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Stream bed organic carbon and biotic integrity

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ABSTRACT

1. Allochthonous carbon is the basis of the detrital food web in low-order, warmwater stream ecosystems, and stream-bed sediments typically function as carbon reservoirs. Many of the same factors that govern carbon input and storage to streams (e.g. riparian vegetation, large wood, heterogeneous boundaries) have also been identified as key attributes of stream fish habitat.
2. Effects of channel incision on sand-bed stream carbon reservoirs and indices of biological integrity (IBIs) based on fish collections were examined for four streams exhibiting a range of incisement in northern Mississippi. Observed mean C concentrations (mass percentage) ranged from 0.24 $\pm$0.36% for a non-incised stream to only 0.01 $\pm$ 0.02% for a severely incised channel, and were not correlated with large wood (LW) density, perhaps because LW density at one site was elevated by a habitat rehabilitation project and at another site by accelerated inputs from incision-related riparian tree fall. Fish IBI was positively correlated with bed C ($r = 0.70$, $p = 0.003$), and IBIs for reference streams were more than 50% greater than those computed for the most severely degraded sites.
3. More testing is needed to determine the efficacy of stream bed C as an indicator, but its importance to warmwater stream ecosystems, and the importance of covarying physical and hydrologic conditions seems evident.

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KEY WORDS: streams; channel incision; erosion; carbon; benthic organic matter; large wood; fish; indices; index of biotic integrity

INTRODUCTION

Allochthonous input of organic matter (OM) such as leaves, twigs and larger wood into stream ecosystems often forms the basis of the detrital food web (Minshall, 1967; Fisher and Likens, 1973; Vannote *et al*., 1980). Exclusion of leaf litter can trigger major changes across trophic levels in small, forest streams (Wallace *et al*., 1997). OM input as detrital litter is gradually broken down into finer particulate organic

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matter (POM), through a combination of processes. POM influences denitrification rates (Kemp and Dodds, 2002), stream energy budgets (Cummins, 1974), and populations of consumers (Webster, 1983).

Streams with mobile beds (i.e. beds moved by stream flow at least several times a year) store OM in their beds. For example, half or more of OM storage was in sediments in first-order Virginia coastal plain streams (Smock *et al*., 1989). Since buried OM is processed more slowly than that on the stream-bed surface, subsurface deposits may function as reservoirs that gradually release OM to downstream habitats (Metzler and Smock, 1990; Tillman *et al*., 2003). POM concentrations in stream beds reflect a balance among inputs, transport, and retention (Wallace *et al*., 1982; Metzler and Smock, 1990; Jones, 1997). POM retention has been linked to the local hydraulic regime (bed material size, channel slope, water depth, etc.) (Jones, 1997), density of riparian vegetation, and presence of instream retentive structures such as leaf litter and small wood (Adams, 1998) and large wood (LW) formations (Bretschko, 1990; Allan, 1995; Hauer and Lamberti, 1996; Laitung *et al*., 2002; Brookshire and Dwire, 2003; Morara *et al*., 2003), as well as catchment land-use (Maloney *et al*., 2005). Organic C levels tend to be higher in finer sediments than in coarser materials (Leichtfried, 1995; Sutherland, 1999), suggesting that physical features associated with hydraulic retention such as LW (Shields and Smith, 1992; Wallace *et al*., 1995; Shields *et al*., 2003) may trap and retain both finer sediments and associated OM (Haschenburger and Rice, 2004). Human perturbations such as flow augmentation (Hauer, 1989), LW removal (Bilby and Likens, 1980), and channel incision (Stofleth *et al*., 2004) tend to reduce OM levels in stream beds.

Since features that control OM input and retention such as instream LW, abundant riparian vegetation and stable banks have been associated with various measures of aquatic habitat quality (Shields *et al*., 1994, 1995a; Sullivan *et al*., 2004) and fish community vitality in streams draining agricultural catchments (e.g. Talmage *et al*., 2002; Sullivan *et al*., 2006), we hypothesized that warmwater stream fish community status might be positively correlated with OM concentrations. Warmwater stream fish species are adapted to a diverse environment that includes zones of very low, or no, velocity, irregular boundaries, abundant LW and frequent interactions among main channel, backwater, and floodplain environments. For example, pool habitats are important refugia for larger piscivores from terrestrial predators and act to damp hydraulic extremes associated with droughts (Schlosser, 1987), yet the lower velocities that occur in pools during normal flows provide hydraulic retention (Stofleth *et al*., 2005) that increases the likelihood of OM retention. Furthermore, many fish species native to warmwater streams in the US use LW for cover, feeding, egg attachment or nesting cover (Warren *et al*., 2002). Although some streams have elevated bed OM levels owing to human perturbations (e.g. wastewater inputs), we hypothesized that OM levels are indicative of physical habitat quality as well as providing a food base for benthic invertebrates. If this hypothesis is correct, measuring bed OM concentrations provides another way to assess stream habitat quality. Further, efforts to conserve or rehabilitate stream habitats must remediate the processes and features that retain OM and not merely focus on channel forms or instream structure.

STUDY SITES

Warmwater streams in the south-eastern coastal plain of the US are characterized by pulse inputs of water and OM that occur throughout the year. Non-incised channels are dominated by LW and frequently exchange materials with adjacent floodplains and wetlands. Unfortunately, few such channels remain in northern Mississippi. Here, European settlement, which began in the 1830s, was followed by deforestation, cultivation, rapid erosion of hillsides and accelerated valley sedimentation (Happ *et al*., 1940). Between 1840 and 1930 landowners and drainage districts attempted to improve utility of valley bottoms by channelizing the streams. Channelization by federal agencies also occurred between 1930 and 1965. These activities led to channel incision and loss of riparian vegetation. The channel incision process has been termed ‘channel evolution’, and has been described using a five-stage conceptual model by Simon (1989)

