version 2.12.2; R Development Core Team, Vienna, Austria). I compared *r*-values among treatments with a 1-way analysis of variance (ANOVA).

I estimated the expected particle production in mixed-species treatments with double or triple logarithmic models. For example,
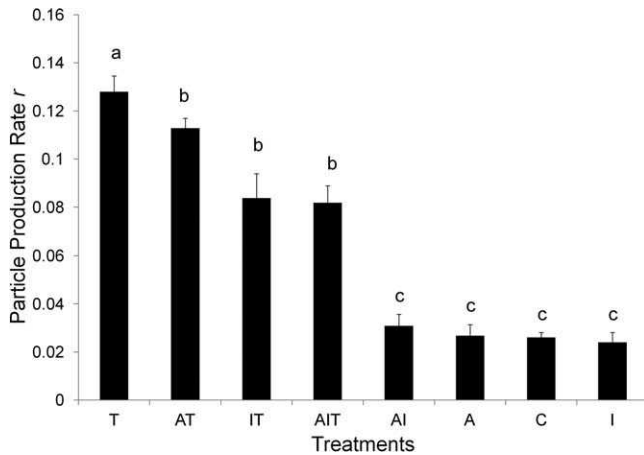
FIG. 1.   Mean (+1 SE) particle production rates expressed as the mean unitless coefficient (r) that controlled the change in particle production rate over time in each experimental treatment. Bars with the same letter are not significantly different (Tukey Honestly Significant Difference). A = Amphipod (*Hyalella azteca*), T = Trichoptera (*Limnephilus* sp.), I = Isopoda (*Caecidotea* sp.), C = Control.

$$M_t = 0.5r_1\ln(t) + 0.5r_2\ln(t) - b_1 - b_2,$$

which simplifies to

$$M_t = \ln(t^{0.5r_1}t^{0.5r_2}) - b_1 - b_2.$$

These models were parameterized with r and b values from single-species treatments in a manner similar in concept to double and triple exponential models used for estimating expected decomposition rates in mixed-leaf-species treatments. This method produces more accurate predictions of mixed species treatments than simply averaging together the total particles produced in each single-species treatment (see Wieder and Lang 1982, Ostrofsky 2007). I used t-tests to compare the observed and expected total particles produced by day 24 for each treatment (Dunn–Sidak-adjusted $\alpha = 0.013$).

I expressed the average particle size distribution for each replicate as the proportion of particles in each size class through time. I compared arcsin(x)-transformed particle size distributions among treatments with a multivariate analysis of variance (MANOVA). I estimated the expected particle distributions for mixed-species treatments by averaging single-species distributions and compared observed and expected distributions with t-tests (Dunn–Sidak adjusted $\alpha = 0.013$ to control for Type I error).

C:N of particles did not appear to follow any temporal trends, so I collapsed the data into mean values across the sampling period. I compared mean C:N of particles in each size class and treatment over time with a 2-way ANOVA and remaining leaf mass across treatments with a 1-way ANOVA. I calculated the difference between leaf mass loss and particle mass for each replicate and compared values across treatments with a 1-way ANOVA. I used particle mass produced as a predictor of leaf mass loss in a linear regression. These statistical analyses were done in SYSTAT (version 10; SYSTAT Inc., Karnataka, India).

Results

Particle production

Particle production rates differed among treatments ($F_{7,24} = 55.8$, $p < 0.0001$; Fig. 1). The most important factor explaining FPOM r-values was the presence of the functionally dominant detritivore, *Limnephilus* sp. Treatments fell into 3 separate groups: 1) *Limnephilus* sp. treatment had the fastest r, 2) *H. azteca*–*Limnephilus* sp., *Caecidotea* sp.–*Limnephilus* sp., and *H. azteca*–*Caecidotea* sp.–*Limnephilus* sp. treatments had intermediate r, and 3) the *H. azteca*–*Caecidotea* sp., *H. azteca*, *Caecidotea* sp., and control treatments had slow r. Some observed r-values in the mixed-species treatments differed from values predicted by the additive logarithmic models. The *H. azteca*–*Limnephilus* sp. ($t = -8.263$, df = 18, $p < 0.001$), *H. azteca*–*Caecidotea* sp. ($t = -3.125$, df = 18, $p = 0.005$), and *H. azteca*–*Caecidotea* sp.–*Limnephilus* sp. treatments ($t = -9.456$, df = 66, $p < 0.001$) had significantly faster r than expected, whereas the *Caecidotea* sp.–*Limnephilus* sp. treatment did not differ from expected ($t = -2.734$, df = 18, $p = 0.014$) (Fig. 2).

