



Influence of large woody debris on stream insect communities and benthic detritus

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Received 24 December 1998; in revised form 12 August 1999; accepted 3 December 1999

Key words: stream habitat management, benthic macroinvertebrates, leaf processing, particulate organic matter, energetics

Abstract

We examined the extent to which benthic detritus loadings and the functional feeding group structure of stream insect communities respond to channel modifications produced by experimental addition of large woody debris (LWD, entire logs) to Stony Creek, Virginia. Benthic detritus loadings per sample did not change after LWD additions, but large increases in pool habitats created by LWD increased net detritus by an estimated 27 kg (25%) in the 250 m of stream receiving LWD. A large increase in the proportional area of pool habitats may result in a dominance of collector-gatherers and corresponding decreases in shredders and scrapers. Functional feeding group community structure in pools was similar spatially and temporally. Riffles were spatially convergent, but differed temporally. Community structure was significantly different between pools and riffles. The results indicate possible large scale influences in overall community structure due to channel alterations by LWD, but little within-habitat change.

Introduction

Invertebrate communities in forested, temperate streams are thought to be structured on the basis of detritus processing with several functional feeding groups evolved to capitalize on energy leakage of the larger particle detritivores (Cummins, 1974; Vannote et al., 1980). Allochthonous inputs (especially leaves) appear to be a very important energy source driving community structure (Minshall, 1967). Anderson et al. (1978) found that invertebrate standing crops in leaf debris were two orders of magnitude higher than on wood. This relationship appears to remain intact for detritus trapped in the substratum as well (Egglishaw, 1964; Rabeni & Minshall, 1977; Flecker, 1984).

Because the majority of a stream's energy input

comes in a relatively short pulse from autumn litter-fall (Cuffney & Wallace, 1989), the retention capacity of structures such as LWD becomes very important for providing a food reservoir throughout the year. Experimental additions of whole-leaf detritus in a Pacific Northwest stream resulted in greater abundance of the collector-gatherer and collector-filterer functional feeding groups (sensu Cummins, 1973) than before additions (Richardson & Neill, 1991). The presence of LWD increased retention of coarse particulate organic matter. This allowed for more complete leaf processing at the site by shredders. Subsequently, more fine particulate organic matter was made available, which secondarily supported higher densities of collector-gatherers and collector-filterers (Richardson & Neill, 1991).

Relative to other non-mineral substrates, the residence time of LWD is much longer and it provides a

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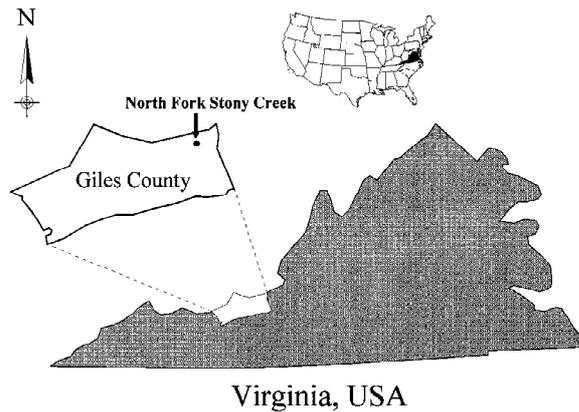


Figure 1. Location of Stony Creek in the Appalachian Mountain region of Virginia, U.S.A.

stable base that resists disturbances. It often maintains a dominant influence in structuring channel morphology (Keller & Swanson, 1979; Bilby, 1984; Andrus et al., 1988; Hilderbrand et al., 1997) and sediment retention (Megahan, 1982). It also provides a major storage mechanism through the physical capture of entrained organic materials in debris dams and by slowing throughput (Bilby & Likens, 1980; Speaker et al., 1984; Smock et al., 1989; Trotter, 1990). These properties may increase an aquatic system's stability, resiliency and resistance to disturbance.

Secondarily, LWD can influence retention, thereby potentially affecting invertebrate communities by increasing the amount of depositional areas and changing the proportional abundance of pool and riffle habitats. However, little information exists regarding secondary effects. The purpose of this paper is to report relations found between benthic detritus dynamics, experimental additions of LWD and the benthic macroinvertebrate community of a small forested stream in the middle Appalachians.

