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Primary Research Paper

# Invertebrate community and stream substrate responses to woody debris removal from an ice storm-impacted stream system, NY USA

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**Abstract**

We assessed the influence of ice-storm-derived debris dams on aquatic macroinvertebrates and stream substrates in a high-gradient watershed in the eastern Adirondack Mountains of New York State. Using a modification of electrofishing techniques, invertebrates were collected once before (June 2000) and once after (June 2001) wood removal from the downstream reach in each of six pairs of reaches (second and third-order streams). Stream substrates were also mapped in 2000 and 2001 to evaluate shifts in dominant substrates within a reach following wood removal. The following metrics were used to compare the invertebrate communities before and after wood removal: genera similarity, Shannon–Weiner equitability, taxa richness, dominant taxon, percent dominance and functional feeding group relative abundance. The changes in removal reaches were evaluated relative to changes in upstream reference reaches using a Before-After Control-Impact (BACI) design and analysis. Stream substrates did not change significantly in response to wood removal, although a trend toward coarser substrates was observed following removal. Following wood removal, the relative proportion of grazers increased upstream and downstream from removed dams in all streams; however, comparisons of other metrics indicated no significant response to removal. Invertebrate responses to wood removal were lower than expected, perhaps due to the presence of abundant boulder-formed pools in this high gradient system.

## Introduction

Large-extent physical disturbances, such as ice storms, can produce wide-ranging impacts on ecosystem structure and function (Dale et al., 2001; Bernhardt et al., 2003). In January 1998, a severe ice storm occurred in the northeastern U.S. and eastern Canada (DeGaetano, 2000), producing extensive damage to tree limbs throughout the forested landscape (Millward & Kraft, 2004). Direct impacts from damage to trees produced openings in the forest canopy (Duguay et al., 2001; Rhoads et al., 2002), and wood was deposited in abundance onto the forest floor (Hooper et al., 2001) and into streams (Kraft et al., 2002). Woody debris in streams can affect stream geomorphology (Montgomery et al., 1995), stream sediments (Diez et al., 2000), stream nutrients (Vallett et al., 2002), and stream biotic communities (Lemly & Hilderbrand, 2000). By manipulating debris dams and woody debris in ten stream reaches in this study, we evaluated the influence of ice storm-derived wood deposition on both the lotic invertebrate community and stream substrate composition.

Woody debris in streams provides habitat and retains nutrients used by a wide variety of stream invertebrates (Elliott, 1986; O'Connor, 1991; Weigelhofer & Waringer, 1999). Leaves and particulate organic matter trapped by woody debris and debris dams provide abundant food for invertebrates and can increase nutrient uptake in streams (Newbold et al., 1982; Smock et al., 1989;

Raikow et al., 1995). Wood also provides a surface on which algae and other microorganisms can accumulate, creating a biofilm that augments invertebrate food sources (Hax & Golladay, 1993; Phillips & Kilambi, 1994a, b). Additionally, pools formed by wood provide slow-water habitat that contribute to invertebrate community diversity at the stream reach scale (Wallace et al., 1995; Lemly & Hilderbrand, 2000). These pools also serve as a refuge for drifting invertebrates during high flow events (O'Connor, 1991; Palmer et al., 1996).

In streams, woody debris directly and indirectly influences invertebrate taxon richness and invertebrate community composition. Wood provides a carbon source, acts as substrate, retains sediment and creates stream features such as pools. The importance of woody debris as structure and substrate for colonization is particularly apparent in streams with fine substrates (Smock et al., 1989), but wood can also provide invertebrate habitat when streambeds are more stable (Johnson et al., 2003). Johnson et al. (2003) also found that macroinvertebrate communities associated with woody debris were more diverse than invertebrate communities not associated with wood. Invertebrate community responses to LWD manipulations may be attributable to local changes in the physical characteristics of the stream, such as velocity and substrate (Wallace et al., 1995; Lemly & Hilderbrand, 2000). For example, Diez et al. (2000) found that woody debris and debris dam removal from high gradient streams in northern Spain led to significant decreases in the retention of fine materials and an increase in coarse substrates. In highly disturbed streams, following the eruption of Mount Saint Helens, woody debris removal increased scour of fine sediments and exposure of gravel beds (Lisle, 1995). The specific addition of woody debris to a stream reach can also increase pool area, however, the extent of this increase may depend upon the abundance of other stream features that contribute to pool formation such as upstream channel constrictions and boulders (Hilderbrand et al., 1997; Thompson & Hoffman, 2001).

