

Macroinvertebrate response to stream restoration by large wood addition

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ABSTRACT

We examined the aquatic macroinvertebrate community response to habitat rehabilitation activities in an incised, sand-bed stream. Seventy-two large wood (LW) structures were placed along 2 km of Little Topashaw Creek (37 km² watershed) in north-central Mississippi, USA. Macroinvertebrate collections were made from bed sediments, LW, leaf packs and qualitative multi-habitat sampling during 2 years prior to and 2 years following LW addition. Addition of LW tripled the availability of wood substrate but had no measurable effect on macroinvertebrate abundance or family richness. Ordination analyses revealed subtle differences in community composition between treated and untreated conditions, but these were related to antecedent discharge (occurrence of high flows during the preceding 6 months) and bed sediment composition rather than the availability of LW. Restoration of incising, sand-bed streams must include measures that address perturbed hydrology and degraded water quality as well as instream treatments. Published 2010. This article is a US Government work and is in the public domain in the USA.

KEY WORDS stream restoration; benthos; channel incision; physical habitat; large wood; substrate

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INTRODUCTION

Channel incision, often triggered by urbanization, channel straightening (Simon, 1989) and other anthropogenic processes (Galay, 1983), is a global environmental problem (Petit *et al.*, 1996; Wang *et al.*, 1997; Rinaldi and Simon, 1998; Simon and Rinaldi, 2000; Isik *et al.*, 2008). Channel incision and attendant phenomena have been implicated in physical habitat (Shields *et al.*, 1994, 2008a) and water quality (Shields *et al.*, 2010) degradation in warmwater streams. Channel incision is especially severe in northern Mississippi. Since the European settlement in the early 19th century, stream incision processes have degraded streams through extreme headwater channel erosion, downstream sedimentation and creation of flashy hydrologic regimes and unstable benthic substrates. These processes have been documented through extensive observation and research in north-central Mississippi, where typical streambed degradation of 2–5 m and channel widening of 200–300% has occurred (Thorne, 1997). Channel widening has been associated with drastic reductions in instream large wood (LW; Brooks and Brierly, 2002; Hassan *et al.*, 2005) and organic carbon in bed sediments (Shields *et al.*, 2008a). Some workers have suggested that naturally occurring LW accumulation is a natural recovery process in response to incision (Shields *et al.*, 2000; Wallerstein and Thorne, 2004).

LW is an important component of stream macroinvertebrate habitat, especially in sand-bed streams (Scealy *et al.*, 2007; Nakano *et al.*, 2008). Aquatic macroinvertebrates make use of LW for feeding on wood and associated biofilm, attachment for filter feeding, refuge during spates, oviposition, molting, pupation, predator avoidance, drifting and emergence. Benke *et al.* (1985) estimated that snags represented only 4% of habitat area of Satilla River, Georgia, but supported 60% of total macroinvertebrate biomass and contributed over 78% of drifting macroinvertebrates. They postulated that colonization of LW by macroinvertebrates may be limited by available space (Benke *et al.*, 1984). In some regions, LW is the only suitable stable substrate available to macroinvertebrates, including net-spinning caddisflies (Cudney and Wallace, 1980) and filter-feeding Diptera (Sioli, 1975; Benke *et al.*, 1979).

Since incised streams are often depauperate of LW, addition of wood is a logical rehabilitation measure and is widely used with typical accounts arising from locations as diverse as North Carolina (Wallace *et al.*, 1995), Liechtenstein (Zika and Peter, 2002), Mississippi (Shields *et al.*, 2006) and Australia (Lester and Boulton, 2008). A global review is provided by Nagayama and Nakamura (2009). Effects of wood addition or removal on macroinvertebrate populations are often complex due to other factors such as hydrology, water quality, predation, competition and temporal instability (Entrekin *et al.*, 2009). In addition, many of the macroinvertebrate taxa typical of sandy streams in the southeastern coastal plain are tolerant habitat generalists and typically respond weakly to habitat manipulations (Kaller and Kelso, 2007). Some

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workers report that LW addition for stream rehabilitation led to greater macroinvertebrate diversity (Hilderbrand *et al.*, 1997; Gerhard and Reich, 2000) or greater diversity of particular taxa types (Wallace *et al.*, 1995), but others have not (Spanhoff *et al.*, 2006). Lester *et al.* (2007) added wood to short segments of eight Australian streams and found that richness of macroinvertebrate families and functional feeding groups increased in zones treated with wood. Others noted wood addition had no effect on urban environments (Larson *et al.*, 2001) or forested watersheds (Coleman, 2006). Warren and Kraft (2006) found that wood removal from streams of a mountain watershed in New York had limited effects on macroinvertebrates, perhaps due to the abundance of boulder-formed pools.

This study examined the aquatic macroinvertebrate community response to the addition of LW to an incised stream in a rural watershed in north-central Mississippi. Macroinvertebrates were sampled along with key physical habitat variables before and after the addition of LW in treated and adjacent untreated reaches.

STUDY SITE

Little Topashaw Creek (LTC), an incised, rapidly eroding fourth-order stream in north-central Mississippi draining about 37 km² was selected for study. Watershed land use was dominated by pine and mixed hardwood forest, with only about 12% of the area in cultivation or used as pasture. Cultivated lands were concentrated within the floodplain immediately adjacent to the study reach.

LTC and the downstream drainage were excavated for drainage purposes in the early 1900s, and downstream channels were again channelized in 1967. Systemic response of the entire 800-km² Yalobusha River watershed encompassing our site involved incision of ~2 m in headwaters, aggradation of ~5 m downstream in the main river floodplain and knickpoint migration rates of 0.6–16 m year⁻¹ (Simon and Thomas, 2002). LTC channel width increased by factors of 4–5 between 1955 and 1999. The LTC channel was quite dynamic throughout this study with bank retreat as great as 7.6 m and 60 m of upstream migration of a 0.6-m high headcut during a single flow event. Naturally occurring LW was quite unstable as well; 60% of LW moved or exited the study reach within 12 months (Shields *et al.*, 2004). A geomorphic evaluation performed immediately prior to rehabilitation indicated that the downstream end of the study area was in the aggradational stage V of the Simon (1989) conceptual model of incised channel evolution, while the middle part was stage IV (degradation and bank failure), and the upstream segments were still degrading (stage III) (N.P. Wallerstein, 2000. *Geomorphic evaluation of Little Topashaw Creek: June 2000*, Unpublished report, National Sedimentation Laboratory, Oxford, MS; http://msa.ars.usda.gov/ms/oxford/nsl/wqe_unit/topashaw/geomorphic_evaluation.pdf; Simon and Thomas, 2002).