Methods

The study stream, North Fork Stony Creek (hereafter referred to as Stony Creek), is a third order, low gradient (<5%) stream at approximately 920 m in elevation in the Appalachian Mountains of southwestern Virginia (Figure 1). The creek is surrounded by a mature, second growth mix of soft- and hardwood forest, and dominant substrates are small and large gravels. We selected an 600 m reach in the Jefferson National Forest for LWD additions. This reach was divided

into two, 250 m sections, separated by a 50 m buffer. The upstream section served as an unmanipulated reference, while we added LWD (entire logs) to the downstream section (systematic placement section).

Prior to manipulation, we demarcated pool and riffle habitat units following descriptions by Bisson et al. (1982) and constructed an accurate stream map (using ARC/INFO) for each study section. Runs were classed with riffles, glides were classed with pools and the major pool-forming element (e.g. LWD, boulder) was recorded. Preexisting LWD was also measured and recorded. The stream was re-mapped 1 year after LWD additions. Pool and riffle area were calculated based on these maps, which enabled us to estimate the total weight of benthic detritus retained in each habitat type.

Location and positioning of logs were subjectively determined by our judgements of how best to enhance stream habitats. The log positions used included: 1. positions based on orientation of the log axis to the stream bank in 45° intervals (upstream, perpendicular and downstream; excluding parallel to bank); and 2. orientation to the water surface (dam with entire log submerged or ramp with one end protruding onto bank). Prior to additions, we marked log positions and the length of log needed at a particular site was determined. Selected trees were felled at least 10-m from the stream bank, stripped of limbs and cut to a minimum 4-m length and 25-cm top diameter. Limbs were removed to maintain uniformity between logs. We used a front-end loader with a hydraulic winch to position logs in the stream. Logs were not keyed or otherwise pinned to the channel. Heavy equipment was operated in the riparian zone, but did not enter the channel. We added 50 logs in the systematic placement section of Stony Creek, representing seven local tree species.

We sampled benthic macroinvertebrates and detritus using a 0.1 m² portable invertebrate box sampler (PIBS, Ellis-Rutter Associates, Punta Gorda, Florida, U.S.A.) with 350 µm mesh net. Sampling occurred during late May, before LWD additions and 1 year after LWD additions, also in late May. We collected five paired riffle samples and three paired pool samples per section at randomly determined locations. Members of a pair were collected in similar local habitat conditions to minimize variability. To ensure adequate representation of all habitat types, different pairs were taken in different habitats within pools or riffles (e.g. heads, tails and centers of pools). During collection, the substrate was disturbed to a depth of 8–10 cm and

was agitated for approximately 2 min, which preliminary trials indicated was long enough to collect most organisms. We assumed that all leaf detritus was also collected during sampling. Because of low current velocities in pools, we used a hand operated diaphragm pump when sampling pools to generate the current necessary to carry invertebrates and detritus into the collection net. The maximum depth sampled in pools was limited to the height of the PIBS sampler (~ 0.45 m). Samples were preserved in 95% ethanol.

In the laboratory, we separated organisms and leaf detritus from mineral substrates by elutriation in a column of moving water and collection in a 500 μm sieve. Invertebrates were separated from the detritus by hand with the aid of a magnifying lamp and the mineral substrates were examined for any remaining invertebrates. Organisms were counted and identified to genus when practical. Most Diptera except for members of Tipulidae were identified to family. However, identifications were taken as far as needed to determine trophic relationships (Merritt & Cummins, 1984). Detritus was dried to constant weight and recorded.

To control variability and increase statistical power, we used the mean of each pair as a sample for analysis rather than each individual member. This generally reduced the coefficient of variation for each group by approximately 10%. Analysis of variance (ANOVA) was used to assess the patterns of variability within and among detritus samples and within FFGs. We also used multivariate analysis of variance (MANOVA) with specific contrast statements to test for spatial and temporal differences in FFG abundances. Because of the number of response variables, we set the significance level at $\alpha = 0.01$ for analyses using MANOVA, whereas significance for all other tests was set at $\alpha = 0.05$. All invertebrate and detritus data were normalized using a $\log_{10}(Y+1)$ transformation. All transformed data passed the Kolmogorov-Smirnov one sample goodness of fit test.