Natural or artificial changes in woody debris and debris dam abundance can lead to shifts in the dominant invertebrate taxa and the relative abundance of invertebrate feeding guilds within a stream reach (Elliott, 1986; Smock et al., 1989; Wallace et al., 1995; Lemly & Hilderbrand, 2000). For example, the addition of woody debris to streams in the southern Appalachian Mountains (North Carolina) by Wallace et al. (1995) led to significant decreases in scraper (grazer) and filterer abundances and significant increases in collector and predator abundances, but no significant response in shredder abundance. Alternatively, Hilderbrand et al. (1997), also working in a first-order stream in the Appalachian region (southwest Virginia), found no significant invertebrate response to large woody debris (LWD) additions.

In this paper we evaluate stream substrate and invertebrate community response to the removal of six naturally occurring debris dams in second- and third-order streams of an ice-storm-impacted watershed. Based on research investigating the effects both of the addition and the removal of wood in other similar stream systems, we hypothesized that debris dam removal would induce the following changes: (1) a decrease in the proportion of fine substrates and an increase in coarser substrates; (2) changes in dominant taxon and invertebrate community equitability; (3) decreased similarity in the invertebrate communities between sites of dam removal and comparable sites with unmanipulated dams due to shifts from pool to riffle habitat and a loss of source populations in dams; and (4) decreased relative abundance of shredder and collector feeding guilds and increased relative abundance of filterers and grazers in the vicinity of debris dams. Based on the overall response from the multi-metric analysis, we infer potential indirect impacts of the 1998 ice storm on the invertebrate community via wood deposition.

## Methods

### *Study site*

This study was conducted on second- and third-order streams within the Rocky Branch watershed located in the eastern Adirondack Mountains of New York State (Fig. 1). The study streams were mid- to high-gradient with pool-cascade or pool-riffle flow regimes. Mean bankfull widths were 6.9 m and 11.3 m, respectively for second- and third-order stream reaches. Substrates were

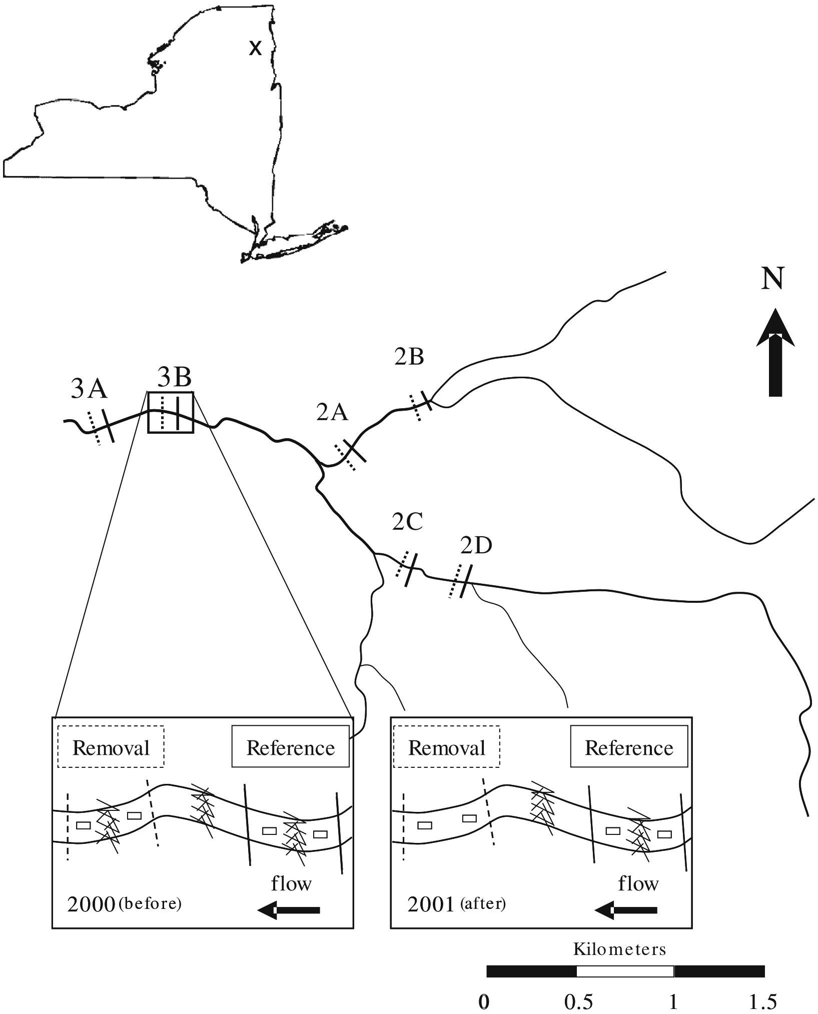


*Figure 1.* Map of Rocky Branch watershed located in the eastern Adirondack Mountains, NY (44° 21′ lat, 73° 41′ lng). Reach pairs are labeled with stream order and reach letter. Solid lines across streams represent reference reaches and dashed lines represent removal reaches. The inset depicts the arrangement of each reach pair. Small rectangles represent invertebrate sampling locations in 2000 and 2001.