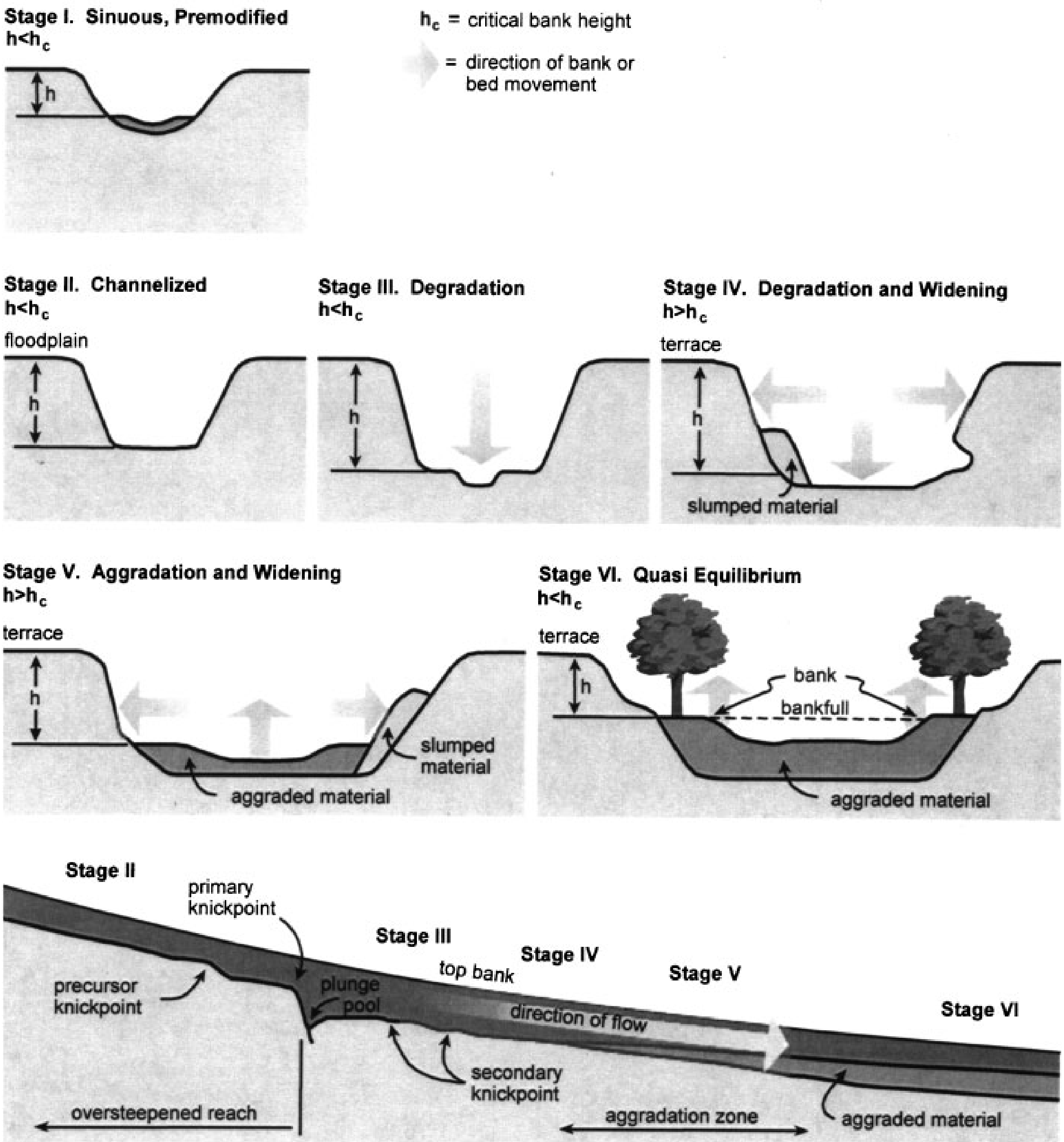

Figure 1. Conceptual model of incised channel evolution. After Simon (1989).

(Figure 1). Briefly, initially stable streams (Stage I) are channelized (Stage II) and respond by deepening (Stage III), which reduces their bed slope. When stream banks exceed a threshold height governed by bank soil strength properties, they cave, leading to rapid channel widening (Stage IV). Eventually, the supply of sediment from failing banks exceeds the ability of the wider, less steep channel to transport them away and lateral bars within the enlarged channel gradually evolve into stable, vegetated berms (Stage V). Thus the natural pattern of incised channel evolution creates a trajectory from a pristine or lightly degraded habitat condition (Stage I) through perturbation (Stage II), rapid and extreme degradation (Stage III and IV) and into gradual recovery (Stage V–VI) (Shields *et al*., 1994).

Four sand-bed streams in north central Mississippi with similar patterns of land use and varying degrees of habitat degradation were selected for study (Table 1 and Figure 2). For purposes of this study, it was assumed that the effect of historical catchment land-use on fish communities varied little among sites and acted as a random variable equally distributed among treatments. Study reaches were selected to be

Table 1. Characteristics of study site catchments

Stream	Catchment area (km^2)	Land use, percentage of catchment area		
		Forest or water	Row crops	Idle or pasture
Toby Tubby Creek	38	69	31	0
Turkey Creek	46	86	0	14
Little Topashaw Creek	37	77	11	12
Hotophia Creek	91	52	8	40

Figure 2. Study streams: (a) Stream 1, (b) Stream 2, (c) Stream 3, (d) Stream 4. Stream 3 is shown 3 years after construction of LW structures for bank erosion control and aquatic habitat rehabilitation. Typical LW structure shown on right side of picture.

Table 2. Characteristics of study streams

Stream	Identification number	Stream order	Mean discharge ($m^3 s^{-1}$)[a]	Stage of incised channel evolution[b]	Additional information
Toby Tubby Creek	1	4	nd	I	Shields *et al*., 1994
Turkey Creek	2	5	nd	early III	Stofleth *et al*., 2004
Little Topashaw Creek before	3-before	4	0.28	III, IV & V	Shields *et al*., 2006
Little Topashaw Creek after	3-after	4	0.53	III, IV & V	Shields *et al*., 2006
Hotophia Creek	4	5	1.7	IV & V	Shields *et al*., 1994, 1995b

[a] Mean is for water year containing bed C sampling dates.
[b] Simon (1989).

representative of a range of incised channel conditions. As part of the site selection process, reaches were classified according to the aforementioned conceptual model using field assessments by experienced observers (Table 2). Hereafter the study reaches are referred to by integers that correspond to their ordinal ranking by stage of channel evolution (Table 2). Streams 1 and 2 were lightly degraded streams with plentiful riparian vegetation and LW. Small (< 60 cm high) beaver dams were common along streams 1 and 2; although these potentially have important effects on stream fish assemblages (Schlosser, 1995; Schlosser and Kallemeyn, 2000) they were not directly addressed in the analysis since they are common natural features just as other types of pool and LW habitat are. All streams had beds comprised primarily of medium sand and average bed slopes ranging from 0.001 to 0.002. Streams 3 and 4 were unstable, deeply incised streams that exhibited characteristics of stages III and IV of incised channel evolution (Simon, 1989): extremely wide and deep channels, high sediment loads, eroding banks, and sandy bars and berms. All streams experienced short-duration high flows in all seasons, but incised channels were flashier (Shields and Cooper, 1994).

Riparian vegetation along all channels was a diverse mixture of bottomland hardwoods, early succession species such as willows (*Salix* spp.) and wetland trees such as baldcypress (*Taxodium distichum*). Plant species assemblages were typical of those in floodplain forests of the south-eastern US (Ricketts *et al*., 1999). Baldcypress was much more common along the lightly degraded streams 1 and 2. Organic matter inputs occurred as leaf fall in the autumn, but input was also distributed throughout the year as many woody species contributed leaves and twigs more or less continually. Furthermore, many of the oaks (*Quercus* spp.) gradually shed dead leaves throughout much of the winter. Stream 3 was sampled before and 3 years after construction of a stream rehabilitation project that consisted of placing 72 LW structures built using almost 1200 felled trees and planting willow cuttings in sandbars within a 2 km long reach as described by Shields *et al*. (2003, 2004, 2006). LW structures were wedge-shaped stacks of criss-crossed trees and whole logs with average dimensions of *ca* 2 m high by 5 m wide by 13 m long (Figure 2(c)). Structures were placed along the toe of concave eroding banks and tended to displace the thalweg and base-flow channel as they filled with sediments. Additional descriptive information regarding these streams and their catchments is available elsewhere (Shields *et al*., 1994, 1995b, 1998, 2001, 2003, 2004, 2006; Stofleth *et al*., 2004).

METHODS

Benthic sediment samples, physical habitat measurements, and fish were collected from selected reaches typical of each study stream. Sampled reaches were separated by 50 m to 600 m of unsampled stream in order to obtain full coverage of habitat types in treated and untreated study reaches. Four, 100 m long reaches were treated as replicates and were sampled at streams 1, 4 and 2; and two, 150-m-long replicate reaches were sampled at stream 3 as part of a larger study: a total of 72 LW structures comprised of 1200 trees were constructed along eroding banks within a 2 km long reach of stream 3 (Shields *et al*., 2006). Streams 1 and 4 were sampled in December 1991 and January 1992, respectively, while reaches of stream 3 were sampled once just prior to and once 3 years after construction of the LW structures, in April–May 2000 and July–August 2003, respectively. Stream 2 samples were collected in August 2003.

Sediment samples were collected at three or four transects placed at uniform intervals along each reach. At each transect, three 250-g samples of the top 10 cm of benthic sediments, including all sizes of OM lying on the bed surface, were collected during base flow (velocities $< 30\,\mathrm{cm\,s^{-1}}$) using a hand trowel or similar instrument to scoop with a motion in the upstream direction. Sample points were located at the channel centreline and within 25% of the base flow width from each water's edge. Thus each reach was represented by 9 to 12 benthic sediment samples. For analysis, all bed samples were dried, ground, forced through a 2 mm sieve, homogenized and subsampled to a weight of 0.5–1.0 g. Subsamples were analysed for total C via dry combustion using a LECO CN2000 at a temperature of 1300–1350°C (LECO CR12 at a temperature of 1400°C for streams 1 and 4) (Sutherland, 1998). Calibration was performed by using LECO soil standards and calibration checked with EDTA, Synthetic C and NAPT exchange soil samples. We assumed that the contribution of inorganic C to total C was negligible owing to the low-pH regime typical of sediments and waters throughout this region and, therefore, total carbon = total organic carbon, the key constituent of instream OM. This assumption was verified by analysing a subset of samples for both total C and total organic C. Variances (*F*-test, $p = 0.45$) and means (*t*-test, $p = 0.31$) of total C and total organic C were not significantly different, and the mean difference between TC and TOC was 0.00009 ± 0.00011 $\mathrm{g\,C\,g^{-1}}$ sediment ($0.009 \pm 0.011\%$).