Particle size distribution

Particle size distributions differed among treatments (Wilks' lambda, $F_{14,46} = 8.5$, $p < 0.0001$; Fig. 3A, B). The *Limnephilus* sp. treatment had a particle size distribution that was skewed heavily toward production of larger particles ($59.6 \pm 0.01\%$ of distribution; mean $\pm$ SE). Mixed-species treatments that included *Limnephilus* sp. tended to have larger particles (*Caecidotea* sp.–*Limnephilus* sp.: 52.3 ± 0.03, *H. azteca*–*Limnephilus* sp.: 52.5 ± 0.03, *H. azteca*–*Caecidotea* sp.–*Limnephilus* sp.: 47.1 ± 0.03: mean % $\pm$ SE of distribution). Mixed- and single-species treatments that did not include *Limnephilus* sp. tended to have more-even particle distributions than treatments that included *Limnephilus* sp. (Fig. 3A, B). The particle size distributions of the mixed-species treatment *H. azteca*–*Caecidotea* sp. (Wilks' lambda, $F_{2,17} = 1.55$, $p = 0.241$) and *Caecidotea* sp.–*Limnephilus* sp. (Wilks' lambda, $F_{2,17} = 2.92$, $p = 0.081$) did not differ
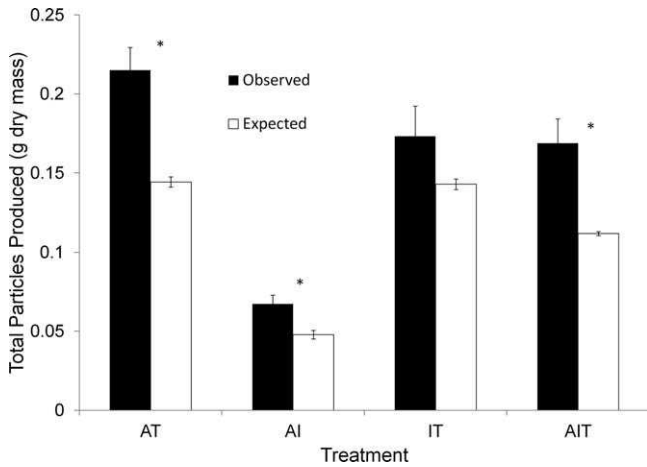
FIG. 2. Mean (±1 SE) observed and expected particle production rates (r) in mixed-species treatments. Expected particle production rates were calculated based on double and triple logarithmic production models informed by single-species treatments. * indicates significant difference between observed and expected values. Treatment abbreviations are as in Fig. 1.

from expected based on linear averaging of single-species combinations (Fig. 4A, B). The particle distributions of the mixed-species treatments *H. azteca–Limnephilus* sp. (Wilks' lambda, $F_{2,17} = 3.9$, $p = 0.042$) and *H. azteca–Caecidotea* sp.–*Limnephilus* sp. (Wilks' lambda, $F_{2,65} = 54.9$, $p < 0.0001$) differed from expected and were skewed toward larger particles than linear averaging predicted (Fig. 4A, B).

Particle stoichiometry

C:N of particles differed among treatments ($F_{6,63} = 5.0$, $p < 0.0001$) and size classes ($F_{2,63} = 7.1$, $p = 0.002$), but the interaction term was not significant ($F_{12,63} = 0.73$, $p = 0.72$) (Fig. 5). Particle size was negatively related to C:N. Particles in the *H. azteca* treatment had the lowest C:N, and particles in the 2-species treatments that included *Limnephilus* sp. had the highest C:N.