dominated by boulders and cobble. Portions of the study watershed have been selectively logged within the last 30 years; however, riparian buffers 5–20 m wide were retained along most streams and along all study reaches. Riparian vegetation consisted of 50–80-year-old mixed hardwood-coniferous forest. Surveys conducted in both 1999 and 2000 indicated that the Rocky Branch watershed incurred greater amounts of ice storm damage relative to other nearby watersheds (Kraft et al., 2002; Millward & Kraft, 2004). The dams generally consisted of numerous small branches from ice-storm-damaged trees aggregated against a few large key pieces of LWD (>25 cm diameter) (Kraft et al., 2002). Brook trout (*Salvelinus fontinalis*) were present at all sites, and slimy sculpin (*Cottus cognatus*) were present in the third-order stream and the lower reaches of one second-order stream. These streams are generally characterized by high flow in the spring and low flow in the summer with some recharge in the fall. General characteristics of the region and additional watershed detail are presented in Kraft et al. (2002) and Warren & Kraft (2003).

*Study design*

To assess the influence of wood and debris dams on the invertebrate community, we used a Before-After Control-Impact (BACI) study design that included impact replicates (Underwood, 1994). Data were collected from six reach pairs consisting of one removal reach and one reference reach (12 total reaches) in June 2000, before habitat manipulation, and in June 2001, approximately one year after woody debris was removed from the downstream reach in each pair. Experimental designs with a downstream reach manipulation and the use of upstream reaches for reference purposes have been applied in a number of other stream studies to avoid unwanted effects of upstream manipulations on downstream reference reaches (Carlson et al., 1990; Noel et al., 1986). Substrates and invertebrate response metrics were compared among paired sites before and after wood removal. The activities associated with the wood removal disturbed the substrates around dams. Because this study focuses on the presence or absence of the debris dam rather than the act of dam removal, the wood and dams in all upstream reference reaches were disturbed to some degree to mimic researcher activity, but not removed. The six reach pairs were located on three streams within the same watershed: two pairs on each of two second-order streams, and two pairs on the third-order (mainstem) stream (Fig. 1). By implementing multiple reach pairs in our study design, we addressed a primary criticism of simpler BACI approaches that do not include spatial replication (Underwood, 1994; Schwarz, 2002).

Reaches and reach pairs in second- and third-order streams were selected and manipulated in a similar fashion. We centered reaches on debris dams, and pairing was based on similarity in debris dam size, function (e.g., location in stream, relative size of pool formed, sediment retained and adjacent substrates), and proximity to other dams. Reach pairs contained the same number of pool-riffle sequences above and below the central dams, and within-pair reaches were similar in length. Overall, the reaches were variable in length between pairs (range from 20 to 85 m) as dictated by these stream geomorphic features. Different pairs within the same stream were always separated by at least one channel-spanning debris dam. Wood removal occurred in August 2000; new wood that recruited into the reaches during the following fall, winter and spring was not removed in 2001, but was minimal in volume.

Stream substrate changes in response to wood removal were measured using coverage maps created before and after the manipulation. Four metrics were used to determine the influence of wood removal on the stream macroinvertebrate community: genera similarity between treatment and reference sites, community equitability, dominant taxa, and functional feeding group relative abundance (Resh et al., 1988; Stone & Wallace, 1998).

*Streambed mapping*

In order to determine if debris dam removal influenced the dominant substrate characteristics, changes in substrate coarseness were evaluated in both reference and removal reaches. Substrates were mapped during May 2000 and May 2001 for all reaches in the third-order stream, and for one of the second-order streams (eight total reaches mapped). We mapped only a subset of the reaches due to logistical constraints. To produce streambed maps, we used a laser range-finder and field computer to collect data along eleven to sixteen transects selected using geodesically-based irregular systematic (GBIS) sampling techniques. By using this GBIS approach, more data are collected from areas of greater substrate variability and less data are collected from areas with uniform substrate, thereby increasing the efficiency by which substrate maps can be produced (Parasiewicz, 1996).