Sampling sites for collections of aquatic macroinvertebrates were in five, 150-m long subreaches along the 3-km stream study reach (Figure 1). One subreach was upstream of the region where LW structures were emplaced, two were within the rehabilitated stretch and two sites were downstream of the treated region. The upstream sampling site was straight, with steep, treeless banks draped with kudzu [*Pueraria montana* (Lour.) Merr. var. *lobata* (Willd.) Maesen & S. Almeida] and almost no LW. The bed was comprised of sand interrupted by several actively advancing knickpoints formed in consolidated cohesive material. The channel was ~20 m wide with vertical banks having bank heights up to 6 m. Deep (50–150 cm) transient pools were immediately downstream of knickpoints, but otherwise the stream was relatively shallow (5–20 cm).

Except for the LWS, the treatment subreaches and the downstream untreated subreaches had similar characteristics (Figure 1). In general, concave banks on the outside of meander bends exhibited mass wasting and sand was accumulating on large point bars opposite failing banks. Channel beds were of shifting 0.2–0.3 mm sand with occasional gravel-sized particles of easily crumbled shale. The channel had an average sinuosity of 2.1 and an average width of 33.3 m, depth of 3.6 m and slope of 0.0025. Although knickpoint migration, width adjustment and sand bar formation observed in the reach were characteristic of classical incised channel evolution (Simon, 1989), fluvial behaviour was perturbed by meandering processes and sediment production from upstream knickpoints. Gully tributaries of the creek intersected channel

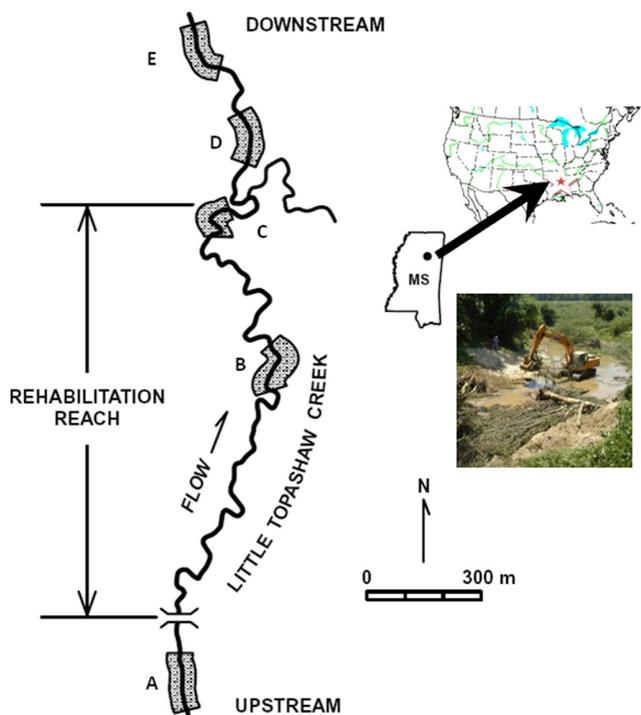


Figure 1. Map of study region, state of MS and study reach locations. Note five shaded subreaches within the study reach: A = upstream reference, B and C = treatment subreaches and D and E = downstream references. Inset photograph shows the construction of one of the 72 LWS added to the rehabilitation reach in the summer of the year 2000.

top bank with an average frequency of 0.01/m. LW input from the stream banks occurred occasionally as high banks failed. Pool habitats were extremely rare, particularly before LW placement, and mean water depths were usually <10 cm.

High flow events tended to be extremely brief (<30 h) and frequent, with base flows generally <0.10 m³ s⁻¹. Water quality degradation reflected flashy hydrology (Shields *et al.*, 2010). Total solids concentrations were commonly over 1000 mg l⁻¹ during storm events, and 824 samples collected across the full range of flow conditions over 6 years averaged 197 mg l⁻¹ (Shields *et al.*, 2010). Current-use pesticide concentrations were greatest in storm events following agricultural applications while historic-use pesticide levels fluctuated with suspended sediment concentrations (Smith *et al.*, 2006). The insecticides methyl parathion and chlorpyrifos were detected in stormwater samples (water + suspended sediment) with concentrations of 0.20 ± 0.42 and 0.30 ± 0.27 µg l⁻¹, mainly associated with spring runoff. Aquatic habitat conditions were marked by extremely shallow base flow (mean depths 5–13 cm) and sand-dominated substrates (bottoms were 71–100% sand) (Shields *et al.*, 2006). Channel bed total organic carbon was less than 0.5% of dry weight for all samples collected, with means about 0.12%, which was about an order of magnitude smaller than for less incised streams nearby (Shields *et al.*, 2008a).

RESTORATION PROJECT

Large wood structures (LWS) were placed along 2 km of the channel (Figure 1) during August and September 2000 to provide streambank stabilization, develop pool habitat and provide cover and substrate. Seventy-two wedge-shaped LW structures were constructed on concave, eroding banks by stacking either woody debris (~10%) or living trees (~90%) in a criss-cross arrangement (<http://ars.usda.gov/Research/docs.htm?docid=5643>). LW structure dimensions averaged 13.9 + 3.9 m in the streamwise direction and 5.3 ± 1.0 m in the transverse direction and were 2.1 ± 0.5 m high. Fifty-eight of the structures were secured to the bed by four or more earth anchors secured to the streambed. To build the structures, 1168 trees were obtained by clearing 3.4 ha of fencerows and ditchlines >10 m from the top bank of the channel. Most trees were harvested more than 200 m from the channel, and no impacts of tree harvest on channel morphology or habitat were observed. Most trees were oaks (*Quercus* sp.), but ash (*Fraxinus* sp.), cherry (*Prunus* sp.), hickory (*Carya* sp.), elm (*Ulmus* sp.), sweetgum (*Liquidambar styraciflua*) and sycamore (*Platanus occidentalis*) were also used (Shields *et al.*, 2004). Structures performed well during the first year after construction. Baseflow-wetted width and depth increased in the modified subreaches by 60% ($p < 0.003$, Mann–Whitney rank-sum test) due to scour adjacent to the LWS and associated beaver dams. Only four of the

72 structures were destroyed, despite three flow events with peaks exceeding 25 m³ s⁻¹, depths >2.5 m and velocities >1.2 m s⁻¹. Comparison of pre- and post-construction channel surveys following the high flows showed insignificant changes in total channel volume despite about 0.3 m of thalweg degradation because of deposition of sand berms adjacent to steep, concave banks. However, high (~40 m³ s⁻¹) flows during the second year (the final year of the macroinvertebrate study described here) triggered progressive failure of about a third of the LWS. This deterioration resulted from decay and breakage, failure of earth anchors, scour of sediments deposited within the structures and undermining of structures by thalweg degradation. Sediments deposited within the LWS were scoured away, and loss of this ballast was followed by failure of the LWS (Shields *et al.*, 2004, 2006).