LW density was measured in each sampled reach using methods described by Barbour *et al*., (1999). Each woody debris formation intersecting the plane of the water surface greater than $0.25\,\mathrm{m^2}$ was recorded. The estimated length and width of each LW formation intersecting the plane of the water surface 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 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. Standing trees and stumps within the stream were also recorded if their length and width exceeded 0.5 m. 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 water surface width by reach length) to obtain LW density. This density is not an expression of the volume of LW, but rather a measure of its relative influence on habitat. Water width and depth were sampled at regularly spaced points along transects in a fashion similar to that prescribed by Gorman and Karr (1978). Qualitative observations of the presence of hydraulic structures, channel width, channel depth and bank vegetation were also recorded. Thalweg sinuosity was computed using plan surveys of the thalweg obtained using total stations or global position systems. About 10% of the bed C sediment samples were collected in duplicate, and duplicates were subjected to sieve analysis to determine bed sediment grain size.

Fish were sampled from the same reaches sampled for bed C and LW using a single pass with a backpack-mounted electroshocker. Each reach was fished for several minutes (electric field application time mean = 9.8 min, SD = 6.1 min). Effort was not significantly greater for the longer (150-m) reaches sampled at LTC than for the 100-m reaches sampled in all other streams (*t*-test, equal variances, $p = 0.146$). Shocking crews, which consisted of one person carrying the electroshocker and two people with dipnets, worked from downstream to upstream, sampling all habitats, with greater concentration on those yielding fish. Fish longer than about 150 mm were identified, measured for total length, and released. Smaller fish, and fish that could not be identified in the field were preserved in 10% formalin and identified and

Table 3. Scoring criteria used to compute indices of relative biotic integrity from fish collections from degraded north-west Mississippi streams. After Shields *et al.* (1995a)

Category	Metric	Scores		
		1	3	5
Species richness and composition	Total number of species	0–9	10–16	$\geqslant 17$
	Number of darter species	0	1	$\geqslant 2$
	Number of sunfish species	0–2	3–4	$\geqslant 5$
	Number of sucker species	0	1	$\geqslant 2$
	Number of intolerant species	0	1–2	$\geqslant 3$
Trophic composition	Proportion of individuals that are members of species classified as tolerant	$\geqslant 35\%$	$20\% \leqslant x < 35\%$	$\leqslant 20\%$
	Proportion of individuals as omnivores	$\geqslant 20\%$	$5\% \leqslant x < 20\%$	$< 5\%$
	Proportion of individuals as insectivorous cyprinids	$\geqslant 50\%$	$10\% \leqslant x < 50\%$	$< 10\%$
Fish abundance and condition	Proportion of individuals as piscivores	$< 1\%$	$1\% \leqslant x < 2\%$	$\geqslant 2\%$
	CPUE, fish per minute	$\geqslant 20$	$8 \leqslant x < 20$	< 8
	Proportion of individuals as hybrids	$\geqslant 2\%$	$0.10\% \leqslant x < 2\%$	$< 0.10\%$
	Proportion of individuals with disease or anomaly	$\geqslant 2\%$	$1\% \leqslant x < 2\%$	$< 1\%$

measured in the laboratory. Fish samples were collected during the autumn when species richness and numbers tend to be higher (Shields *et al.*, 1995a).

Fish collection data were used to compute an index of biotic integrity (IBI, Karr *et al.*, 1986) modified for streams similar to those selected for this study located in our region for each sampled reach (Table 3). The IBI is a widely used tool that has been successfully modified and applied for gauging the severity of environmental perturbations associated with many types of human impacts (e.g. Ganasan and Hughes, 1998; Hughes *et al.*, 1998; Diamond and Serveis, 2001). The scoring criteria used for the modified IBI were identical to those proposed by Shields *et al.*, (1995a), except lower scores were associated with higher proportions of individuals as insectivorous cyprinids and higher values of catch per unit of effort (Table 3). Assemblages typical of warmwater streams disturbed by incision are characterized by large numbers of small cyprinids relative to collections from lightly degraded streams (Shields *et al.*, 1998).

Fish species lists for each collection were used to compute six quantities proposed by Wichert and Rapport (1998) as indicators of ecological integrity in agricultural catchments drained by warmwater streams (Table 4). The number of species in the collection constituted the sixth indicator. Integer scores for habitat orientation, flow preference and feeding group were assigned to each captured fish species by Shields *et al.*, (2000) in such a way that higher scores were associated with greater sensitivity to ecosystem stress. For example, perturbed streams tend to support populations that are characterized by large numbers of a few tolerant, small-bodied species that mature rapidly. In general, omnivorous fish that prefer lotic conditions become more dominant at the expense of specialist feeders that spend part of their life-cycle in lentic habitats.

Values of the first five indicators listed in Table 4 were computed for each site and for each stream as follows:

$$SACS_j = \frac{\sum_{i=1}^{N} SCS_{ij}}{N}$$

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Table 4. Indicators of ecological integrity proposed by Wichert and Rapport (1998) and adapted by Shields *et al*., (2000) for northern Mississippi

Index	Value
Age at maturity	Age for sexual maturity, in years. When male and female differ, average is used
Maximum adult size	Reported maximum length for adults, mm
Habitat orientation	Surface = 1, littoral or vegetation = 2, benthic = 3, general = 4, pelagic = 5
Habitat flow preference	Lotic = 1, lentic = 2, both = 3
Feeding group	Omnivore = 1, herbivore = 2, general invertebrates = 3, fish and large invertebrates = 4, plankton and microcrustaceans = 5
No. of species	Total number of fish species in sample

where $SACS$ = species association characteristic score j, SCS_{ij} = value of indicator j for species i, and N = number of species in collection. Values for indicators for each fish species were gleaned from the literature as described by Shields *et al*., (2000). When different values occurred for the age at maturity for males and females, the average value was used in analysis.

Measured %C values were transformed (arcsine square root) and subjected to a two-way ANOVA with stream and reach as fixed and random effects, respectively. The Holm–Sidak method with alpha adjusted for number of comparisons (Systat Software, Inc., 2004) was used for pairwise comparisons of all possible pairings. Computed indices of biotic integrity were similarly subjected to two-way ANOVA. Bed carbon levels for each sampled reach were compared with LW density values. Similarity of fish species relative abundances for each stream was explored by computing Pearson correlation coefficients for species abundance lists for each stream and by computing Chao's estimator (corrected for unseen species) for Chao's Sørensen abundance-based similarity index (Chao *et al*., 2005) using software by Colwell (2005). Associations between bed carbon concentration and fish indices were explored using nonparametric correlation.

Following these exploratory analyses, data from each reach were assigned to one of two categories: those with mean bed %C$\geqslant$0.15 and those with mean bed %C$\leqslant$0.13. The breakpoint between these two categories was arbitrarily chosen based on a gap in the joint distribution of %C and IBI. Biotic and physical attributes of the two classes were examined by comparing *t*-statistics computed using data and those obtained by randomly resampling the data 5000 times. The null hypothesis (no difference between the high and low %C groups) was rejected when the randomly generated *t*-values exceeded those from the data 5% of the time or less.

RESULTS

Physical habitat conditions exhibited gradients that paralleled stages of channel incision, with riparian cover, canopy and LW density levels declining as channel widths and depths increased (Table 5). Mean LW density values ranged across two orders of magnitude, with highest levels in stream 2, which had well-wooded banks and was experiencing the initial stages of channel incision, triggering accelerated inputs from undermined trees (Figures 1 and 2). All streams were sandy, and all had very shallow water depths except for the non-incised stream 1. Physical habitat effects of LW addition in stream 3 were limited to doubling LW density and a slight increase in water width.