Results

Stream channel and detritus

There were no significant differences in point samples of benthic detritus between treatment sections, between years, or in their interaction (ANOVA, $P > 0.01$). However, channel modifications due to LWD additions resulted in a net increase in benthic detritus throughout the study reach due to a net increase

Table 1. Reach-level channel characteristics in the systematic placement and reference sections of Stony Creek before (May 1993) and after (May 1994) LWD additions

| | Systematic Placement | | Reference Section | |
|---------------------------------|----------------------|------|-------------------|------|
| | 1993 | 1994 | 1993 | 1994 |
| Number of pools | 5 | 10 | 4 | 5 |
| Mean pool length (m) | 10.6 | 14.1 | 16.6 | 13.0 |
| Mean pool area (m^2) | 45 | 55 | 53 | 44 |
| Total pool area | 222 | 546 | 213 | 220 |
| % change in area | | 146 | | 3 |
| Number of riffles | 6 | 7 | 4 | 4 |
| Mean riffle length | 32.1 | 12.8 | 41.8 | 41.5 |
| Mean riffle area | 128 | 55 | 15 | 151 |
| Total riffle area | 768 | 443 | 623 | 615 |
| % change in area | | -42 | | -1 |

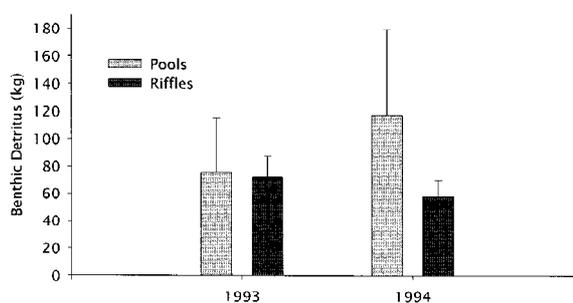


Figure 2. Estimated total benthic detritus (kg) contained within the 600 m study reach before (1993) and one year after (1994) experimental LWD additions. Error bars indicate 2 standard deviations from the mean.

in depositional areas. After LWD additions, total area occupied by pools more than doubled (from 222 m^2 to 546 m^2) concurrent with a 42% decrease in riffle area (from 768 m^2 to 443 m^2 ; Table 1). Pools contained significantly more benthic detritus (9.2 ± 4.8 g per 0.01 m^2) than riffles (3.1 ± 0.7 g per 0.01 m^2), but showed no post-treatment response to LWD additions relative to the reference section. Retention of benthic detritus was, therefore, a function of channel morphology and only indirectly influenced by LWD.

Extrapolating to the entire 600 m study reach (but keeping in mind that the 250 m reference section did not change habitat proportions), total benthic detritus contained in pools increased by 41.7 kg, from 75.5 kg in 1993 to 117.2 kg in 1994 after LWD additions (Figure 2). Net benthic detritus in riffles decreased by 14.3 kg after LWD additions, dropping from 71.6 in 1993 down to 57.3 kg in post-treatment 1994. Focus-

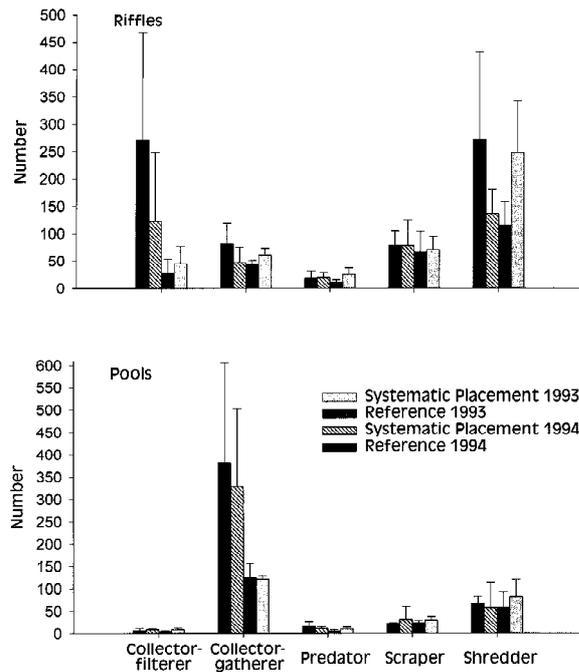


Figure 3. Functional feeding group mean numbers per 0.1 m² by habitat type and treatment section in Stony Creek before (1993) and one year after (1994) experimental LWD additions. Error bars indicate 2 standard deviations from the mean.

ing only on the treatment section receiving LWD, total net change in benthic detritus increased by 25% (27.0 kg).