About 4000 willow (*Salix nigra*) cuttings were planted on point bars and in sediment deposits adjacent to selected LW structures using a water-jetting technique. Similarly, initial survival of willow cuttings was excellent, particularly for those planted at lower elevations adjacent to the baseflow channel (Pezeshki *et al.*, 2007), but only about 40% survived through the end of this study (Martin *et al.*, 2005; Shields *et al.*, 2008b).

METHODS

Macroinvertebrate samples were collected from all five LTC subreaches (Figure 1) on six dates. Three samples were collected before construction (June and September 1999, June 2002). Our experimental design is a before-after-control-impact design that includes sampling sites with and without rehabilitative structures before and after implementation of the structures (Cooperman *et al.*, 2007). Four sampling methods were used during each collection (i.e. all organisms collected from an individual 150-m subreach on a specific date). LW was sampled by brushing approximately 1800 cm² total surface area of submerged (>10 cm diameter) logs and collecting the dislodged material and macroinvertebrates with a standard D-frame aquatic net held downstream. Leaf packs and associated coarse particulate organic matter were sampled by hand-grabbing from two or more accumulation areas (approximately 750 cm³ total volume uncompact leaf material). Streambed substrate sand samples at each site consisted of four 929-cm² samples taken to a depth of 10 cm using a Surber sampler. At the upstream non-treated site, water depth and lack of water velocity required use of an Ekman dredge, but similar area and depths were collected. A qualitative multi-habitat sample was collected to supplement the other sampling methods. It was made primarily by hand picking macroinvertebrates from sticks, limbs, stones, pieces of clay and by the use of a fine mesh (200 µm) aquarium net to obtain aquatic macroinvertebrates from substrate surfaces, vegetation and root mats and the water column. Accumulations of gravel or aquatic macrophytes

were rare, but, if present, these habitats were sampled during the visual multi-habitat collections. Multi-habitat sampling was carried out for approximately 15 min at each site on each date. Below, we have designated the three types of quantitative samples as samples from different 'habitat types' rather than the more traditional term, 'substrates', in recognition of the fact that these samples not only represent different surfaces but different spatial locations in the stream (Growth *et al.*, 1995; Rabeni *et al.*, 2002).

All macroinvertebrates were preserved in the field in 80% ethanol with rose bengal dye and processed in the laboratory. Macroinvertebrates were generally identified to genus with the exception of Chironomidae and most non-insects (family or higher level only, Wright *et al.*, 1995; Downes *et al.*, 2006 in Lester *et al.*, 2007; Marchant *et al.*, 2006). Benthos collections were not subsampled, but processed in their entirety. The primary identification manual was that of Merritt and Cummins (1996). For functional analysis, each family was assigned to a functional feeding group based on the characteristics of the dominant species representing the family in our collections.

Physical habitat data were collected to describe each subreach on each sampling date. Within each reach, 10 transects were placed at 15-m intervals. Along each transect, water depth and substrate were recorded at a point 25 cm from the left water's edge and at four to six additional points spaced at equal intervals (e.g. spacing for four points would be local wetted width divided by 5). Substrate was visually classified as clay, sand, gravel, organic debris or other (usually human made objects or vegetation). Wetted width was measured at each transect with a tape. LW density was measured in each subreach using methods described by Barbour *et al.* (1999). Each piece or accumulation of LW intersecting the plane of the water surface with an enclosing area greater than 0.25 m² was recorded. Estimates were made to the nearest 0.5 m, and formations with length or width less than 0.5 m were not counted. Recorded length was the maximum length of the formation in the direction parallel to the primary flow direction, and the width was the maximum width in the direction perpendicular to the length. The length and width of each LW formation were multiplied together, the resulting products were summed and then this sum was divided by the water surface area within the sampled reach (obtained by multiplying the average wetted width by reach length) to obtain LW density. This index is not an expression of the volume of LW but rather a measure of its relative influence on habitat.

Water velocity and depth were measured at 30-min intervals at the upstream end of the study reach using acoustic Doppler devices and used to compute a series of mean daily discharges for the study period using the approach described by Shields *et al.* (2010). Depth and velocity data were also logged for shorter periods of record from two bends within the study reach. Stream bed sand gradation curves were determined from sieve analysis of 15 samples collected during late summer

base flow from the study reach before (1999) and after (2003) installation of the LWS. Using the aforementioned water velocity, depth and discharge records, the discharge associated with conditions required to entrain the coarser sand particles in the bed ($D_{84} \sim 0.6$ mm) determined from criteria provided by USACE (1994) was estimated to be about 5 m³ s⁻¹. Stream macroinvertebrates reflect both substrate stability (Shields and Milhous, 1992) and impacts of antecedent flows that disturb the benthos (Payne and Miller, 1991; Cooper *et al.*, 2001). We calculated an index of antecedent flows (Q_a) for each sample date (t) by summing the mean daily flows $Q_{md}(t)$ greater than 5 m³ s⁻¹ for the 180 days prior to the sample date:

$$Q_a(t) = \sum_{n=t}^{t-180} Q(t),$$

where $Q_a(t)$ is the antecedent flow index for day t , and $Q(t)$ is given by

$$Q(t) = 0 \text{ if } Q_{md}(t) < 5 \text{ m}^3 \text{ s}^{-1}, \text{ and} \\ Q(t) = Q_{md}(t) \text{ if } Q_{md}(t) > 5 \text{ m}^3 \text{ s}^{-1}.$$