Data collected at each transect point included the relative location of the point and the dominant substrate at that point. The substrate at each point along a transect was placed into one of five categories: large rocks and boulders (>20 cm), medium sized rocks (2–20 cm), small rocks and sand (0.1–2 cm), sediment and clay (<0.1 cm), and particulate organic matter (POM) that included woody debris. Sample points on exposed rocks received no substrate value. Surveys were conducted along the same transects and, where possible, at the same points in both years. Thiessen polygons were established for all mapped reaches using a geographic information system, with the substrate at a given point location representing the entire polygon. The total area for each substrate type was determined within each study reach in 2000 and 2001 by summing the area of all thiessen polygons for a given substrate size.

*Invertebrate sampling*

Invertebrates were collected using a modification of the electrofishing techniques described in Taylor et al. (2001), hereafter referred to as "electrobugging". A modified Hess sampler 0.5 m wide by 1 m long was constructed with 240-micron mesh netting at the upstream and side surfaces and a removable 240-micron collection net at the downstream end. This larger sampling device allowed the anode of the electroshocker to be moved over the substrate within the sampler and ensured a sufficiently large sample to be collected, thereby accommodating the surface conditions within this type of stream. Samples were collected in the thalweg, one to three meters upstream and downstream from the central dam (Fig. 1). The modified Hess sampler was placed to ensure that water flowing through the sampler entered only through the upstream mesh and exited through the downstream net. Using markers set along the streambank, the sampler was placed at the same stream location in 2001 as in 2000.

After the modified Hess sampler and net were set, the anode of the electroshocker was placed inside the sampler and turned on for 90 sec. The net was then removed from the sampler and all invertebrates within the net were immediately preserved in ethanol. Because this collection technique relies on passive transport of immobilized invertebrates, the number of individuals captured may be subject to variability in stream velocity which was not measured in this study. This study therefore focuses on analyses of relative abundance. All sites within a given reach pair were always collected on the same day to control for variability in the timing of emergence.

Aquatic invertebrates were counted and identified to genus, except for Chironimidae (Diptera) and an early instar Plecopteran. The family Chironimidae was included as a separate taxon in community analyses and rarely comprised greater than 5% of a sample (10 of 43 total samples; 4 of 43 had >10% Chironimidae). Early instar Plecoptera were very rare and thus, were excluded from the community analysis. They were also excluded from the assessments of generic richness as it was assumed that the early instar individuals belonged to a genera that was already represented.

We tested responses of the invertebrate community to wood removal using four metrics: (1) genera similarity (Krebs, 1994), (2) Shannon–Weiner equitability (3) the dominant taxon with its proportion of dominance, and (4) proportional changes in functional feeding groups (Merritt & Cummins, 1984). Jaccard's index of generic similarity is a calculation of the proportion of overlap in genera present or absent from a pair of sites independent of relative abundance. Because debris dams are a potential source pool for new taxa, we chose this metric for analyzing presence/absence data. We determined generic similarity according to the equation in Krebs (1994):

$$\frac{(2 \times (A \cap B))}{(A + B)} \tag{1}$$

where A ∩ B is the number of genera in common (found in both site A and site B) and where A + B is the sum of the total number of genera in site A plus the total number of genera in B. Genera similarity was calculated between reference and removal sites and values were compared before and after the wood removal.

The Shannon–Weiner equitability index was used to test for differences in relative abundance of genera using following equation:

$$(-1) \times \sum_{i=gen_1}^{gen_n} (P_i \times \log_{10}(P_i)) \tag{2}$$

where $gen_1$ = the first genus in a sample, $gen_n$ = the last genus in a sample and $P_i$ = the proportion of the sample accounted for by genus *i*.

Five functional groups were designated for this study: grazer/scrapers (hereafter referred to as "grazers"), collector/gatherers, shredders, predators, and filterer/suspension feeders. Invertebrates were assigned to functional feeding groups (feeding guilds) using Merritt & Cummins (1984), Stone & Wallace (1998) and local expertise (Barbara L. Peckarsky, Cornell University, personal communication). For the purposes of this study, generalist invertebrate taxa were classified into a single functional feeding group based on information available for local groups and based on generalized family classifications. For example, two baetid genera, *Procleon* and *Acentrella*, that could be either grazers or gatherers were classified as grazers. The elmid beetles, *Optioservus* and *Stenelmis* (grazers or gatherers), were classified as gatherers. The ephemerellid mayfly, *Drunella* spp., was classified as a predator. All functional feeding group classifications for invertebrates within this study are reported in Warren (2002). Individuals from the family Chironomidae were not identified to genus, and therefore could not be placed into feeding guilds (Chironomids were present in 51% of all samples; when present, Chironomids were generally rare).

### *Analysis*

Two comparisons were made for each of the four metrics: (a) the differences between reference and removal reaches upstream of debris dams before versus after wood removal ("upstream reference-removal" comparisons) and (b) the differences between reference and removal reaches downstream of debris dams before versus after wood removal ("downstream reference-removal" comparisons).