Reach-mean C levels ranged from 0.54% to 0.01%, while the mean of all data was 0.18%. Mean and standard deviation of C were an order of magnitude higher for streams 1 and 2 than for stream 4 (Figures 3 and 4). Carbon levels were intermediate for stream 3, and mean concentrations were essentially unchanged there 3 years after installation of LW structures and willow planting. Two-way ANOVA of %C indicated that differences based on stream were significant ($p<0.001$), but differences based on reach within a given

Table 5. Physical habitat characteristics of study reaches[a]

Stream no.	Stage of incised channel evolution	Bankline covered by woody vegetation (%)	Canopy (%)	LW density[b] ($m^2\,km^{-2}$)	Thalweg sinuosity	D_{50} (mm)	Water width (m)	Channel width (m)	Water depth (cm)	Channel depth[c] (m)
1	I	71	62	41 900 $\pm$ 35 500	1.3	0.40	6.2 $\pm$ 0.9	7–9	35 $\pm$ 24	1–2
2	early III	85	65	170 948 $\pm$ 77 000	1.3	0.45	5.1 $\pm$ 1.8	12	nd	3
3-before	III, IV & V	27	25	46 500 $\pm$ 40 800	2.1	0.28	3.0 $\pm$ 1.0	33 $\pm$ 7	11 $\pm$ 11	4–6
3-after	III, IV & V	45	27	111 800 $\pm$ 43 600	2.2	0.29	4.0 $\pm$ 1.4	38 $\pm$ 12	9 $\pm$ 5	4–6
4	IV & V	28	4	1500 $\pm$ 3000	1.4	0.40	17.7 $\pm$ 4.4	37–58	16 $\pm$ 8	3–7

[a] Values separated by a short dash (–) represent maxima and minima. Values separated by $\pm$ are means followed by standard deviations. Channel width and depth for Turkey Creek (stream 2) are estimates.
[b] Units refer to a visual estimate of the sum of the areas of large wood formations in the plane of the water surface divided by the water surface area in a given reach (Barbour *et al*., 1999).
[c] Difference between top bank and thalweg elevation.

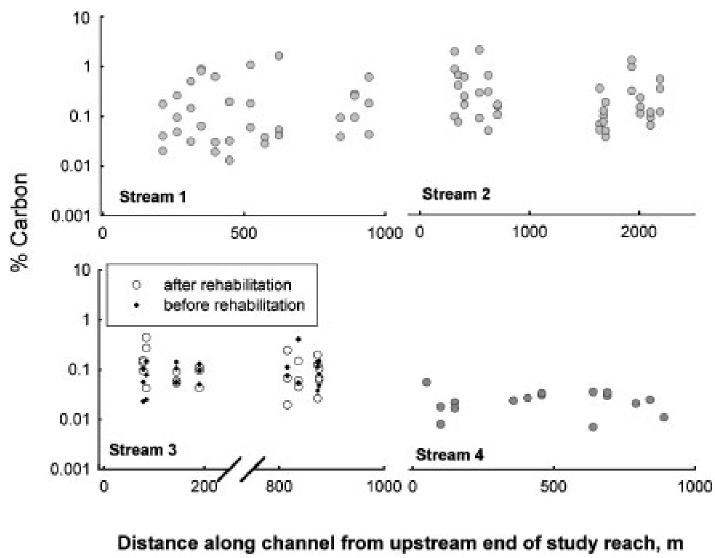

Figure 3. Total carbon in bed sediment samples versus downstream distance for study streams.

stream were not. Furthermore, a longitudinal trend was not evident for any stream (Figure 3). Pairwise multiple comparisons indicated that bed C concentration for the highly degraded stream 4 was significantly lower than for the other streams, and that stream 3 (both before and after rehabilitation) was significantly lower than the lightly incised stream 2 ($p < 0.05$) (Figure 4). Reach-mean sediment %C was not correlated with LW density ($n = 16$, $r = 0.41$, $p = 0.12$).

Fish collections totalled 2429 individuals representing 39 species (Table 6 and Appendix). Rates of capture (catch per unit effort) ranged from 5–35 fish per minute of electrical field application, but differences in stream-mean rates were not significant ($p = 0.148$). Collections (a collection is all the fish sampled from one of the sampled reaches on a given date) comprised 16–575 fish representing 5–21 species. Slightly incised stream 2 yielded 23 species while the deeply incised and widened stream 4 yielded only 12.

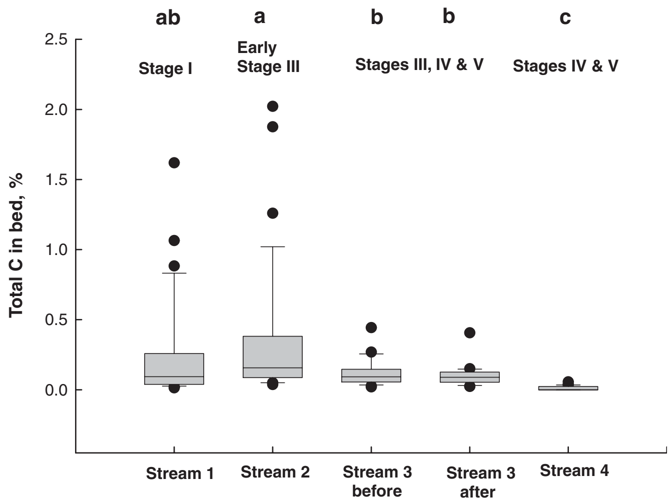

Figure 4. Distribution of total carbon in bed sediments of incised, sand-bed streams. Boxes represent limits of 25th and 75th percentiles, central line represents median, whiskers represent 10th and 90th percentiles, and solid dots are outliers that fall above the 90th percentile or below the 10th percentile. Box plots with the same letter above them are not significantly different (ANOVA of arcsine square-root-transformed data, $p < 0.001$).

Table 6. Characteristics of fish collections from selected reaches of sand-bed streams in north central Mississippi. Except for total number, tabulated values are means for all collections. Means in the same row followed by the same letter or by no letter are not significantly different

Stream number	1	2	3-before	3-after	4
Stage of incised channel evolution	I	Early III	III, IV & V	III, IV & V	IV & V
Fish IBI	45[c]	45[c]	26[a]	37[b]	29[a]
No. of species	10[a]	18[b]	7[a]	18[b]	7[a]
No. of darter species	1.0	3.3	0.5	0.5	0.3
No. of sunfish species	4[b]	3[ab]	0.5[a]	4[ab]	2.8[ab]
No. of sucker species	0.8	1.0	1.0	0.0	0.0
No. of intolerant species	1.0[ab]	4.3[b]	3.0[ab]	1.0[ab]	0.0[a]
% tolerant species	1[b]	18[a]	41[a]	29[a]	30[a]
% omnivores	2[a]	14[ab]	7[a]	23[b]	6[a]
% insectivorous cyprinids	17[a]	25[a]	83[b]	56[ab]	46[ab]
% piscivores	18.77	0.00	0.31	0.00	1.18
Fish per minute	19	7	23	16	12
% hybrids	0.0	0.0	0.0	0.0	14.8
% anomalies	0.0	0.0	0.0	0.0	0.0
Total no. of fish (all collections)	386	623	213	941	266

Six of these 12 were small-bodied cyprinids and a seventh was the opportunist *Gambusia affinis*. Collections from stream 1 included two darters (family Percidae) while stream 2 yielded five species of darters. Across-stream differences in fish assemblages were striking (Table 6); only three of the 39 species were common to all four streams, and correlation coefficients between species abundance lists ranged from −0.074 (1 with 2) to 0.419 (3 with 4). Streams 2 and 3-after had the greatest number of species (15) in common. Similarity indices between collections were a minimum (0.00 ± 0.00) for a pair containing a collection from stream 1 and one from stream 3-before, and, excluding pairs of collections from the same stream, were greatest (0.751 ± 0.141) for a pair containing collections from 3-after and 2.

Fish IBI values ranged from 24 ('very poor to poor' integrity class) to 48 ('good'), which compares with a possible range of 12–60 (Karr *et al*., 1986) and a reported range of 24–50 for 51 collections from streams in this region (Shields *et al*., 1995a). As for %C, two-way ANOVA of IBI indicated that differences based on stream were significant ($p < 0.001$), but differences based on reach were not. Fish IBI for the non-incised and lightly incised streams 1 and 2 were significantly greater than for the incised streams 3 and 4; the rehabilitated stream 3 was intermediate between these two extremes (Table 6). Fish IBI and several of its component metrics were significantly correlated with mean bed sediment total carbon concentration (Table 7). Variation in reach-mean bed %C explained 49% of the variation in fish IBI values. None of the Wichert indicators except for number of species was correlated with %C; however, when data from the lightly degraded stream 2 were excluded, three of five indicators (maximum size, habitat flow preference and feeding group) were correlated with %C ($r > 0.56$, $p \leqslant 0.06$). Shields *et al*. (2000) found the Wichert indicators were significantly correlated with physical measures of large-scale perturbations in higher-order streams in this region.