Leaf mass loss

Leaf mass remaining at the end of the experiment differed significantly among treatments ($F_{7,24} = 72.0$, $p < 0.0001$). Treatments fell into 2 groups: 1) *Limnephilus* sp., *H. azteca–Limnephilus* sp., *Caecidotea* sp.–*Limnephilus* sp., and *H. azteca–Caecidotea* sp.–*Limnephilus* sp. treatments had more leaf mass loss, and 2) control, *H. azteca*, *Caecidotea* sp., and *H. azteca–Caecidotea* sp. treatments had less leaf mass loss. Leaf mass loss was a highly significant predictor of particles produced (adjusted $R^2 = 0.84$, $F_{1,30} = 164.5$, $p < 0.001$).

Discussion

In this system, the relationship between shredder richness, particle production rates, and leaf mass loss was most heavily affected by a single species, *Limnephilus* sp., whose particle production rate was up to $10\times$ higher per unit mass than that of *H. azteca* and *Caecidotea* sp. This result suggests that the late-
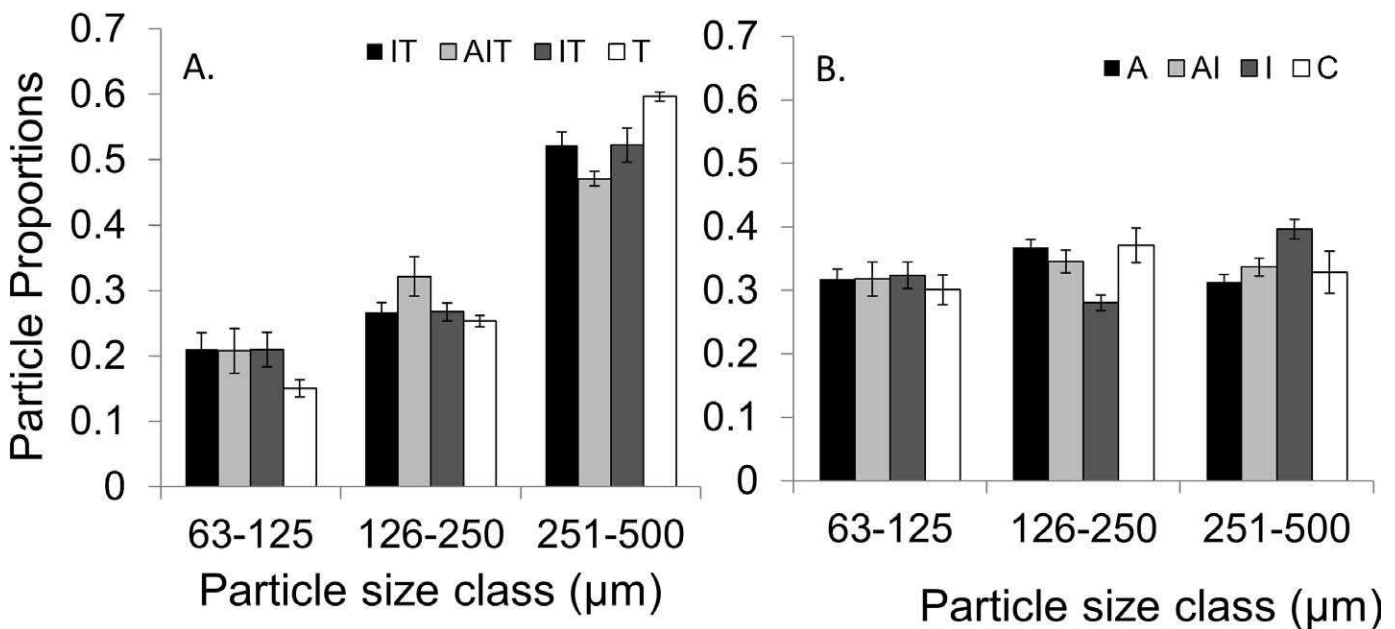