DATA ANALYSIS

Principal components analysis was used to explore physical differences among the sample dates and sites. A matrix of physical habitat data was created containing a row for each sample site and date (5 sites \times 6 dates = 30 rows) and a column for each of the five physical habitat variables: mean water depth, mean wetted width, % bed covered with sand, LW density and $Q_a(t)$. Each entry within the matrix was $\log(x + 1)$ transformed, and this matrix was used as both the main and secondary matrix in PC-ORD version 4.41 (McCune and Mefford, 1999). Sites and physical habitat variables were evaluated with a joint plot, with the length and direction of the vectors graphically representing the strength and direction of the physical habitat vector loadings along influential axes. Results of this ordination were used to place collections into groups or categories based on physical reach conditions. One-way analysis of variance (ANOVA) using condition as the grouping variable of the physical habitat variables (antecedent flow index, mean water depth, LW density and % bed surface covered by sand) were then used to validate our assignment of collections to habitat categories [ANOVA on ranks and all pairwise multiple comparison (Dunn's method) except for % sand, which was standard ANOVA, Holm-Sidak comparison procedure]. Two-way ANOVA (Holm-Sidak comparison procedure) using reach condition and habitat type (leaf packs, bed sediments or wood) were then used to compare the abundance [data $\log_{10}(x + 1)$ transformed], relative abundance (data arcsine square root transformed) and family richness of macroinvertebrates found in each of the reach condition categories. Two-way ANOVA were also used to examine relative abundance (data arcsine square root transformed) of dominant families and

functional feeding groups (Merritt and Cummins, 1996) among the habitat types and reach condition categories. In addition, six metrics of biological condition (MDEQ, 2003; index configuration 2 for northwest bioregion, pp. 3–17) were computed for each collection: % Chironomidae (number of Chironomidae/total number of macroinvertebrates), % clingers (number of macroinvertebrates that cling to habitat features/total number of macroinvertebrates), dipteran taxa richness (number of dipteran taxa), % Ephemeroptera non-inclusive of Caenidae (number of Ephemeroptera excluding Caenidae/total number of macroinvertebrate captures), filterer taxa richness (number of filter-feeding taxa) and % tolerant taxa (tolerant taxa richness/total macroinvertebrate taxa richness). These metrics were also subjected to ANOVA to examine differences among reach condition categories. All ANOVA were run using Sigmastat 3.5 software with $p < 0.05$ for significance.

For purposes of ordination analysis, a matrix containing taxa abundances at the family level for each collection was created. Non-metric multidimensional scaling (NMS) and ancillary graphical and correlation analyses (McCune and Grace, 2002) were run using PC-ORD 4.41 software (McCune and Mefford, 1999) in order to detect response of the macroinvertebrate community to gradients of physical habitat conditions: specifically, wetted width, water depth, antecedent flow, substrate (% bed surface covered with sand) and LW density, all characterized at the sub-reach scale. NMS ordination was performed to assess similarities among the 30 collections based on abundances of the 31 most common taxa. As many zero counts were found in the 30 collections \times 31 taxa data matrix, values were subjected to Beals smoothing (McCune and

Grace, 2002) prior to NMS. Sorenson distances were constructed with NMS from the data matrix with a random starting configuration and 10 runs with real data using the autopilot ‘slow and thorough’ mode in PC-ORD. NMS ordination was assessed with Monte Carlo tests of the probability that a similar final stress could be obtained by chance and by interpreting the final stress in real data (McCune and Grace, 2002). Taxa that had correlation coefficients >0.70 between their Beals-smoothed abundances and site scores along influential NMS axes were noted. An overlay of the physical habitat data onto the influential ordination axes showed which ones were most related (Pearson correlations of habitat variables and NMS axis 1 and 2 scores) to assemblage structure. We also assessed the response of macroinvertebrates found in different habitats to physical gradients by running similar NMS analyses using only macroinvertebrates collected from leaf packs, only those found on LW and only those found in stream bed sediments due to substrate-specific responses reported by others (Jahng and Lorenz, 2008).

RESULTS

A principal components analysis of physical habitat variables produced three axes, which explained 82.2% of the variance in the habitat variables. The first two axes explained 66.7% of the variance (Figure 2). PC axis 1 explained 42.2% of the variation in environmental conditions, and largest vector loadings on this axis included LW density ($r = -0.758$) and wetted width ($r = -0.746$). Treated reaches had lowest plotting positions along this axis, indicating greater values of LW density and narrower width. Antecedent discharge correlated with

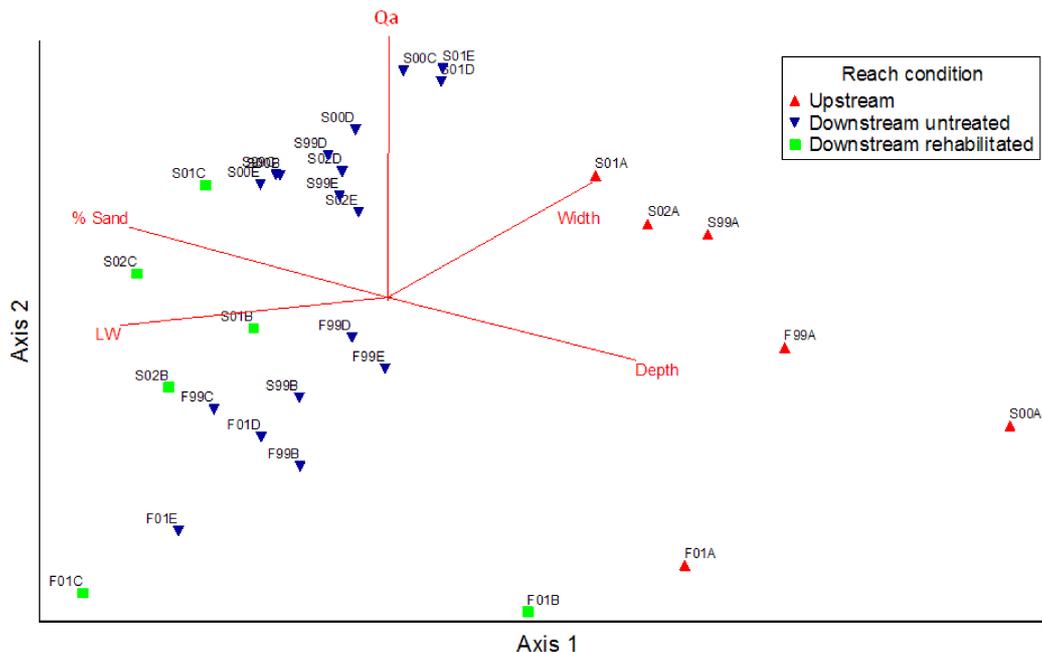


Figure 2. Principal components analysis using physical habitat variables across all collections (collection = all organisms collected from an individual 150-m subreach on a specific date). These two axes explained 66.7% of the variation in the physical habitat data. Labels indicate season (S = spring, F = fall), year (e.g. 99 = 1999, 01 = 2001), and subreach (Figure 1A–F). Influential habitat variables with vector loadings >0.200 are shown (red vectors).