Functional feeding groups

Five functional feeding groups were represented in the insect community of Stony Creek (Table 2). Collector-gatherers numerically dominated the feeding group structure (Figure 3). Shredders, scrapers, collector-filterers and predators followed in abundance. All groups except predators exhibited a significant association with either pools or riffles. Collector-gatherers were significantly more abundant in pools mainly due to the Chironomidae, whereas all remaining functional feeding groups were greater in riffles. Predators, although not significant (ANOVA, $P=0.07$), were more numerous in riffles.

Community structure based on FFGs was similar both spatially and temporally between treatment sections for pools, and was spatially similar for riffles in 1993, but differed significantly between years in riffles. However, a large number of Simuliidae, having not yet emerged in the reference section during 1994, produced a significant difference (MANOVA,

Table 2. Major benthic insect taxa identified in Stony Creek and their functional feeding group allocation.

| Taxon | Functional feeding group | | | | |
|-------------------|--------------------------|----------|---------|--------------------|----------|
| | Collector Gatherer | Shredder | Scraper | Collector Filterer | Predator |
| Diptera | | | | | |
| Ceratopogonidae | | | | | X |
| Chironomidae | X | | | | |
| Empididae | | | | | X |
| Nymphomyiidae | | | X | | |
| Simuliidae | | | | X | |
| Tabanidae | | | | | X |
| Tipulidae: | | | | | |
| Dicranota | | | | | X |
| Hexatoma | | | | | X |
| Pedicia | | | | | X |
| Pilaria | | | | | X |
| Tipula | | X | | | |
| Ephemeroptera | | | | | |
| Baetidae | X | | | | |
| Ephemerellidae: | | | | | |
| Ephemerella | | X | | | |
| Eurylophella | | X | | | |
| Ephemeridae: | | X | | | |
| Ephemera | | X | | | |
| Heptageniidae: | | | | | |
| Epeorus | | | X | | |
| Stenonema | | | X | | |
| Leptophlebiidae: | | | | | |
| Habrophlebia | | | X | | |
| Potamanthidae: | | | | | |
| Potamanthus | | | | | X |
| Plecoptera | | | | | |
| Chloroperlidae | | | | | X |
| Nemouridae: | | | | | |
| Amphinemura | | X | | | |
| Shipsa | | X | | | |
| Peltoperlidae: | | | | | |
| Tallaperla | | X | | | |
| Perlidae: | | | | | |
| Eccoptura | | | | | X |
| Perlodidae: | | | | | |
| Isoperla | | | | | X |
| Trichoptera | | | | | |
| Hydropsychidae: | | | | | |
| Cheumatopsyche | | | | | X |
| Diplectrona | | | | | X |
| Hydroptilidae: | | | | | |
| Palaeagapetus | | X | | | |
| Lepidostomatidae: | | | | | |
| Lepidostoma | | X | | | |
| Limnephilidae: | | | | | |
| Neophylax | | X | | | |
| Pycnopsyche | | X | | | |
| Odontoceridae: | | | | | |
| Psilotreta | | | X | | |
| Philopotamidae: | | | | | |
| Dolophilodes | | | | | X |

Continued on p. 183

Table 2. Continued

| Taxon | Functional feeding group | | | | |
|--------------------|--------------------------|----------|---------|-----------|----------|
| | Collector Gatherer | Shredder | Scraper | Collector | Predator |
| | | | | Filterer | |
| Polycentropodidae: | | | | | |
| Polycentropus | | | | | X |
| Rhyacophilidae: | | | | | |
| Rhyacophila | | | | | X |