FIG. 3. Mean (±1 SE) proportions of particles in the small (63–125 μm), medium (126–250 μm), and large (>250 μm) size classes in treatments with (A) and without (B) *Limnephilus sp*. Treatment abbreviations are as in Fig. 1.
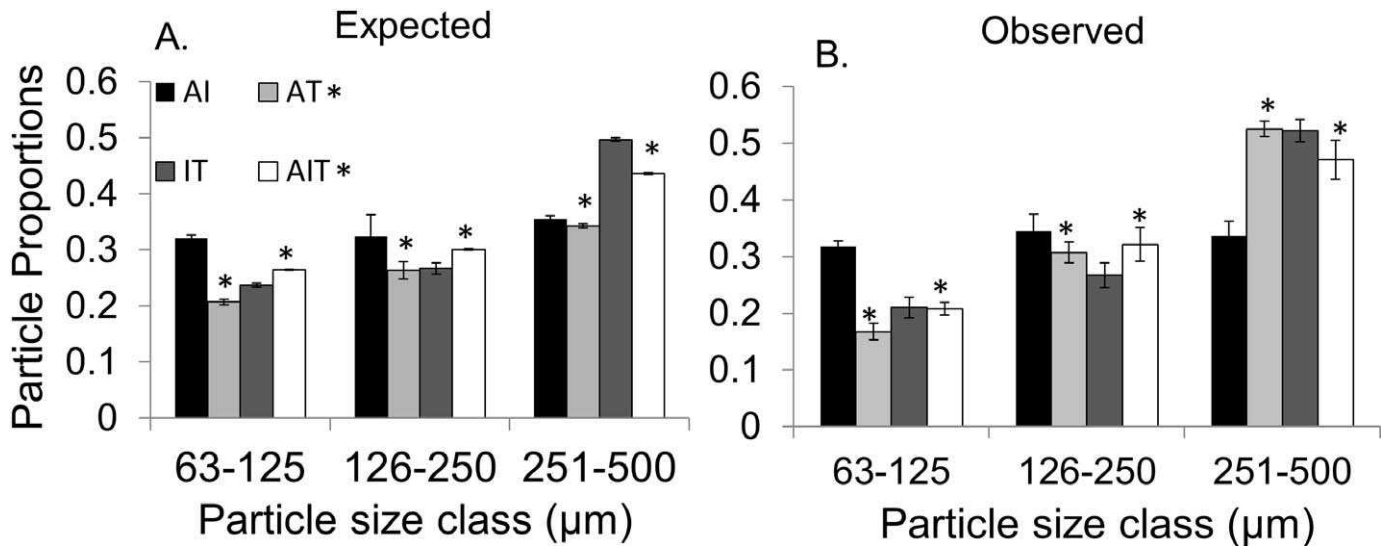
FIG. 4. Mean (±1 SE) expected (A) and observed (B) proportions of particles in the small (63–125 μm), medium (126–250 μm), and large (>250 μm) size classes. Expected values were predicted from linear averages of the single-species particle-size distributions. * indicates significant difference between observed and expected values. Treatment abbreviations are as in Fig. 1.

instar *Limnephilus* sp. used in this experiment is a functionally dominant species that is far more efficient, per unit mass, at converting CPOM to FPOM than the other numerically dominant detritivores present in the surveyed streams.

Based on metabolic-scaling theory, smaller taxa should process leaves faster (per unit biomass) than larger taxa because they have faster metabolisms. For example, Patrick and Fernandez (2012) found that *Lepidostoma* sp. processed leaves much faster than *Pycnopsyche guttifer*. *Lepidostoma* sp. is $^1/_{14}$ the size of *P. guttifer*. However, in my study, the smaller taxa processed leaves more slowly than the larger taxon. My result was surprising because *Limnephilus* sp. is 4 to 25× larger than the other species used and shredder biomass was balanced explicitly among treatments. However, limnephilid caddisflies are often the functionally dominant detritivores in streams (Herbst 1980, 1982, Eggert and Wallace 2007, Creed et al. 2009). Creed et al. (2009) found that *Pycnopsyche gentilis* was both a competitive dominant and a very effective shredder. The advantages of greater size, strength, or morphological adaptations in chewing parts might outweigh the effect of metabolism on leaf processing rates. Thus, making predictions based on metabolic scaling might be inappropriate when comparing phylogenetically different groups. An alternative explanation is that the replacement design may have increased intraspecific competition in treatments with smaller organisms at higher densities. Intraspecific competition would have slowed leaf

processing and could have offset the metabolic differences between species.