Reference-removal comparisons were conducted separately for upstream samples and downstream samples because we expected different wood removal responses between these habitats. Because second- and third-order sites were selected in a similar manner, data from second- and third-order pairs were combined and analyzed together (this also increased statistical power). As part of the BACI analysis, the reference sites reflected natural fluctuations in community structure. The comparisons between reference and removal reaches were used to determine if changes in the removal reach invertebrate community resulted from the experimental manipulation.

A non-parametric Wilcoxon sign-rank test with an additional randomization test was used to compare the mean difference between reference and removal sites before versus after wood removal. Due to the small sample sizes, the additional randomization test was included to more rigorously evaluate the significance of observed responses (Manly, 1997). The additional randomization was conducted if the sign-rank *p*-value was greater than 0.005 or less than 0.2 (these values were chosen to ensure that, beyond these extreme bounds, the randomization would not change the significance of a result). The randomization analysis compared the z-value from the initial sign-rank analysis to z-values from 1000 iterations of the same analysis using the same pair values, randomly switching the sign of the differences, thereby creating a separate distribution of z-values. The *p*-value derived from this analysis (implemented using SAS v. 8.0) was determined by the proportion of z-values greater than that of the observed data.

Differences in stream substrates were assessed in a similar fashion by comparing the proportion of the streambed occupied by each of the substrate size classes before and after the experimental manipulation in the areas mapped just above and below debris dams. The proportion of the substrate for each size category in 2000 was subtracted from the proportion in 2001; this difference was then used to compare sites using similar analyses as described above.

## Results

### *Substrates*

There were no significant differences in the proportion of substrate particle sizes between reference and removal sites in response to wood manipulations ($p > 0.05$ for all). There were non-significant trends toward a relative increase in larger substrates in the removal reaches from 2000 to 2001 in response to the removal. The proportion of small substrates increased in almost all sites (i.e. three of the four removal reaches and all of the reference reaches in the year following wood removal), however, the relative increase of small substrates was consistently, although not significantly, smaller in removal reaches relative to reference reaches ($p = 0.07$).

### *Invertebrate community*

*Baetis* was the genus the greatest abundance in 10 of 11 reference sites (one reference sample was

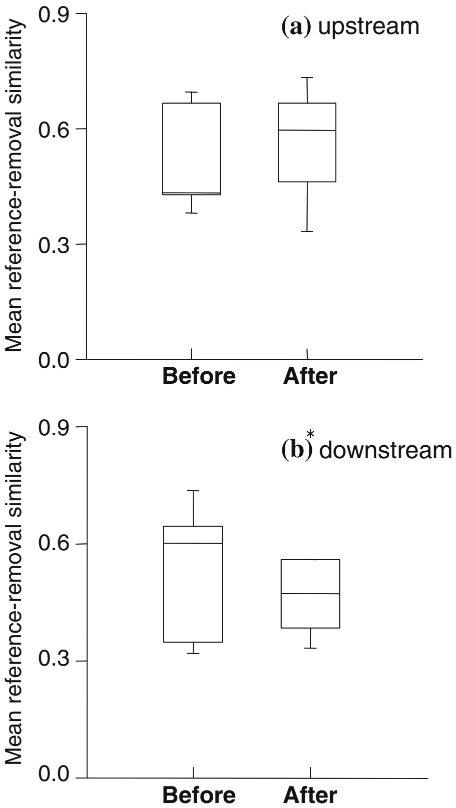


*Figure 2.* Box plot indicating genera similarity between reference and removal sites (a) upstream, and (b) downstream of debris dams, before versus after wood removal in second- and third-order streams. Similarity did not change significantly in response to wood removal ($p > 0.1$) according to a Wilcoxon sign-rank test. The central horizontal line in each box represents the median value. Boxes encompass the middle 50% of values. Whiskers indicate the presence of values up to 1.5 times the range of the middle 50% of the values. Asterisks and O's indicate values beyond this range.

lost) and 11 of 12 removal sites in 2000, before wood removal. After wood removal, the dominant genus was either *Epeorus* (6 of 12 reference and 7 of 11 removal site samples), or *Baetis* (See Supplementary table[1]). *Baetis* and *Epeorus* were both characterized as grazers and this was verified by the presence of diatoms in an evaluation of gut contents from preserved individuals.

Similarity index values did not change significantly in response to wood removal between the reference and removal site samples upstream or

[1] Electronic supplementary material is available for this article at <http://dx.doi.org/10.1007/s10750-006-0218-9> and accessible for authorised users.