A scatterplot of reach mean bed %C versus fish IBI suggests two categories of sites (Figure 5), with streams 1 and 2 (incision stages I and III) in one category and streams 3 and 4 (incision stages III–V) in the other. All seven collections from reaches with mean bed C $\geqslant$ 0.14% had IBI values of $\geqslant 42$ ('fair' to 'good') while eight of the nine collections from reaches with mean bed C $\leqslant$ 0.13% had IBI values of $\leqslant 38$ ('fair-poor' to 'very poor'). Furthermore, mean bed %C values for sites with mean bed C $\geqslant$ 0.14% was about five times greater than for the mean for the other group (Table 8), even though the means of LW density were not significantly different. Mean fish IBI was about 30% lower for the incised group and means of the percentage of individuals representing tolerant species, the percentage of individuals that were classified as insectivorous cyprinids, and the Wichert feeding group score were all significantly different for the two groups ($p \leqslant 0.027$).

Following LW addition, fish collections from stream 3 showed an increase in the number of species, the percentage of fish classified as omnivores, and IBI values (Table 6), but mean bed C did not increase

Table 7. Spearman rank-order correlation coefficients (r) and significance levels (p) for correlations between mean total carbon in bed sediments and fish index of biotic integrity (IBI), key components of the IBI and Wichert indices. Bold font indicates correlations with $p < 0.10$

	r	p
Fish IBI	**0.720**	**0.001**
No. of species	**0.540**	**0.031**
No. of darter species	**0.498**	**0.049**
No. of sunfish species	0.009	0.969
No. of sucker species	**0.642**	**0.007**
No. of intolerant species	**0.702**	**0.002**
% tolerant species	**−0.583**	**0.018**
% omnivores	0.187	0.476
% insectivorous cyprinids	**−0.432**	**0.091**
% piscivores	0.060	0.822
Fish per minute	−0.329	0.207
Age at maturity	0.338	0.194
Maximum adult size	0.309	0.238
Habitat orientation	−0.163	0.541
Habitat flow preference	0.370	0.153
Feeding group	0.198	0.456

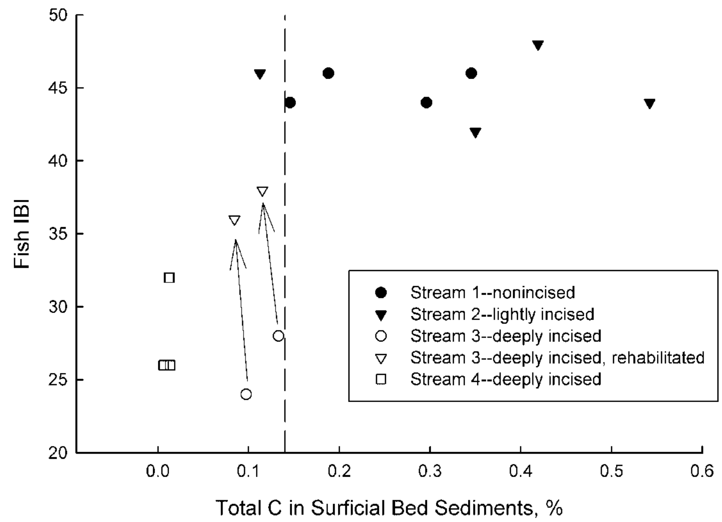

Figure 5. Total carbon in surficial bed sediments versus fish IBI for sampled reaches of sand-bed streams in north central Mississippi. Each point represents a single reach sampled for bed C and fish. Vertical line shows %C = 0.14.

Table 8. Comparison of descriptors of fish samples from sand-bed streams in north central Mississippi with relatively high and low organic C concentrations in their beds. Bold font indicates significant differences

Quantity	Reaches with mean bed %C > 0.14	Reaches with mean bed %C < 0.13	*p*
% carbon	**0.327**	**0.065**	**0.0001**
LW density, $m^2 km^{-2}$	93,000	58,000	0.39
Fish IBI	**44.9**	**32.0**	**0.0004**
Catch per unit of effort	13.6	14.5	0.85
No. of species	13.6	10.6	0.28
No. of darter species	1.71	0.89	0.358
No. of sunfish species	3.4	2.7	0.32
No. of intolerant species	2.4	1.3	0.23
% individuals of species classified as tolerant	**0.084**	**0.31**	**0.0014**
% omnivores	0.078	0.10	0.54
% insectivorous cyprinids	**0.21**	**0.54**	**0.0073**
% piscivores	0.11	0.006	0.096
Age at maturity, yr	1.3	1.3	0.94
Maximum size, mm	239	185	0.11
Habitat orientation	2.9	2.941	0.99
Habitat flow preference	1.6	1.595	0.43
Feeding group	**3.8**	**3.4**	**0.027**

(Figures 3 and 4). In fact, concurrent sampling of fish in untreated reaches immediately upstream and downstream from the treated reach showed that fish populations along the entire stream experienced recovery in the post-rehabilitation period irrespective of reach-scale treatment (Shields *et al.*, 2006). Species richness approximately doubled upstream from, downstream from, and within the reach where wood was added, suggesting that the entire stream may have been recovering from some sort of stressful acute event.

Fish community composition in the reach where wood was added shifted towards one typical of a lightly degraded reference site, but similar shifts occurred in the untreated reaches downstream, which had relatively high levels of naturally occurring LW.

DISCUSSION

Degraded, incised reaches sampled in this study had less OM in their bed sediments than non-incised or lightly incised sites, probably reflecting the higher velocities, flashier hydrology, frequent bed movement and lack of riparian vegetation and debris typical of incising streams (Shields *et al.*, 1994). Spatial distribution of OM in the reference streams was highly non-uniform as reported by Metzler and Smock (1990), producing large sample variances (Figures 3 and 4) that are indicative of the relatively high levels of physical heterogeneity and diversity that are important aspects of stream ecosystems (Gorman and Karr, 1978; Palmer *et al.*, 1997). Bed sediment C was higher for streams with greater riparian canopy, as noted by Hauer (1989). Riparian canopy is typically reduced by the bank erosion that follows channel incision because it destroys riparian buffers and produces wider channels that require taller vegetation for canopy cover.

The mass per unit mass concentrations of total C within this data set ranged from near detection limits (0.01%) to as much as 2%, but isolated values in the order of 10% were reported for different reaches of the same streams by Stofleth *et al.*, (2004). Observations of stream-bed organic carbon (OC) concentration (mass percentage) reported by others vary roughly between 0.1% and 10% (Table 9), and some differences are likely owing to variation in analytical methods. Most published data for stream-bed sediments are for ash-free dry matter (AFDM). Arbitrary conversions of AFDM to organic C by dividing the former by a constant ~ 2 are common, but incorrect, according to Sutherland (1998), who found values of OM/OC for Hawaiian stream bed sediments to range from 6.2 to 27.4. Use of a dry combustion carbon analyser is preferred to AFDM determined by loss on ignition for POM (Sutherland, 1999; Cambardella *et al.*, 2000). With this caveat in mind, examination of published data shows that lowland, sand-bed stream sediments tend to have OM content greater than those of gravel and cobble streams, but lower than for depositional zones along lowland streams such as abandoned channels or natural levees (Table 9). A more global survey indicated that lowland and small mountain streams tend to have higher levels of benthic OM than those in arid, tundra or boreal settings (Webster and Meyer, 1997).

Our findings regarding bed C levels may have been perturbed by seasonal effects, but we feel these are probably minor. Streams 1 and 4 (non-incised and incised, respectively) were sampled in winter, and streams 2 and 3 (non-incised and incised, respectively) were sampled in summer. The literature indicates that OM input to upland (montane) streams and to streams in higher latitudes is highly seasonal, with a major pulse corresponding to leaf fall in autumn (e.g. Webster *et al.*, 2001). However, information on seasonal variation in bed OM levels was not found in the literature. Owing to the long growing season and the nature of riparian vegetation, warmwater streams in the south-eastern coastal plain of the US are characterized by pulse inputs of water and OM that occur throughout the year. Major inputs are associated with overbank flows that convey detritus from the floodplain into the channel. POM concentrations in stream beds reflect a balance among input, transport and retention.