Positive effects of detritivore richness on leaf mass loss have been found in most experiments in which species richness was manipulated (Srivastava et al. 2009, Gessner et al. 2010). The increased particle production rate observed in mixed-species treatments in my study was a sampling effect (i.e., caused by the specific taxa used in the study; Huston 1997, Loreau et al. 2001, Hooper et al. 2005). *Limnephilus* sp. clearly had a dominant species effect in these treatments, and synergistic positive effects on decomposition detected in mixed-species treatments probably were caused, in part, by release of *Limnephilus* sp. from intraspecific competition. I also observed synergistic increases in particle production rate in the *Hyalella azteca–Caecidotea* sp. treatment. Therefore, the positive effects of richness in my study could have been caused by facilitation between species, in addition to the dominant species effect of *Limnephilus* sp.

Particle size distributions across treatments reflected the sizes of particles produced by each species individually. Species identity and size have large effects on fecal size (Wotton 1990, Wotton and Malmqvist 2001), and the FPOM in the mesocosms was primarily egested leaf material. The largest shredder, *Limnephilus* sp., tended to produce more large particles than the other shredders (probably because *Limnephilus* sp. was so much larger than the other shredders), with the consequence that mixed-species treatments containing *Limnephilus* sp. tended
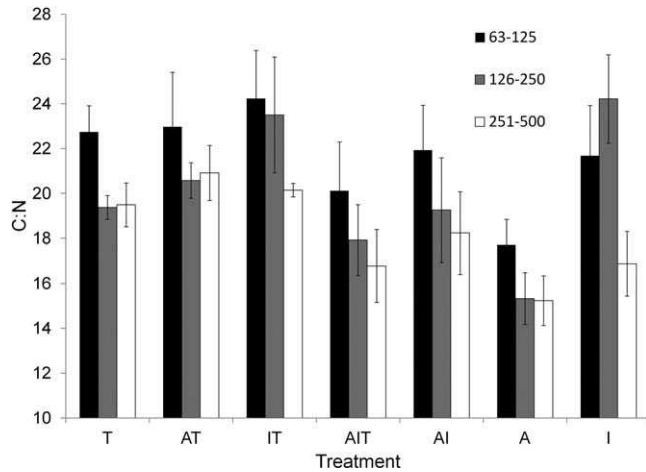
FIG. 5. Mean (±1 SE) particle molar C:N of particles in each size class in each treatment. Treatment abbreviations are as in Fig. 1.

to have larger particles than treatments from which *Limnephilus* sp. was absent. Thus, *Limnephilus* sp. increased the rate of particle production and increased the proportion of large particles.

The finding that larger particles had lower C:N conflicts with reports that larger particles tend to have a higher C:N than smaller particles (Sinsabaugh and Linkins 1990, Bonin et al. 2000, Atkinson et al. 2009). The conflicting results might stem from the source of the particles being studied. Particles collected from large streams and rivers probably consist of a mixture of fine benthic organic matter (FBOM) and seston from terrestrial and aquatic sources that may have been present in the stream for various amounts of time. Most of the N in such particles should be present in the microbial communities growing on the surface of the particle (Sinsabaugh and Linkins 1990, Bonin et al. 2000). Thus, smaller particles with a larger surface-to-volume ratio tend to have lower C:N. The particles in my experiment were freshly produced and came from insect frass and messy feeding. The N in these particles might reflect the amount of N that passed through the invertebrate gut rather than the ratio of surface area for bacterial growth to mass of the particle. If this surmise is correct, then differences among the single-species treatments in particle C:N should indicate differences in taxon-specific assimilation efficiencies (Allan 1995, Wotton and Malmqvist 2001).