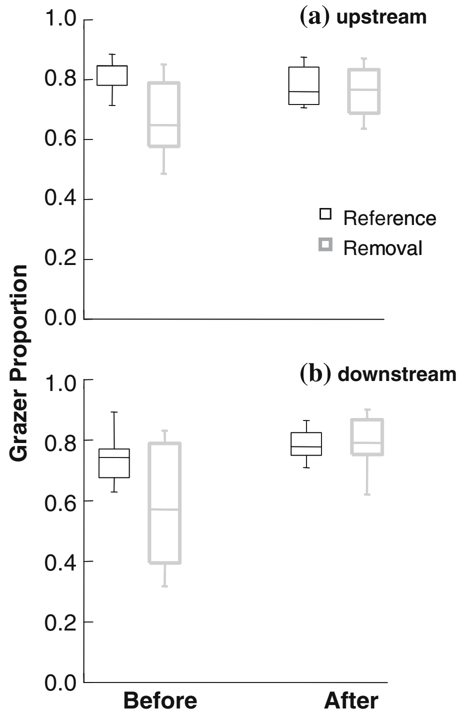


*Figure 3.* Box plot indicating grazer relative abundances in reference and removal sites in upstream (a) and downstream (b) sites, before versus after wood removal in second- and third-order streams. Grazer relative abundance increased significantly in response to wood removal ($p < 0.02$) according to a Wilcoxon sign-rank test. See Figure 2 for Box plot description.

downstream of debris dams ($p > 0.50$ for upstream and downstream reaches; Fig. 2). Similarly, no significant changes were found in community equitability upstream or downstream of the manipulation in response to debris dam removal ($p > 0.2$ for both).

Grazers were the dominant feeding guild in this system, accounting for greater than 70% of all invertebrates in the majority of sample collections. Overall (all sites combined and analyzed in aggregate) the relative abundance of grazers increased significantly from 2000 to 2001 ($p < 0.03$). By comparing differences between the reference and removal sites from one year to the next, the BACI analysis accounted for this overall increase in grazers across the study system and grazer relative abundance increased more in the wood removal reaches than in the reference reaches (downstream $p < 0.02$; upstream $p < 0.01$; Fig. 3). No significant changes were observed in the rela-

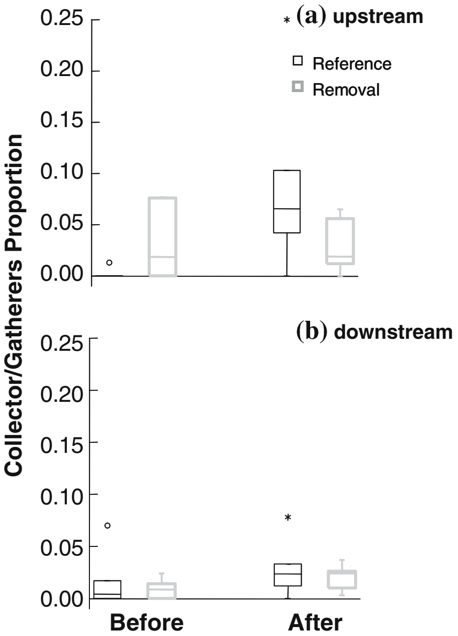


*Figure 4.* Box plot indicating collector/gatherer relative abundances in reference and removal sites in upstream (a) and downstream (b) sites, before versus after wood removal in second- and third-order streams. Collector/gatherer relative abundance did not change significantly in response to wood removal ($p > 0.05$) according to a Wilcoxon sign-rank test. See Figure 2 for Box plot description.

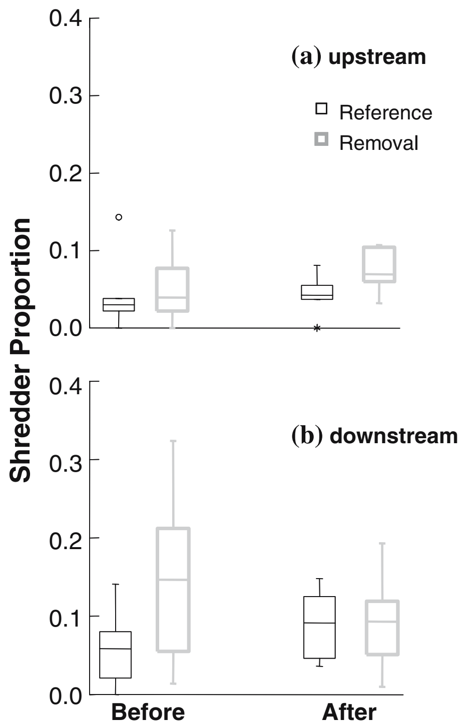


*Figure 5.* Box plot indicating shredder relative abundances in reference and removal sites in upstream (a) and downstream (b) sites, before versus after wood removal in second- and third-order streams. Shredder relative abundance did not change significantly in response to wood removal ($p > 0.05$) according to a Wilcoxon sign-rank test. See Figure 2 for Box plot description.

tive proportion of the other major functional feeding groups in response to wood removal ($p > 0.05$ for all, Figs. 4–6).