The lightly degraded streams 1 and 2 contained more LW than the incised channels 3 and 4, but reach LW density was not positively correlated with bed %C, as has been reported by others (e.g. Bilby and Likens, 1980; Hauer, 1989; Lepori *et al.*, 2005; Maloney *et al.*, 2005). This may reflect the fact that elevated levels of LW density at streams 2 and 3 were caused by accelerated inputs from the riparian zone driven by channel incision (Downs and Simon, 2001) and a large-scale LW addition project, respectively. The

Table 9. Published values for organic matter in stream bed sediments

Location	Analytical method	Sample	Reported magnitude (means or ranges)	C as percentage of dry sediment weight[a]	Source
Small gravel-bed river, Switzerland	AFDM	40-cm-deep cores	1.5 to 8.0 kg m^{-2}	0.3–1.6	Naegeli *et al.* (1995)
4th-order gravel-bed river, New Zealand	AFDM	Cores between 10 and 50 cm below bed surface	0.4–0.8 g AFDM POM per 4000 cm^3 sediment	0.005–0.010	Olsen and Townsend (2005)
Forested, mountain stream, North Carolina	AFDM	10-cm-deep cores	88–1568 g AFDM m^{-2}	0.07–1.25	Wallace *et al.* (1995)
1st-order sand-bed blackwater stream, Virginia	AFDM	20-cm-deep cores	4.8 kg AFDM m^{-2}	1.6	Metzler and Smock (1990)
2nd-order sand-bed river overlying iron pan in north-western lowlands of Germany	AFDM	25–40-cm-deep cores	~0.2% to 6.6% of sediment dry weight, 'varied around 1%'	0.2–6.6	Cleven and Meyer (2003)
2nd–3rd-order sandy streams on coastal plain, Georgia	AFDM	10-cm-deep cores excluding POM > 1.6 cm diameter	0.09% to 0.2% of sediment dry weight	0.09–0.20	Maloney *et al.* (2005)
6th-order sand-bed blackwater river on coastal plain, Georgia	AFDM	24-cm-deep cores	869 g CBOM and 1903 FBOM m^{-2} bed	0.92	Benke and Meyer (1988)
Streams and rivers in south-eastern USA	AFDM	Various	10–5270 g m^{-2} BOM (excluding wood)	0.0033–1.75	Jones (1997)
Two coastal plain blackwater streams, one impacted by prolonged heated discharge from nuclear plant, South Carolina	AFDM	30-cm-deep cores of stream bed and stream banks	<1–30% AFDM	<1–30	Hauer (1989)
4th-order gravel-bed river, grasslands, bedrock canyon, New Zealand	Elutriated and dried @ 100°C	50-cm-deep freeze cores	0.6–71.7 g POM L^{-1}	0.05–5	Boulton and Foster (1998)
Outlet from karstic spring on River Rhone floodplain, cobble, gravel	Carbon analyser	Sediment samples from 20-cm depth below bed surface	0.1–1.0 × 10^3 mg L^{-1}	0.008–0.8	Chafiq *et al.* (1999)
3rd-order sand and gravel-bed river, basaltic catchment, Hawaii	Carbon analyser	5-cm-deep cores	6.7 g OC kg^{-1}	0.67	Sutherland (1999)
San Joaquin River and tributaries, California		Top 6 cm of recently deposited fine sediments	0.05–1.7 TOC (% of dry weight)	0.05–1.7	Gilliom and Clifton (1990)
Freshwater fluvial sediments			1.5–23.8 g OC kg^{-1}	0.15–2.38	Means *et al.* (1980)
Freshwater sediments (both lotic and lentic environments)	Carbon analyser	Scooped from top 5 cm	0.03–11.8%OC	0.03–11.8	Suedel and Rodgers (1991)
Four sand-bed streams in with mixed cover catchments, northern Mississippi	Carbon analyser	Scooped from top 10 cm	0.00[b]–0.95%C	0.01–0.95	This study

[a] Published data converted to percentage of dry weight by assuming a bulk specific gravity for stream-bed sediments of 1.25 except for Olsen and Townsend (2005), who published a porosity value of 20% for their samples, which equates to a bulk specific gravity of 2.0.
[b] Below detection limits.

addition of LW to stream 3 for rehabilitation did not increase bed %C, even though LW density was increased by ~70%. Evidently the efficiency of the added LW formations as POM retention devices is not fully reflected by simple density, since LW placed parallel to the flow direction along the channel margins has less impact on high flow velocities than LW that projects into or spans the channel (Shields and Gippel, 1995). Sediments trapped within the LW structures often shifted baseflows toward the opposite bank, leaving much of the LW out of water (Figure 2(c)) and reducing the frequency of leafpack formation (S. Testa, personal communication). The added LW also promoted local scour in the base-flow channel (Shields *et al*., 2004), which could have depressed local C levels. Finally, many of the LW structures failed during the second and third high flow seasons following construction (Shields *et al*., 2004), just prior to post-rehabilitation sampling, which may have released trapped OM.

Fish populations displayed interesting differences among the sampled sites that paralleled gradients in bed sediment %C. These responses were somewhat surprising in light of findings by others that stream benthic macroinvertebrates in this region are more strongly influenced by water quality than by physical processes associated with channel incision (Maul *et al*., 2004). Indeed, given the wide range of chemical, geomorphic and hydrologic variables that influence fish, the dichotomy in fish assemblages suggested by Table 8 is striking. Apparently fish in this region are adapted to streams with abundant sources of allochthonous matter and heterogeneous physical conditions that include zones that trap and retain OM of various sizes. Previous work has documented the sensitivity of the relative abundances of piscivorous centrarchids and their cyprinid prey to pool habitat and cover, physical features which contribute to C retention (Shields *et al*., 1997, 1998, 2003). The findings presented here suggest that the physical and hydrologic effects of channel incision and its causes produce perturbations in stream bed C and fish assemblage structure. The differences in fish assemblages in stream reaches with relatively high and low bed C content (Table 8) are consistent with previous findings regarding impacts of channel incision on fish and their habitats (Shields *et al*., 1994). As stable pools are eliminated by channel incision, widening and aggradation of coarse, sandy bed material (Figure 1), piscivores are replaced by small-bodied, rapidly reproducing opportunists such as cyprinids (Shields *et al*., 1998). Species such as darters give way to those more tolerant of shallow depths and shifting bed materials.

It is not known if the observed shifts in fish IBI are partially due to reductions in bed C or may simply depend on the same factors governing bed C. Although biotic indices are powerful tools, they cannot convey causal relationships or information about fundamental ecological processes (Hughes *et al*., 1998). It is interesting that fish IBI responded positively to LW addition at stream 3 but bed C did not. Shifts in fish community composition probably reflected physical habitat changes due to LW addition. Although LW addition doubled mean water depth and increased LW density by a factor of three (Shields *et al*., 2006), it did not result in improved C retention.

To summarize, stream bed C concentrations (assumed equivalent to OC concentrations) were found to vary between detection limits (0.01%) and about 2% in sand-bed streams in north central Mississippi. Means and variances of C were one to two orders of magnitude lower in severely incised channels than for a non-incised stream. Reach-mean C concentration explained 49% of the variance in an index of biotic integrity computed using fish collections from the same reach, and values of the index and two of its components were significantly different for incised and lightly degraded stream reaches. We do not propose general use of benthic OC as an ecological indicator without much additional work. Clearly, situations are likely to occur in which bed C levels may be elevated owing to human perturbations, but fish communities are severely impaired by water quality degradation and habitat modifications (e.g. agricultural drainage ditches). However, we note that efforts to restore and manage warmwater sand-bed stream ecosystems will fall short if they do not recreate conditions that promote higher levels of bed OC. Restoring stream form (channel width, depth and sinuosity) alone will not fully address ecosystem rehabilitation unless processes responsible for OC input and retention also are allowed to recover.

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REFERENCES

Adams JC. 1998. The role of leaf litter and small wood in the retention of fine particles during storms in an Appalachian headwater stream. MS thesis, Virginia Polytechnic Institute and State University, Blacksburg.

Allan JD. 1995. *Stream Ecology*: *Structure and Function of Running Waters*. Kluwer: Netherlands.

Barbour MT, Gerritsen J, Snyder BD, Stribling JB. 1999. *Rapid Bioassessment Protocols for Use in Streams and Wadeable Rivers*: *Periphyton*, *Benthic Macroinvertebrates and Fish* (2nd edn). EPA 841-B-99-002, US Environmental Protection Agency; Office of Water: Washington, DC.