Crustaceans produce cellulases and are capable of digesting cellulose in leaves (Chamier 1991, Walters and Smock 1991), whereas the limnephilid caddisflies used in this experiment have little ability to digest cellulose (Martin et al. 1991). The N-poor particles produced by *Limnephilus* sp. could be a result of

passage of C-rich cellulose through their guts undigested, and the high rate of feeding could be a result of compensatory feeding dynamics (Gessner et al. 2010). This explanation fits the results mechanistically because the species that consumed leaves the fastest also released the most organic particles per unit leaf material consumed.

Processing chains that begin with leaf decomposition are an important component of stream food webs (Short and Maslin 1977, Wallace et al. 1982, 1991, Webster and Benfield 1986), and the effect of shredder diversity and abundance on decomposition rates is well studied. However, these 2 lines of research have not been thoroughly integrated (Heard and Richardson 1995). The role of shredder assemblages in determining the characteristics of the initial products of decomposition, fine organic particles, within the processing chain has not been well investigated (Heard and Richardson 1995, but see Wotton and Malmqvist 2001 and Navel et al. 2010). I found that shredder assemblage composition had significant effects on particle production, size distribution of particles produced, and particle C:N. This result suggests that understanding how the composition of a shredding assemblage affects decomposition rates may not yield full understanding of how a shredding assemblage will affect the detritus processing chain because of differences in how shredder assemblages affect particle size spectra and stoichiometry.

Changing the particle size spectrum may affect the collecting and filtering assemblages in streams. Particle size preferences differ among filter feeders. Thus, changing the particle size spectrum could affect the species composition of the filtering guild (Schroder 1987, Wotton 1977, 1990). For example, in Tenderfoot Creek, one of the streams surveyed for my study, several different hydropsychid caddisflies (*Hydropsyche morosa*, *Hydropsyche betteni*, and *Cheumatopsyche* sp.) are very common in riffles (CJP, unpublished data). Each of these species produces nets with different sized mesh openings, and each species has a specific particle-size preference (Runde and Hellenthal 2000a, b). If the mass of particles moving through the system remained constant, but the particle size spectrum shifted to larger particles, *Cheumatopsyche* sp., a small-particle specialist, might be at a disadvantage and experience a reduction in density, whereas *H. betteni*, a large-particle feeder, might respond positively to the spectrum shift. In this context, a more even particle size distribution might support a more diverse group of filter feeders.

Shifts in particle size also may affect the mobility and export rates of organic material from stream reaches. Less force is required to move smaller

particles from the substratum, and smaller particles travel farther before settling than larger particles (Webster et al. 1987, Wallace et al. 1991, Minshall et al. 2000, Thomas et al. 2001). A small shift in the particle size spectrum could yield a significant change in FPOM residence time and standing stock when scaled up to the entire body of organic material present in a reach. A 100-μm downward shift in particle size could double the rate at which particles are lost from a reach and more than double the distance that they travel (Thomas et al. 2001). In the streams on which my experiment was based, such a shift could translate into a decline from 80 g FBOM/m^2 to 20 g/m^2. Such an effect could lead to a meaningful negative effect on the production of the microbial and collector–gatherer assemblages in a stream reach.

In the shredder-driven system described here, functional differences in particle production among shredder species could affect the linked filterers and collector-gatherers. Thus, knowing the rate at which decomposition occurs may not always tell us how detritivores are affecting stream benthic communities. Additional information about where the products of decomposition (FPOM) are going and what form those products take is needed to understand how decomposition rates will affect linked trophic groups.

My results show that the composition of shredder assemblages could exert considerable influence over characteristics of the particles being exported downstream. In my study system, a single dominant species was the most important factor in determining fine-particle production. Detritivore community composition could similarly affect the characteristics of the products of decomposition in terrestrial systems. Leaf decomposition rates are very important, but my results show that different shredder assemblages with similar decomposition rates could have substantially different effects on the physical form of the FPOM they are producing and on the stoichiometric ratios of the particles. Leaf mass loss is only part of the story, and the individual effects of species on the fate of particles produced via decomposition also have an important place in our understanding of how biota regulate decomposition.

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