PC axis 2 ($r = 0.627$). This ordination analysis suggested that our collections might be viewed as three groups based on reach conditions: (1) the upstream untreated reach, which was straight, characterized by pools below low scarps, and nearly devoid of woody riparian vegetation or LW; (2) untreated reaches downstream, which were shallower and loaded with LW from bank erosion and (3) downstream reaches after treatment, which had much greater levels of LW loading (Table I). It is important to note that this grouping places reaches B and C in the downstream untreated group prior to rehabilitation and in the downstream treated group after rehabilitation. Although this may be a bit unorthodox, the principal component analysis (PCA) and ANOVA (Table I) indicate that it is a sound approach for classifying sampled subreaches based on physical habitat attributes.

A total of 68 422 macroinvertebrates representing 149 taxa and 79 families were collected for this study. Thirty-two families were found in collections from all three 'reach condition' categories defined in Table I. Chironomids dominated all collections (82% of all captures) but were slightly less dominant in treated reaches. Macroinvertebrate density was smaller in the upstream reach A, but this difference was not significant (Table II). Furthermore, the abundance of organisms found within a

given habitat (bed sediment, LW and leaf pack) was not influenced by reach condition ($p = 0.619$). However, numbers captured from each of the three sampled habitat types were significantly different (Table II, $p < 0.001$). Leaf packs were densely colonized by macroinvertebrates, with 77% of all captures occurring in leaf pack collections and only 14% in bed sediments, 8% on wood substrates and 1% in visual collections. Fifty-nine of the 79 families collected during the study were represented in leaf pack collections, and 16 families were found only in leaf packs. However, it should be noted that the gear types used to sample sediments, leaf packs and wood were not strictly comparable in terms of the space or volume of habitat covered. The distribution of individuals among the sampled habitats was similar across reach conditions (Table III).

Taxa richness was about 50% smaller in the untreated upstream subreach A (Table IV). The average number of families found in each type of habitat was similar across sites, except fewer families that were represented in leaf packs in the upstream subreach. This may reflect the lack of sources along subreach A and the highly transient nature of leaf packs there due to the lack of LW and other retentive structures (see photo and statistics for subreach A in Table I). Six families comprised 97%

Table I. Summary of physical conditions in sample unit groupings suggested by PCA (Figure 2).

Location (refer to Figure 1)	Antecedent flow index	Mean (SD) water depth, cm	Mean (SD) wetted width, m	Mean (SD) LW density, $m^2 km^{-2}$	Mean (SD) % bed covered with sand
 Subreach A	37.5 (32)	30 (8) ^a	6.3 (0.9) ^a	0.4 (0.30) ^a	64.8 (23.9) ^a
 Subreaches B and C prior to rehabilitation, D and E	33.9 (25.2)	7 (4) ^b	5.1 (1.4) ^{a,b}	6.3 (3.2) ^b	87.6 (8.1) ^b
 Subreaches B and C after rehabilitation	48.0 (41.0)	13 (9) ^{a,b}	4.3 (1.2) ^b	41.5 (8.2) ^c	84.2 (11.2) ^b

Entries in the same column with different superscript letters are significantly different ($p < 0.05$), ANOVA on ranks, all pairwise multiple comparison (Dunn's method) except for % sand, which was standard ANOVA, Holm-Sidak comparison procedure.

Table II. Mean number of individuals per collection by reach condition and habitat type.

Reach condition	Leaf packs	Bed sediment	Wood	Sum of all habitats
Upstream	1024	397	254	1675
Downstream untreated	1987	328	184	2498
Downstream rehabilitated	1845	171	68	2084

No significant differences were found among the three reach conditions, but habitat types were all significantly different from each other [$p > 0.05$, two-way ANOVA, data $\log_{10}(x + 1)$ transformed].

Table III. Mean % of captures by reach condition and habitat type.

Reach condition	Leaf packs	Sediment	Wood
Upstream	58	21	21
Downstream untreated	78	16	6
Downstream rehabilitated	85	12	3

No significant differences were found among the three reach conditions, but leaf packs were significantly different from sediment and wood ($p > 0.05$, two-way ANOVA, Holm-Sidak method, data arcsine square root transformed prior to ANOVA).

Table IV. Mean number of families per collection by reach condition and habitat type.

Reach condition	Leaf packs	Sediment	Wood	All habitat types
Upstream	11.5 ^a	10.5	7.8	10.1 ^a
Downstream untreated	20.7 ^b	11.8	11.3	14.9 ^b
Downstream rehabilitated	21.7 ^b	13.0	11.7	14.9 ^b

Entries in the same column with different superscript letters are significantly different ($p < 0.05$, two-way ANOVA, Holm-Sidak comparison procedure).

of all captures, while 63 families were represented by fewer than 40 captures. Six taxa were found only in streambed sediments, while three were found only on wood. Dominance patterns varied little among the three site types (Table V). Although the most common families were similarly dominant across the three site types, there was a significant interaction ($p = 0.040$) between site type and family, rendering interpretation of this ANOVA difficult (Table V).

Nine functional feeding groups were represented in macroinvertebrate collections, with gathering collectors comprising 86%, filtering collectors 8% and herbivorous shredders 3% of individuals captured. Gathering collectors were primarily (95.3%) chironomids, while

filtering collectors were primarily (75.5%) Hydropsychidae and herbivorous shredders were annelids (97.2%). Exclusive of chironomids, the total collection of macroinvertebrates was dominated by collecting filters (43.9% of all non-Chironomidae), collecting gatherers (23.0%), shredding herbivores (14.3%), scrapers (9.4%) and predators (7.2%). Relative abundance of functional feeding groups was similar across site types except for shredding herbivores, which were more dominant in the rehabilitated reaches (Table VI).

Tolerance metrics varied little across reach conditions. There was no significant difference among the tolerance metrics computed using the composite collections and those from leaf packs and LW. Bed collections exhibited differences in % Ephemeroptera non-inclusive of Caenidae for the untreated upstream and downstream rehabilitated groups, and qualitative multi-habitat collections produced smaller values for % clingers in the untreated upstream reach than for the other two categories.