Table 3. Relationships between abundance of insects (mean no/0.1 m²) and substratum detritus (mean g/0.1 m², dry weight) in Stony Creek

| | Reference section | | | | Systematic placement | | | |
|---------------|-------------------|------|-------|------|----------------------|------|-------|------|
| | Riffles | | Pools | | Riffles | | Pools | |
| | 1993 | 1994 | 1993 | 1994 | 1993 | 1994 | 1993 | 1994 |
| Detritus | 3.9 | 2.1 | 5.1 | 13.0 | 3.7 | 3.2 | 9.1 | 9.8 |
| Diptera | 55 | 312 | 109 | 343 | 78 | 167 | 100 | 308 |
| Plecoptera | 119 | 277 | 59 | 65 | 251 | 139 | 82 | 57 |
| Coleoptera | 66 | 73 | 23 | 20 | 70 | 72 | 26 | 31 |
| Ephemeroptera | 5 | 30 | 8 | 49 | 6 | 6 | 21 | 18 |
| Trichoptera | 7 | 14 | 5 | 6 | 23 | 15 | 11 | 5 |

$P < 0.0001$) in community structure between riffles of the systematic placement and reference sections in 1994. No interactions were significant. Additionally, FFG community structure was significantly different between pools and riffles (MANOVA, $P < 0.0001$). Relationships between substratum detritus and abundance of insects are given in Table 3.

Discussion

Detritus retention in forested streams appears to be greatly enhanced by the presence of LWD. Although the effect is most often attributed to debris dams (Bilby & Likens, 1980; Speaker et al., 1984; Smock et al., 1989; Trotter, 1990; Jones & Smock, 1991; Ehrman and Lamberti, 1992), the current study demonstrates the importance of the secondary effect of LWD by modifying channel morphology and thereby creating depositional areas. We predicted that benthic detritus retention would increase after LWD additions. This should be expressed as a Section \times Year effect. There was a weak (not significant) effect in Stony Creek, but detritus amounts actually decreased slightly in riffles after LWD additions, while amounts in pools increased in both treatment sections through time. We accept the original prediction that LWD additions in-

crease benthic detritus, but for a different reason. Detritus amounts per sample remained nearly equal for each habitat type and experimental section through time. However, the proportional area of pools changed substantially in the systematic placement section due to additions of LWD. Decreased current velocities in pools resulted in deposition and increased detritus loadings. Rather than LWD increasing detritus retention per unit area, LWD increased depositional area and a corresponding overall net increase in benthic detritus (25% increase in the section receiving LWD). Extrapolating to the reach level, the logical extension is a huge increase in the amount of stored detritus due to increased area of pools. We did not sample debris dams. Inclusion of these retention sources with additions of LWD undoubtedly increased detritus loadings by another factor, although most detritus stored in dams was above the water line.

Speaker et al. (1984) reported that riffles trapped leaves more efficiently than pools regardless of substrate type. We found just the opposite in the current study, but our sampling included leaf fragments and organic materials on top of the substrate as well. It is possible that the greater storage ability of pools limited detritus supply to riffles, but not likely. The differing results might also arise from substrate size differences. The study section of Stony Creek contained few of the coarser substrates typically found in riffles. Even a small percentage of these coarse substrates interspersed among gravels probably influence (and increase) detritus retention in riffles of most streams because of the coarse substrate's hydraulic influences on flow direction and deposition.

Numerous studies have documented changes in benthic macroinvertebrate community structure in response to changing or contrasting environmental conditions (Woodall & Wallace, 1972; Newbold et al., 1980; Haefner & Wallace, 1981; Murphy & Hall, 1981; Gurtz & Wallace, 1984; Wallace et al., 1988). However, community differences in all of these studies occurred on a changing background template of terrestrial vegetation succession influencing the stream. In these cases, the influence is not only through allochthonous inputs, but also in the amount of sunlight allowed into the stream, temperature change, etc. In the current study, the background environmental template was held constant while local channel conditions were manipulated. Because of this, we expect any changes occurring to be based solely on habitat associations of taxa, net changes in detritus retention and the hydraulic properties of the stream. The quantity

or quality of energy inputs should have remained similar, but their residence times were manipulated by our treatments.