## Discussion

We hypothesized that debris dam removal would alter local stream habitat conditions, leading to significant changes in streambed morphology and invertebrate community composition. Our results, however, revealed no significant change in substrate size distributions and few invertebrate community changes in response to debris dam removal. These results are more consistent with those of Hilderbrand et al. (1997) than those of Wallace et al. (1995), two similar studies also conducted in small high gradient streams in eastern North America. Although, the relative abundance of grazers did increase in response to wood removal, as expected, other invertebrate and physical habitat responses to wood removal were not observed. We speculate that the relatively steep gradients and abundant stable boulders present at all sites mitigated the effects of debris dam removal, especially during summer low flows. Additionally, variability in function of naturally occurring debris dams in the eastern Adirondack Mountains may have obscured the effect of dam removal relative to studies where wood was anthropogenically placed and anchored in a stream.

In a number of studies the impacts of woody debris and debris dams on invertebrate communities have been associated with modifications of stream physical habitat and flow (e.g. Smock et al., 1989; Wallace et al., 1995; Lemly & Hilderbrand, 2000). Other investigations have specifically focused upon invertebrates present directly on and in close association with the wood itself (e.g. Johnson et al., 2003). Much of the wood contained within our study debris dams was dry at the time of mid-year sampling and wood decom-

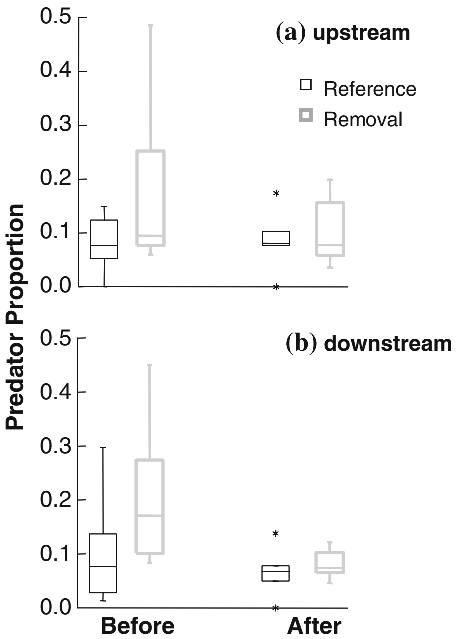


*Figure 6*. Box plot indicating predator relative abundances in reference and removal sites in upstream (a) and downstream (b) sites, before versus after wood removal in second- and third-order streams. Predator relative abundance did not change significantly in response to wood removal ($p > 0.05$) according to a Wilcoxon sign-rank test. See Figure 2 for Box plot description.

position was likely minimal due to the relatively short period of time since its deposition by the ice storm. As such, wood within resulting debris dams likely provided a low quality food source for invertebrates, which may partially explain why we did not observe more dramatic changes in the invertebrate community.

The influence of ice-storm-derived debris dams may also have been limited in these stream systems due to the prevalence of pool-forming boulders (Warren & Kraft, 2003). This interpretation is consistent with conclusions of Hilderbrand et al. (1997), who also worked in a high gradient system in which abundant boulders and bedrock influenced stream hydraulics. In situations where wood is responsible for creating pool habitat, debris dams can influence the invertebrate community through the creation of local depositional habitats with low stream energy (Lemly & Hilderbrand, 2000). Although debris dams created pools at some locations in our study, wood frequently accumulated against large boulders that contributed significantly to pool formation and pools were still present after wood was removed. Debris dam removal generally reduced the size of upstream pools, but did not always entirely eliminate their presence. This observation was supported by substrate response data that showed no significant changes in substrate size distributions.

Our results are consistent with observations by both Hilderbrand et al. (1997) and Wallace et al. (1995) regarding the role of stream gradient in regulating the influence of woody debris on invertebrate community composition and abundance. Wallace et al. (1995) attributed many of the differences between their work and that of Smock et al. (1989) to regional variability and, in particular, to differences in stream gradient between the two systems. Smock et al. (1989) found in a low gradient stream that shredders were more abundant at locations where debris dam addition was greater; but Wallace et al. (1995) found no significant changes in abundance of this functional feeding group following the addition of wood to higher gradient streams. The steep gradients of our study streams were more similar to gradients within streams studied by Wallace et al. (1995). Although gradient was not specifically noted in the paper by Johnson et al. (2003), who found several effects of debris dam removal on invertebrate communities, their study streams in Michigan and Minnesota were likely lower gradient than those within our study.