Benke AC, Meyer JL. 1988. Structure and function of a blackwater river in the southeastern U.S.A., *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie* **23**: 1209–1218.

Bilby RE, Likens GE. 1980. Importance of organic debris dams in the structure and function of stream ecosystems. *Ecology* **61**: 1107–1113.

Boulton AJ, Foster JG. 1998. Effects of buried leaf litter and vertical hydrologic exchange on hyporheic water chemistry and fauna in a gravel-bed river in northern New South Wales, Australia. *Freshwater Biology* **40**: 229–243.

Bretschko G. 1990. The dynamic aspect of coarse particulate organic matter (CPOM) on the sediment surface of a second order stream free of debris dams. *Hydrobiologia* **203**: 15–28.

Brookshire ENJ, Dwire KA. 2003. Controls on patterns of coarse organic particle retention in headwater streams. *Journal of the North American Benthological Society* **22**: 17–34.

Cambardella CA, Gajda AM, Doran JW, Wienhold BJ, Kettler TA. 2000. Estimation of particulate organic and total organic matter by weight loss-on-ignition. In *Assessment Methods for Soil Carbon*, Kimble JM, Follett RF, Stewart BA (eds). CRC Press: New York; 349–359.

Chafiq M, Gilbert J, Claret C. 1999. Interactions among sediments, organic matter, and microbial activity in the hyporheic zone of an intermittent stream. *Canadian Journal of Fisheries and Aquatic Sciences* **56**: 487–495.

Chao A, Chazdon RL, Colwell RK, Shen TJ. 2005. A new statistical approach for assessing compositional similarity based on incidence and abundance data. *Ecology Letters* **8**: 148–159.

Cleven EJ, Meyer EI. 2003. A sandy hyporheic zone limited vertically by a solid boundary. *Archiv für Hydrobiologie* **157**: 267–288.

Colwell RK. 2005. EstimateS: Statistical estimation of species richness and shared species from samples. Version 7.5. User's guide and application published at: http://purl.oclc.org/estimates

Cummins KW. 1974. Structure and function of stream ecosystems. *BioScience* **34**: 631–641.

Diamond JM, Serveiss VB. 2001. Identifying sources of stress to native aquatic fauna using a watershed ecological risk assessment framework. *Environmental Science and Technology* **35**: 4711–4718.

Downs PW, Simon A. 2001. Fluvial geomorphological analysis of the recruitment of large woody debris in the Yalobusha River network, Central Mississippi, USA. *Geomorphology* **37**: 65–91.

Fisher SG, Likens GE. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. *Ecological Monographs* **43**: 421–439.

Ganasan V, Hughes RM. 1998. Application of an index of biological integrity (IBI) to fish assemblages of the rivers Khan and Kshipra (Madhya Pradesh), India. *Freshwater Biology* **40**: 367–383.

Gilliom RJ, Clifton DG. 1990. Organochlorine pesticide residues in bed sediments of the San Joaquin River, California. *Water Resources Bulletin* **26**: 11–24.

Gorman OT, Karr JR. 1978. Habitat structure and stream fish communities. *Ecology* **59**: 507–515.

Happ SC, Rittenhouse G, Dobson GC. 1940. Some principles of accelerated stream and valley deposits in northern Mississippi. Technical Bulletin no. 695, United States Department of Agriculture, Washington, DC.

Haschenburger JK, Rice SP. 2004. Changes in woody debris and bed material texture in a gravel-bed channel. *Geomorphology* **60**: 241–267.

Hauer FR. 1989. Organic matter transport and retention in a backwater stream recovering from flow augmentation and thermal discharge. *Regulated Rivers*: *Research and Management* **4**: 371–380.

Hauer FR, Lamberti GA. 1996. *Methods in Stream Ecology*. Academic Press: New York.

Hughes RM, Kaufmann PR, Herlihy AT, Kincaid TM, Reynolds L, Larsen DP. 1998. A process for developing and evaluating indices of fish assemblage integrity. *Canadian Journal of Fisheries and Aquatic Sciences* **55**: 1618–1631.

Jones JB. 1997. Benthic organic matter storage in streams: influence of detrital import and export, retention mechanisms, and climate. *Journal of the North American Benthological Society* **16**: 109–118.

Karr JR, Fausch KD, Angermeier PL, Yant PR, Schlosser IJ. 1986. Assessing biological integrity in running waters: a method and its rationale. Special Publication no. 5, Illinois Natural History Survey, Champaign, IL.

Kemp MJ, Dodds WK. 2002. Comparisons of nitrification and denitrification in prairie and agriculturally influenced streams. *Ecological Applications* **12**: 998–1009.

Klimetz L, Simon A. 2006. Characterization of stream morphology and sediment yield for the Big Black and Tombigbee River Basins, Mississippi. USDA Report 54, National Sedimentation Laboratory, Oxford, MS.

Laitung BL, Pretty JL, Chauvet E, Dobson M. 2002. Response of aquatic hypomycete communities to enhanced stream retention in areas impacted by commercial forestry. *Freshwater Biology* **47**: 313–323.

Leichtfried M. 1995. Organic matter in bed sediments and energy source for lotic ecosystems (a compilation of a long term study). *Biologia* **91**: 77–93.

Lepori F, Palm D, Malmqvist B. 2005. Effects of stream restoration on ecosystem functioning: detritus retentiveness and decomposition. *Journal of Applied Ecology* **42**: 228–238.

Maloney KO, Mulholland PJ, Feminella JW. 2005. Influence of catchment-scale military land use on stream physical and organic matter variables in small southeastern plains catchments (USA). *Environmental Management* **35**: 677–691.

Maul JD, Milam CD, Cooper CM, Testa S, Feldman DL. 2004. The influences of stream habitat and water quality on macroinvertebrate communities in degraded streams of northwest Mississippi. *Hydrobiologia* **518**: 79–94.

Means JC, Wood SG, Hassett JJ, Banwart WL. 1980. Sorption of polynuclear aromatic hydrocarbons by sediments and soils. *Environmental Science and Technology* **145**: 1524–1528.

Metzler GM, Smock LA. 1990. Storage and dynamics of subsurface detritus in a sand-bottomed stream. *Canadian Journal of Fisheries and Aquatic Sciences* **47**: 588–594.

Minshall GW. 1967. Role of allochthonous detritus in the trophic structure of a woodland springbrook community. *Ecology* **48**: 139–149.

Morara GO, Mathooko JM, Leichtfried M. 2003. Natural leaf litter transport and retention in a second-order tropical stream: the Njoro River, Kenya. *African Journal of Ecology* **41**: 277–279.

Naegeli MW, Uehlinger U, Hartmann U, Meyer EI. 1995. POM-dynamics and community respiration in the sediments of a floodprone prealpine river (Necker, Switzerland). *Archiv für Hydrobiologie* **133**: 339–347.

Olsen DA, Townsend CR. 2005. Flood effects on invertebrates, sediments and particulate organic matter in the hyporheic zone of a gravel-bed stream. *Freshwater Biology* **50**: 839–853.

Palmer MA, Hakenkamp CC, Nelson-Baker K. 1997. Ecological heterogeneity in streams: why variance matters. *Journal of the North American Benthological Society* **16**: 189–202.

Ricketts TH, Dinerstein E, Olson DM, Loucks CJ *et al*. 1999. *Terrestrial Ecoregions of North America*: *A Conservation Assessment*. World Wildlife Fund — United States and Canada. Island Press, Washington, D.C.

Schlosser IJ. 1987. A conceptual framework for fish communities in small warmwater streams. In *Community and Evolutionary Ecology of North American Stream Fishes*, Matthews WJ, Heins DC (eds). University of Oklahoma: Norman, OK; 17–24.

Schlosser IJ. 1995. Disperal, boundary processes, and trophic-level interactions in streams adjacent to beaver ponds. *Ecology* **76**: 908–925.

Schlosser IJ, Kallemeyn LW. 2000. Spatial variation in fish assemblages across a beaver-influenced successional landscape. *Ecology* **81**: 1371–1382.

Shields FD, Cooper CM. 1994. Riparian wetlands and flood stages. In *Proceedings of the 1994 Conference*, *Hydraulic Engineering '94*, Controneo GV, Rumer RR (eds). American Society of Civil Engineers: New York; 351–355.

Shields FD, Gippel CJ. 1995. Prediction of effects of woody debris removal on flow resistance. *Journal of Hydraulic Engineering* **121**: 341–354.