Subtle but distinct biological similarities among the sample units are shown graphically in the NMS ordinations (Figure 3 and Tables VII–IX). When collections from all habitats and gear types are considered (Figure 3a), the ordination shows slightly greater similarity among rehabilitated reaches than among the degraded reaches. Rehabilitated reaches tended to plot in a region lower on axis 2 than the untreated reaches, which were more widely scattered in the ordination plane. Beals-smoothed abundances of macroinvertebrate taxa were strongly related to the NMS axes. Families of dobsonflies (Corydalidae), caddisflies (Hydroptilidae), mayflies (Isonychiidae and Caenidae) and the water mites (Hydracarina) were all positively correlated with axis 1 ($r > 0.80$), which was also positively correlated with family richness ($r = 0.597$, $p < 0.001$, Spearman's rank order correlation) (Table IX). The Isonychiidae are often found in vegetation along edges of streams with moderate current—conditions similar to

Table V. Mean % of captures comprised by the six most dominant families.

Reach condition	Chironomids	Baetidae	Hydropsychidae	Annelida	Heptageniidae	Simuliidae
Upstream	75.6	2.9	2.5	10.6 ^a	0.6	0.9
Downstream untreated	80.3	3.9	6.8	0.7 ^b	2.2	2.3
Downstream rehabilitated	72.5	5.4	11.0	1.9 ^{a,b}	2.7	1.9

Entries in the same column with different superscript letters are significantly different ($p < 0.05$, two-way ANOVA, Holm-Sidak comparison procedure). Data were transformed (arcsine square root) prior to ANOVA.

Table VI. Mean % of captures comprised by functional feeding group exclusive of chironomids.

Reach condition	Filtering collectors	Gathering collectors	Shredding herbivores	Scrapers	Predators	Parasites
Upstream	8.9	86.5	0.6 ^a	2.3	1.5	0.2
Downstream untreated	10.7	80.9	3.2 ^b	2.8	1.9	0.3
Downstream rehabilitated	3.8	81.1	10.9 ^c	0.8	3.0	0.3

Entries in the same column with different superscript letters are significantly different ($p < 0.05$, two-way ANOVA, Holm-Sidak comparison procedure). Data were transformed (arcsine square root) prior to ANOVA.

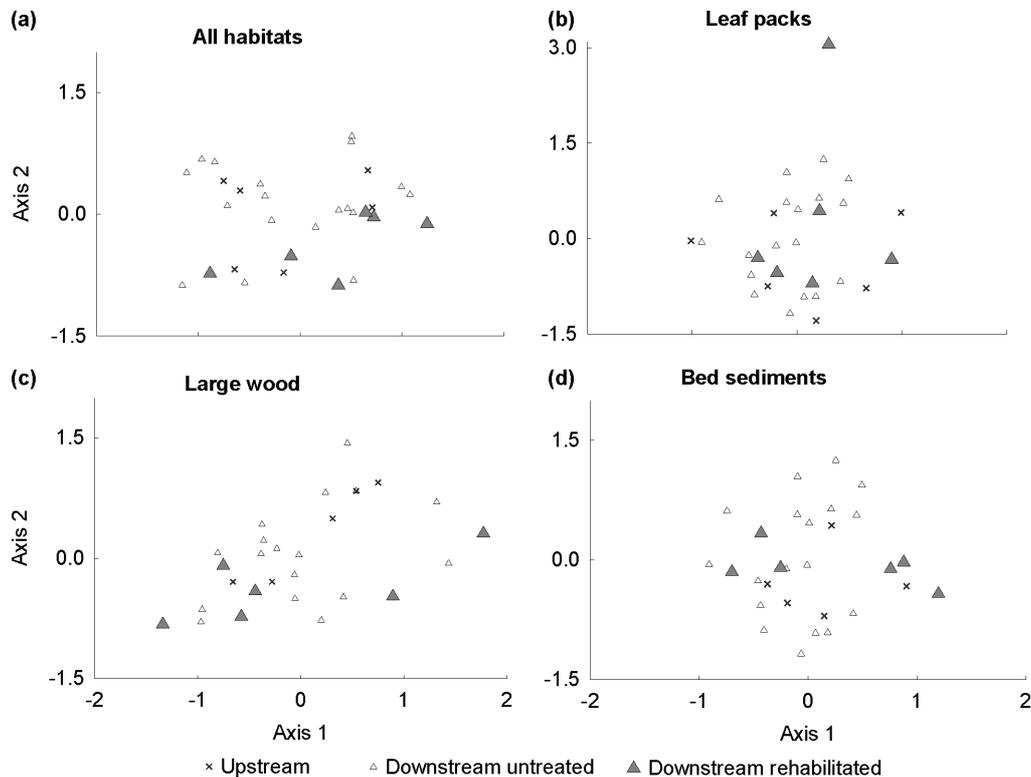


Figure 3. Non-metric multidimensional scaling (NMS) showing sample unit groupings based on PCA and ANOVA of physical habitat variables.

Table VII. Results of NMS ordination using data from all collections and those from only leaf packs, large wood and bed sediments.

	All habitats	Leaf packs	Large wood	Bed sediments
Final stress	7.66	10.98	7.46	12.47
Cumulative r^2	0.944	0.941	0.971	0.906
Taxa used in ordination	22	19	13	11
No. of collections	30	30	29	30
Minimum abundance	27	24	12	16
No. of axes in NMS ordination	3	2	2	2

those found in the untreated upstream reach A (Table I). Elmidae, often associated with submerged LW, were positively correlated with axis 2 ($r = 0.75$), while the tolerant worms Annelida, the Dipteran midges Ceratopogonidae and Ancylidae snails were negatively correlated with axis 2 ($r < -0.74$) (Table IX). NMS scores were significantly correlated with several tolerance

metrics (Spearman's rank order correlation). Axis 1 was positively related to % Dipteran taxa, % Ephemeroptera non-inclusive of Caenidae, filterer taxa ($r > 0.37$, $p < 0.045$) and inversely related to % Chironomidae ($r = -0.43$, $p = 0.019$). Axis 2 was inversely proportional to % filtering taxa, and axis 3 was inversely proportional to % Ephemeroptera non-inclusive of Caenidae ($r < -0.45$, $p < 0.013$ in both cases).

Leaf pack ordination (Figure 3b) featured a rehabilitated collection that plotted as an outlier on axis 2 (Figure 3b). This collection represents leaf pack samples from one of the treated reaches collected in the Fall of 2001, about 1 year after the rehabilitation project was completed. These samples contained only two taxa: 526 animals classified as chironomids and 11 Eucopepoda. Leaf pack collections from this reach on the other five sampling dates produced an average of 967 organisms representing an average of 9.4 taxa. Leaf packs became smaller and less common in this subreach following rehabilitation, perhaps due to construction impacts (heavy equipment in creek) or to the fact that LWS trapped leaves above baseflow stage. Other collections

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Table VIII. Habitat variables correlated ($r^2 > 0.25$) with axes from NMS ordination using data from all collections and those from only leaf packs, large wood and bed sediments.