Differences between our study and Johnson et al. (2003) may also be explained by differences in invertebrate sampling techniques. Johnson et al. (2003) collected invertebrates from the wood itself as well as a variety of other stream habitats. In this study we focused on invertebrates within the main channel of the stream in close proximity to the debris dams, but not within the debris dams. As such, we were testing for an invertebrate community shift in response to a lost source population or a change in substrate resulting from dam removal, and we did not assess invertebrates lost in the wood itself. We are confident that mobile macroinvertebrates comprised a majority of stream invertebrates in our sampling locations, however, the electrobugging technique employed in this study may have under-represented sessile macroinvertebrates. This limitation in our collection method is consistent throughout all sampling, thus comparisons between locations and dates remain valid. Taylor et al. (2001) designed and verified their adaptation of electrofishing gear in a Colorado mountain stream where sessile macroinvertebrates were less common (B. Peckarsky, Cornell University, personal communication).

Independent of sample location or treatment (upstream or downstream, before or after), grazers were the dominant feeding guild at most study sites. At the time of year of our collections, streams often support relatively high grazer abundances, even in headwater streams within forested watersheds (Georgian & Wallace, 1983). However, we did not expect grazer dominance at almost all sites, particularly in areas upstream of debris dams with abundant detritus. We speculate that the loss of riparian canopy branches during the 1998 ice storm (Kraft et al., 2002) may have increased light availability and nutrients to the stream, thereby leading to increased algal growth and subsequent increases in grazer relative abundance. Previous studies have reported increases in grazer abundance in response to increased light availability resulting from streamside logging (Hawkins et al., 1982; Noel et al., 1986; Carlson et al., 1990; Ulrich et al., 2000). The significant increase in overall grazer relative abundance across most sites from 2000 to 2001 was particularly noteworthy considering the seven-fold increase in stream nitrate ($NO_3^-$) observed in response to the 1998 ice storm (Bernhardt et al., 2003; Houlton et al., 2003). This increase in nitrate along with greater light penetration due to canopy loss from the ice storm could have led to a subsequent increase in algal and biofilm abundance. Many streams are nitrogen (N) limited (Perrin and Richardson, 1997; Peterson et al., 2001), and Tank & Dodds (2003) specifically found that primarily productivity was N-limited in forested New Hampshire streams similar to our study streams. Increases in algal and biofilm abundance could in turn lead to increased grazer abundance (Perrin & Richardson, 1997; Biggs et al., 2000; Hall et al., 2001). We ultimately expect that summer invertebrate communities within our study area will shift away from grazers and towards greater shredder and collector abundance, as terrestrial inputs increase following forest re-growth over the stream and periphyton growth decreases in response to greater shade in the post-ice storm forest.

Wallace et al. (1995) specifically highlighted the need for studies that address the role of LWD and debris dams in structuring stream invertebrate communities in other regions to strengthen our ability to generalize those effects. We hypothesized that debris dam removal would decrease similarity between reference and removal sites upstream from the dams in eastern Adirondack streams, due to changes in substrate and litter retention. We also expected a decrease in downstream similarity in response to changes in upstream source populations, though we anticipated that this response could be limited by fewer changes in downstream substrate composition. Contrary to these expectations, no significant changes in generic similarity were observed in response to wood removal. This result suggests that debris dams did not strongly influence the presence or absence of mobile taxa in or on the streambed within these reaches. In conjunction with the similarity results, the Shannon–Weiner equitability analysis – taking into account relative abundance as well as species richness – indicated little community response in the second and third-order streams. The observed invertebrate response to debris dam removal in second- and third-order streams of Rocky Branch is generally consistent with results from a slightly different wood manipulation study conducted in first-order streams of this system (Warren, 2002).

## Conclusions

These results support the conclusion that during summer, woody debris in the high-gradient boulder-dominated study system has little impact on the invertebrate community relative to other stream systems. Overall, wood deposited by the 1998 ice storm had little influence on the invertebrate community in this stream system within three years after its deposition. We expect that the influence of ice-storm-generated debris dams on the overall stream invertebrate community will increase as wood within debris dams decays and organic debris continues to accumulate behind dams. The small number of significant responses to wood removal observed during our study suggests that the role of woody debris and debris dams was largely overshadowed by the influence of other dominant habitat structures, such as boulders. In lower gradient streams or in steep streams with fewer boulders, we expect that wood from ice storms would have had a much greater influence on the stream invertebrate community.


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