Shields FD, Smith RH. 1992. Effects of large woody debris removal on physical characteristics of a sand-bed river. *Aquatic Conservation*: *Marine and Freshwater Ecosystems* **2**: 145–163.

Shields FD, Knight SS, Cooper CM. 1994. Effects of channel incision on base flow stream habitats and fishes. *Environmental Management* **18**: 43–57.

Shields FD, Knight SS, Cooper CM. 1995a. Use of the index of biotic integrity to assess physical habitat degradation in warmwater streams. *Hydrobiologia* **312**: 191–208.

Shields FD, Cooper CM, Knight SS. 1995b. Experiment in stream restoration. *Journal of Hydraulic Engineering* **121**: 494–502.

Shields FD, Knight SS, Cooper CM. 1997. Rehabilitation of warmwater stream ecosystems following channel incision. *Ecological Engineering* **8**: 93–116.
Shields FD, Knight SS, Cooper CM. 1998. Rehabilitation of aquatic habitats in warmwater streams damaged by channel incision in Mississippi. *Hydrobiologia* **382**: 63–86.
Shields FD, Knight SS, Cooper CM. 2000. Cyclic perturbation of lowland river channels and ecological response. *Regulated Rivers*: *Research and Management* **16**: 307–325.
Shields FD, Morin N, Cooper CM. 2001. Design of large woody debris structures for channel rehabilitation. In *Proceedings of the Federal Interagency Sedimentation Conferences*, *1947 to 2001*, *Seventh Conference Proceedings*. CD-ROM, Washington, DC; II-42–II-49.
Shields FD, Knight SS, Morin N, Blank JC. 2003. Response of fishes and aquatic habitats to sand-bed stream restoration using large woody debris. *Hydrobiologia* **494**: 251–257.
Shields FD, Morin N, Cooper CM. 2004. Large woody debris structures for sand bed channels. *Journal of Hydraulic Engineering* **130**: 208–217.
Shields FD, Knight SS, Stofleth JM. 2006. Large wood addition for aquatic habitat rehabilitation in an incised, sand-bed stream, Little Topashaw Creek, Mississippi. *River Research and Applications* **22**: 803–817.
Simon A. 1989. A model of channel response in disturbed alluvial channels. *Earth Surface Processes and Landforms* **14**: 11–26.
Smock LA, Metzler GM, Gladden JE. 1989. The role of debris dams in the structure and functioning of low-gradient headwater streams. *Ecology* **70**: 764–775.
Stofleth JM, Shields FD, Fox GA. 2004. Organic carbon concentrations in hyporheic zone sediments: a tool for measuring stream integrity. In *Proceedings of the 2004 World Water and Environmental Resources Congress*: *Critical Transitions in Water and Environmental Resources*, Sehlke G, Hayes DF, Stevens DK (eds), CD-ROM, American Society of Civil Engineers: Reston, VA.
Stofleth JM, Shields FD, Fox GA 2005. Hyporheic and total storage exchange in small sand-bed streams. In *Proceedings of the 2005 World Water and Environmental Resources Congress*: *Impacts of Global Climate Change*, Walton R (ed.). Proceedings 173 (587), American Society of Civil Engineers: Reston, VA.
Suedel BC, Rodgers JH. 1991. Variability of bottom sediment characteristics of the continental United Status. *Water Resources Bulletin* **27**: 101–109.
Sullivan SMP, Watzin MC, Hession WC. 2004. Understanding stream geomorphic state in relation to ecological integrity: evidence using habitat assessments and macroinvertebrates. *Environmental Management* **34**: 669–683.
Sullivan SMP, Watzin MC, Hession WC. 2006. Influence of stream geomorphic conditions on fish communities in Vermont, U.S.A. *Freshwater Biology* **51**: 1811–1826.
Sutherland RA. 1998. Loss-on-ignition estimates of organic matter and relationships to organic carbon in fluvial bed sediments. *Hydrobiologia* **389**: 153–167.
Sutherland RA. 1999. Distribution of organic carbon in bed sediments of Manoa Stream, Oahu, Hawaii. *Earth Surface Processes and Landforms* **24**: 571–583.
Systat Software, Inc. 2004. *Sigmastat 3.1 User's Manual*. Systat Software, Inc.: Richmond, CA.
Talmage PJ, Perry JA, Goldstein RM. 2002. Relation of instream habitat and physical conditions to fish communities of agricultural streams. *North American Journal of Fisheries Management* **22**: 825–833.
Tillman DC, Moerke AH, Ziehl CL, Lamberti GA. 2003. Subsurface hydrology and degree of burial affect mass loss of invertebrate colonization of leaves in a woodland stream. *Freshwater Biology* **48**: 98–107.
Vannote RL, Minshall GW, Cummins KW, Sedell JR, Cushing CE. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* **37**: 130–137.
Wallace JB, Ross DH, Meyer JL. 1982. Seston and dissolved organic carbon dynamics in a southern Appalachian stream. *Ecology* **63**: 824–838.
Wallace JB, Webster JR, Meyer JL. 1995. Influence of log additions on physical and biotic characteristics of a mountain stream. *Canadian Journal of Fisheries and Aquatic Sciences* **52**: 2120–2137.
Wallace JB, Eggert SL, Meyer JL, Webster JR. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. *Science* **277**: 102–104.
Warren ML, Haag WR, Adams SB. 2002. Forest linkages to diversity and abundance in lowland stream fish communities. In *Proceedings of a Conference on Sustainability of Wetland and Water Resources*, Holland MM, Stanturf JA, Warren ML (eds). May 23–25 2000, University of Mississippi, Oxford. USDA Forest Service, General Technical Report SRS-50; 168–182.
Webster JR. 1983. The role of benthic macroinvertebrates in detritus dynamics of streams: a computer simulation. *Ecological Monographs* **53**: 383–404.
Webster JR, Meyer JL. 1997. Organic matter budgets for streams: a synthesis. *Journal of the North American Benthological Society* **16**: 141–161.

Webster JR, Benfield EF, Hutchens JJ, Tank JL, Golladay SW, Adams JC. 2001. Do leaf breakdown rates actually measure leaf disappearance from streams? *International Review of Hydrobiology* **86**: 417–427.
Wichert GA, Rapport DJ. 1998. Fish community structure as a measure of degradation and rehabilitation of riparian systems in an agricultural drainage basin. *Environmental Management* **22**: 425–443.

APPENDIX: FISH CAPTURED FROM STREAMS IN NORTH-WEST MISSISSIPPI FOR THIS STUDY

Family	Species	1	2	3-before	3-after	4
Atherinidae	***Labidesthes sicculus***	3				
Catostomidae	***Carpiodes carpio***					9
	Erimyzon oblongus		8	2		
	Ictiobus bubalus					20
Centrarchidae	***Lepomis cyanellus***		24	14	23	28
	Lepomis gulosus		1			
	Lepomis macrochirus	28	8	1	9	34
	Lepomis megalotis		24		34	33
	Lepomis punctatus	1				
	Micropterus punctulatus	4				12
	Micropterus salmoides	6		2	6	
Clupeidae	***Dorosoma cepedianum***					3
Cyprinidae	***Cyprinella camura***	12	35			114
	Cyprinella venusta	2		43	231	119
	Luxilus chrysocephalus		30	41	4	
	Lythrurus umbratilis		8		6	
	Notropis atherinoides	50				
	Notropis rafinesquei		15	144	233	20
	Pimephales notatus	8	25	94	110	
	Pimephales vigilax				15	23
	Semotilus atromaculatus		46			
Fundulidae	***Fundulus olivaceus***	7	53	4	17	35
Ictaluridae	***Ameiurus natalis***		2	2	3	3
	Ictalurus punctatus	1				20
	Noturus miurus		2	1	3	
	Noturus phaeus	1	22		5	
Lepisosteidae	***Lepisosteus oculatus***	5				4
	Lepisosteus osseus					2
Percidae	***Etheostoma chlorosomum***	1				
	Etheostoma fusiforme		2			
	Etheostoma lynceum		10			
	Etheostoma nigrum		12		12	
	Etheostoma proeliare	5				
	Etheostoma artesiae		8			1
	Percina sciera	11	9			
Petromyzontidae	***Icthyomyzon gagei***		21			
Poeciliidae	***Gambusia affinis***		9		3	