	All habitats	Leaf packs	Large wood	Bed sediments
Axis 1	None	None	<u>Antecedent discharge</u>	Antecedent discharge
Axis 2	None	None	None	<u>% sand</u>

Underline indicates negative r .

Table IX. Macroinvertebrate taxa with Beals-smoothed abundances that have correlations with NMS axes such that $r^2 > 0.50$.

	All habitats	Leaf packs	Large wood	Bed sediments
Axis 1	Corydalidae Hydroptilidae Isonychiidae Hydracarina Caenidae	Coenagrionidae <u>Hydrophilidae</u> Heptageniidae	Tipulidae Annelida Hydroptilidae <u>Simuliidae</u> <u>Baetidae</u> Heptageniidae <u>Hydropsychidae</u>	Simuliidae <u>Elmidae</u> <u>Gomphidae</u>
Axis 2	Elmidae <u>Ancylidae</u> Ceratopogonidae <u>Annelida</u>	Eucepoda Corydalidae <u>Hydroptilidae</u> <u>Elmidae</u> Isonychiidae Ceratopogonidae <u>Caenidae</u> <u>Hydropsychidae</u>	Elmidae Annelida <u>Caenidae</u>	Ceratopogonidae Annelida <u>Baetidae</u>

Underline indicates negative r .

from rehabilitated reaches clustered low on axis 1 relative to untreated reaches, but physical habitat variables were not related to the ordination axes (Table VIII). Axis 1 was positively correlated with the abundance of stream mayflies, Heptageniidae and inversely related to abundances of the pond damselflies, Coenagrionidae and the water scavenger beetles, Hydrophilidae (Table IX).

LW NMS ordination (Figure 3c) showed rehabilitated collections plotting generally lower on axis 2 than other units. Axis 2 was positively ($r > 0.74$) related to the Beals-smoothed abundances of the wood-dwelling Elmidae and worms (Annelida) and inversely ($r = -0.95$) related to the tolerant, silty-bottom dwelling mayfly taxa, Caenidae (Table IX). Axis 1 in this ordination was inversely related to antecedent discharge ($r = -0.73$, Table VIII). Smoothed abundances of two taxa were positively related to plotting position on axis 1, while five were inversely related ($r < -0.77$).

Collections from bed sediments produced an ordination with axes that were positively related to antecedent discharge (axis 1, $r = 0.59$) and inversely related to the fraction of bed surface covered with sand (axis 2, $r = -0.54$) (Table VIII). Both these variables are strong indicators of the substrate stability. Abundance of the black flies (Simuliidae) was positively related to axis 1 ($r = 0.90$), while abundances of representatives of Elmidae and the Gomphidae dragonflies were inversely related to axis 1 ($r < 0.80$) (Table IX). Abundances of family Ceratopogonidae biting midges and worms (Annelida)

were positively related to axis 2 ($r > 0.71$), while Baetidae were inversely related to axis 2 ($r = -0.79$).

DISCUSSION

Stream macroinvertebrate communities in dynamic systems such as LTC reflect the integration of biotic influences and abiotic influences such as substrate, water quality and large-scale factors that govern local hydraulics such as hydrology, channel planform and channel evolution. Prior to the rehabilitation project, physical differences among the five sampled subreaches were mainly due to differences in channel evolution and riparian vegetation (LW loading). Temporal differences in habitat quality were largely driven by hydrology and water quality issues linked to hydrology (Smith *et al.*, 2006; Shields *et al.*, 2010). Our rehabilitation project, which included the addition of LW to two of the five subreaches modified only one of these physical habitat components. The influence of rehabilitation was superimposed on pre-existing physical gradients.

Separate NMS ordinations for leaf packs, LW and bed sediments showed differences in key taxa within each habitat assemblage (Table IX). The LW and bed sediment ordinations (Figure 3c and d) illustrated the importance of high flow events and bed sediment stability in controlling the LTC macroinvertebrate assemblages. Hydrologic history, especially of extreme events, has a strong influence on ecosystem structure and function (e.g. organic carbon

dynamics; Shields *et al.*, 2008a) and stream macroinvertebrate abundance (Payne and Miller, 1991) and community composition (Cooper *et al.*, 2001). In a study of other incising streams in Mississippi, Cooper *et al.* (2001) found a total macrobenthos reset after extreme flows to be a widespread phenomenon. In that study, changes associated with rehabilitation were overshadowed by long-term recovery from major disturbances caused by over 1470 mm of rainfall in a few months prior to initial sampling. Maul *et al.* (2004) presented results of benthic macroinvertebrate sampling in 1999 at 44 stream sites in the region encompassing LTC, and 17 of these sites were resampled in 2000. Degraded streams such as LTC exhibited high levels of temporal instability (between-year variation) relative to less-impacted sites. Furthermore, few physical habitat variables were influential in structuring macroinvertebrate communities, but % substrate as sand and several water quality variables were important influences (Maul *et al.*, 2004). Others have found similar negative correlations between % substrate as sand and stream macroinvertebrates in the southeast (Sawyer *et al.*, 2004), upper Midwest (Entrekin *et al.*, 2007) and western USA (Cover *et al.*, 2007; Bryce *et al.*, 2010).

In some streams, large amounts of LW can stabilize a channel during high flows (Gerhard and Reich, 2000). Smith *et al.* (1993) measured a fourfold increase in bedload transport at bank-full discharge when all LW was removed from a small, gravel-bed stream. Although LTC current velocities inside the LWS during high flows was roughly one tenth of those observed in the open channel, major hydrologic events had sufficient power to exceed critical velocity for sand movement even within the LWS, and such erosion increased as the LWS decayed (Shields *et al.*, 2003, 2004, 2006). Workers in other regions have reported diminishing effects of LW addition with time due to structural failure (Frissell and Nawa, 1992). At any rate, NMS ordination seemed to indicate that reach-scale hydrologic characteristics (i.e. flashy high flows) were more important in structuring the LTC macroinvertebrate community than more local beneficial impacts due to LWS. These findings regarding scale effects corroborate earlier results (Nislow *et al.*, 2002; Smiley and Dibble, 2005; Hrodey *et al.*, 2008) when specific details of each study are considered. Furthermore, others have reported transient or unfavourable macroinvertebrate responses to reach-scale restorations with LW (Moerke *et al.*, 2004; Entrekin *et al.*, 2009) and to LW removal (Warren and Kraft, 2006) and other types of habitat manipulations (Brooks *et al.*, 2002).