The River Continuum Concept (RCC; Vannote et al., 1980) predicts shredder dominated assemblages driven by allochthonous energy inputs in small, forested streams such as Stony Creek. While a somewhat heuristic model, RCC is still a useful starting point in forested watersheds. By default, RCC implies a positive relationship between detritus and shredders, with the remainder of the processing community (functional feeding groups) adapted to exist on incomplete energy transformation by shredders. Insect abundances and detritus amount were positively related for most insects in studies by Egglisshaw (1964) and Minshall & Minshall (1977). Hildrew et al. (1991) reported a positive relationship for shredders whereas Townsend & Hildrew (1984) reported all other functional feeding groups declined in more highly retentive areas. Conversely, no relationship could be determined by Petersen & Cummins (1974).

Stony Creek was dominated by shredders. Paradoxically, shredders dominated riffles relative to pools, although pools contained significantly more detritus. A large portion of the detritus in pools appeared to be broken down into very small fragments relative to riffles. Riffles may contain higher quality detritus than pools. The size fraction in pools is possibly too small to be of use to shredders, or the smallest size fraction somehow inhibits feeding or respiration by shredders and the other groups negatively related to pools and detritus amount. Detritus could also be just a surrogate for an unmeasured habitat characteristic. Another possibility is that the sampling protocol excluded shredder habitats – we did not sample leaf packs or detritus trapped on debris dams because these represented a minor portion of available habitats. Most detritus associated with debris dams was above the waterline for most of the year. Sometimes, large amounts of whole leaf detritus were collected in pool samples, and these would figure into the final analysis unless physical conditions within these areas (e.g. low dissolved oxygen levels) precluded invertebrates.

In Stony Creek, collector-gatherers demonstrated a significant positive relationship with detritus, predators showed no correlation, and shredders, scrapers and collector-filterers a significant negative relationship. All functional feeding groups were closely associated with either pools or riffles. Overall, collector-gatherers were the most abundant group and inhabited pools almost three-to-one over riffles. In contrast,

shredders were the next most abundant group and numerically dominated riffle habitats almost four-to-one over pools. In the treatment sections where LWD additions substantially increased pool surface area at the expense of riffle area, we should expect to see a net decrease in abundances of all groups except collector-gatherers. The most pronounced decrease should occur for shredders, but could also substantially reduce scraper and collector-filterer numbers. In contrast, collector-gatherers should experience a large net increase.

Theoretically, the decrease in shredders could have major impacts on the assemblage structure because shredders are the initial component in processing allochthonous detritus inputs. Cuffney & Wallace (1989) reported a dramatic decline in FPOM export levels after the decimation of the shredder population by insecticide application. While drought conditions exacerbated the decrease, invertebrate removal accounted for 75% of the reduction. This decrease might potentially cause food limitations for the other functional groups, resulting in an overall decrease in abundance which could impact higher trophic levels. Richardson & Neill (1991) reported increases in collector-gatherer and collector-filterer densities in response to increased inputs of whole leaf detritus in experimental stream channels. While they attributed the increases to higher survival, it could also result from a lifting of food limitations. However, this last statement probably cannot be tested because effects might take several years to detect due to the fact that the amount of FPOM stored in the stream channel is much greater than the amount exported (Cuffney & Wallace, 1989). Even with a time lag introduced in detritus decomposition, the large increase in stored detritus coupled with mechanical abrasion and microbial decomposition of leaf particles will probably be sufficient to maintain the FPOM reservoir.

Despite the changes in benthic detritus loadings found in our study, insect community structure as measured by abundance of functional feeding groups remained similar spatially and temporally. However, community structure differed substantially between pools and riffles, and LWD additions greatly shifted the pool/riffle relationships. This indicates that whereas benthic insect communities may be structurally resistant to changes in energy inputs at the habitat unit scale (pool, riffle), changes in habitat proportions due to LWD or other structures may potentially reshape the overall trophic relations at larger spatial scales.

Acknowledgements

The USDA Forest Service Southern Research Station provided funding for this project under cooperative agreement 29-825. We thank R. Allen, G. Annis, J. Bates, B. Beaty, J. Burress, A. Dolloff, S. Gerken, J. Harefield, K. Harpster, T. Huffman, K. Leftwich, K. Newman, M. Underwood and S. White for field and lab assistance. D. Orth and R. Voshell provided important insights throughout this project, while S. Barras and K. Engelhardt provided excellent reviews of the manuscript. We thank M. Underwood for preparing the stream location map.

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