Response to LW addition to LTC may have also been retarded by degraded habitat conditions in the stream above the study reducing the number of colonizing taxa in drift. Additionally, there were no high-quality inoculating streams within a reasonable distance. Nearby streams provided a limited source of adults for immigration to re-establish populations. All streams in the region within ~15 km to the west and southwest (prevailing winds) have been channelized and have poor habitat much like LTC. Only two streams > 10 km to the south have benthic

habitat of good quality. Barlow *et al.* (2004) found that aerial recolonization of stream fauna below dams in Australia was highly dependent on satisfactory adult dispersal and suitable habitat. In a review of active and passive dispersal of freshwater macroinvertebrates, Bilton *et al.* (2001) observed that active dispersal is relatively uncommon apart from flight.

NMS ordinations indicated that the habitat types we studied—stream beds, leaf packs and LW—support different assemblages of macroinvertebrates. The important and unique role of LW as macroinvertebrate substrate has been reported by workers studying a variety of river types (Benke *et al.*, 1979, 1984; Johnson *et al.*, 2003; Coe *et al.*, 2006; Angradi *et al.*, 2009). Our data further underscore the importance of leaf pack habitat in sandy streams such as LTC (Dobson and Hildrew, 1992; Palmer *et al.*, 1996; Entrekin *et al.*, 2009). Leaf pack collections produced 77% of individuals and 75% of taxa (families) (Tables III and IV). Leaf packs were in short supply in all subreaches, but the paucity of riparian vegetation along subreach A implies that leaf packs found there were imported, and the straight channel and lack of LW there implies that leaf packs were also quite transient. Leaf pack collections from the untreated subreach A produced only about half as many taxa, on average, as the downstream subreaches (Table IV). On average, collections from downstream subreaches yielded 35 times as many shredding herbivores as the upstream subreach, highlighting the importance of leaf pack habitat to that group (Roeding and Smock, 1989; Dobson and Hildrew, 1992). Qualitative observations indicate that leaf pack frequency and quality may also have been somewhat depressed in the rehabilitated subreaches due to construction impacts (Knudsen and Dilley, 1987), perhaps leading to the ordination pattern in Figure 3b. Others have observed the pronounced influence of watershed land use, particularly riparian corridor vegetation on macroinvertebrate assemblage structure (Hrodey *et al.*, 2008; Jowett *et al.*, 2009; Jahnig *et al.*, 2009; Miserendino and Masi, 2010).

Functional redundancy occurring within sampling units might have influenced NMS ordinations and, subsequently, our interpretations of community responses among habitat types and sub-reaches. The number of taxa in the best represented functional group, predators, was large (72 of 149 total taxa encountered) and representation of predators in each reach condition group used to plot NMS ordinations was also large (31 in rehabilitated reach condition subsets, 54 in downstream untreated subsets and 44 in the upstream site). However, even when functional guilds contain a large variety of taxa, they may be limited due to individual member taxa that vary in ability to function dependent on the experienced range of environmental conditions (Wellnitz and Poff, 2001; Poff *et al.*, 2003). The ability of functional guilds to perform their anticipated functions, especially in an environment that is subject to wide variety of changing conditions as observed at our study reach, may crucially depend on this 'response diversity' aspect of functional redundancy (Laliberte *et al.*, 2010). While response diversity

was high for the predator guild of our study, four of nine guilds included fewer than five taxa, and omnivores were represented by only a single taxon. Yet, despite this paucity of taxa for some guilds, the inability of rehabilitation effects to clearly shift NMS plotting of macroinvertebrate communities away from the untreated site plots may reflect that sufficient functional redundancy was present over the entire study reach and that the communities reacted similarly to more overwhelming forces acting on the stream than were caused by LWS addition (Schofield *et al.*, 2008), emphasizing the importance of over-encompassing factors related to spatial scale when conducting research wherein community-level biological data are used to assess success or failure (Vaughn, 2010).

Findings here are consistent with previously published work on the effects of the LTC project (Shields *et al.*, 2008b). Stream rehabilitation effects on physical habitat were modest and transient, while hydrology and water quality were not changed. Initially, LWS were effective in stabilizing eroding banks within the treated reach by inducing deposition of sand berms adjacent to steep, caving banks. Field measurements (Shields *et al.*, 2004, 2006) and numerical simulations (He *et al.*, 2009) showed that the LWS were effective in providing velocity shelter during higher flows, and baseflow water depth doubled in the treated reach while submerged LW availability tripled. Fish biomass and richness as well as the incidence of larger individuals increased in the treated reach during the period of observation (Shields *et al.*, 2006), but similar changes occurred up- and downstream. By the last year of the study presented here, 31% of the LWS had been destroyed and 22% were damaged (Shields *et al.*, 2004). Furthermore, the rehabilitation efforts had no effects on stream bed carbon content (Shields *et al.*, 2008a) or on hydrologic characteristics, which were extremely flashy relative to a less-degraded reference stream (Shields *et al.*, 2010). LTC sediment and nutrient concentrations were correlated with discharge during high flows, and mean turbidity levels were about twice those for the reference stream (Shields *et al.*, 2010). The rehabilitation project also had no discernible effect on water quality. The rehabilitation project did not result in reach-scale, measurable changes in macroinvertebrate abundance and richness. Although available LW substrate was tripled by LW addition, the mean number of macroinvertebrates sampled from LW in treated reaches after LW addition was only about one third the pre-construction mean. Smaller numerical density of macroinvertebrates on the introduced wood may reflect its younger age (Hrodey *et al.*, 2008; Entrekin *et al.*, 2009) or tree species differences (Drury and Kelso, 2000) relative to naturally occurring LW in untreated reaches.

CONCLUSIONS

Addition of 72 LWS made from about 1100 logs to 2 km of Little Topashaw Creek, Mississippi, tripled the availability of LW substrate at baseflow but had no measurable effect on macroinvertebrate abundance or family

richness. Ordination analyses revealed more subtle differences in community composition between treated and untreated conditions, but these were related to antecedent discharge (occurrence of high flows during the preceding 6 months) and bed sediment composition rather than the availability of LW. Restoration of incising, sand-bed streams in landscapes such as the LTC watershed must include measures that address perturbed hydrology and degraded water quality. A combination of instream and watershed-scale measures appears to be required (Shields *et al.*, 2007).

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