

Influence of landscape geomorphology on large wood jams and salmonids in an old-growth river of Upper Michigan

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Abstract

We investigated the structure of large wood jams (LWJ) and their use by brook trout (*Salvelinus fontinalis*, Mitchell) and other fish in four geomorphically-distinct sections of the Little Carp River, a small river flowing through an uncut, old-growth, northern hardwood-conifer forest along the south shore of Lake Superior, Upper Michigan. We characterized nine LWJ per section and then electroshocked fish at three randomly selected LWJ per section. Structural characteristics of LWJ (e.g., total volume of wood, number of logs) varied with geomorphology at the scale of approximately one km. Differences in the abundance of fish associated with LWJ were not statistically significant among LWJ and non-LWJ portions of stream across all study reaches. Factors that explained most variability in the proportion of salmonids at LWJ (valley constraint, volume and number of pieces in the jam) reflected both large-scale geomorphology and characteristics of LWJ. If emulating an old-growth system is the goal for restoring habitat, attention should be given to the correlation of LWJ with larger-scale geomorphology of the reference river. However, it cannot be assumed that LWJ restoration will necessarily increase brook trout abundance near LWJ in a system similar to the Little Carp River as we observed low overall correlation between brook trout abundance and LWJ.

Introduction

Stream and riparian restoration projects often include the addition of large wood (pieces greater than 10 cm diameter and 1 m in length; Gregory & Davis, 1992; Slaney & Zaldokas, 1997; Booth et al., 2001). Large wood has a variety of functions in stream ecosystems including an influence on stream channel morphology and dynamics, riparian forest structure and dynamics, sediment storage, stream flow, organic matter processing, and the formation of wildlife habitat (Naiman & Bilby, 1998; Gurnell et al., 2002; Naiman et al., 2002; Gregory et al., 2003). Because of the potential for

large wood to provide valuable in-stream habitat, wood additions to streams often aim at improving habitat for fish species (Lowe, 1996; Cederholm et al., 1997a, b; Dominguez & Cederholm, 2000; Lehane et al., 2002). However, in many cases the most effective amounts and arrangements of added wood for both fish habitat and other ecosystem functions remain unclear (Cederholm et al., 1997a; Hilderbrand et al., 1997a, b; DuBois et al., 2001).

Uncertainty associated with addition of large wood to streams is apparent when considering the potential influences of large wood on salmonids. While some studies have suggested that young

salmonids preferentially use large wood habitat, especially when several pieces have aggregated to form large wood jams (LWJ) (Bilby & Bisson, 1998; Sundbaum & Näslund, 1998; Flebbe, 1999), other studies have found that large wood habitat in streams has a variable or negligible effect on the distribution of juvenile salmonids (e.g., Cederholm et al., 1997a; Berg et al., 1998). For example, Ford & Lonzarich (2000) found no significant correlation between density of juvenile coho salmon (*Oncorhynchus kisutch*, Walbaum) and large wood in two Lake Superior tributaries. DuBois et al. (2001) similarly documented no significant change in brook trout or total salmonid biomass in stream reaches up to 3 years after the amount of large wood was increased in three Lake Superior tributaries. Discrepancies between studies suggest that much remains unknown regarding how salmonids use large wood in streams of the northern Lake States, and thus many stream restoration professionals remain undecided about the most effective use of large wood for restoring salmonid habitat.

It is becoming increasingly evident, however, that an improved understanding of the connection between landscape characteristics and the arrangement of large wood fish habitat may increase the effectiveness of LWJ additions to streams (Flebbe 1999, Dominguez & Cederholm 2000, Streb, 2001; Bisson et al., 2002; Wing & Skaugset, 2002). Large wood jams in a river system influence stream characteristics in a variety of ways depending on hydrology, stream materials, and the characteristics of the wood itself (Abbe, 2000; Gurnell et al., 2002, Dolloff & Warren, 2003). Consequently, the influence of large wood on stream fish assemblages likely changes with the landscape. Within different geomorphic settings, certain LWJ characteristics or distributions appear to be typical (Swanson, 2003), and it follows that fish use of jams reflects the larger-scale setting. Where flow is highest and stream channel least amenable to trapping wood, (as is characteristic of larger streams) jams form along channel margins (Bilby & Bisson 1998) where they may be less likely to directly influence fish populations. Bilby and Ward (1989) also found that the characteristic and function of wood in forming pools and trapping sediment changed relative to stream size. Because the aggregation of wood in channels reflects

stream size and other aspects of large-scale geomorphology, the influence of LWJ on fish assemblages is probably not the same everywhere along a stream, partly in response to position in the watershed (Richmond & Fausch 1995) and other aspects of spatial context (Warren and Kraft 2003).

In 2003, we began a study to investigate the formation and distribution of LWJ along the Little Carp River, a small river flowing through an old-growth, northern hardwood-conifer landscape of the northern Lake States, and the effects of these LWJ on salmonid populations. The Little Carp watershed is one of the few remaining watersheds in the northern Lake States that was never harvested, providing a unique opportunity to study the character and distribution of natural LWJ and their associated fish assemblages in order to develop reference information for stream restoration projects aimed at returning manipulated systems to less anthropogenically altered conditions. Our overall objective was to examine the relationships between LWJ and salmonid populations in different geomorphic settings of this old-growth watershed. Although we evaluated the composition and structure of the entire fish assemblage associated with the LWJ, most attention was given to salmonids, particularly brook trout, an endemic species in the waters of our study area. In addition to resident stream brook trout, coaster brook trout (a native, anadromous form) were found in our study area until the mid 1900s. Recently, restoration efforts have included stocking thousands of young coaster brook trout in these streams, but the fate and behavior of these young fish remains unknown. A first step in understanding the fate of these stocked brook trout in the Little Carp River will be to evaluate the association of resident brook trout with habitat components like LWJ, providing a baseline for comparison with stocked brook trout over time. Thus, the specific study objectives of this study were to: (1) quantify how LWJ differ among different geomorphic sections; (2) determine how fish abundance and size differ between portions of stream at LWJ and away from LWJ, with particular attention to resident salmonids; and, (3) examine environmental factors of geomorphology and LWJ structure that influence any apparent associations of salmonids (particularly resident

brook trout) with LWJ. Our overall hypothesis was that the distribution and structure of LWJ would vary by geomorphic setting, which in turn would correspond with the abundance and length of salmonids near LWJ.

Methods

Study site

Along the south shore of Lake Superior in the Porcupine Mountains Wilderness State Park (PMWSP) occurs the largest contiguous tract of virgin northern hardwood-conifer forest between the Adirondack and Rocky Mountains (Davis 2003). The Little Carp River flows through the south-central portion of this old-growth landscape for a length of about 20 km (Fig. 1). The river channel passes from a low-gradient (1%), relatively open valley near the source (Mirror Lake) through a high-gradient (3–5%), constrained section with rock-plane bedding, into a mid-gradient (2–3%), relatively unconstrained section, and then finally onto a mid-gradient (1–3%) section of clay-lake plain before emptying into Lake Superior.

Riparian forests consist of eastern hemlock (*Tsuga canadensis* (L.) Carr.), northern white cedar (*Thuja occidentalis* L.), yellow birch (*Betula alleghaniensis* Britt.), and sugar maple (*Acer saccharum* Marsh.). Maximum tree height is approximately 40 m, with mean height of the tallest trees in the study area roughly 25 m and mean dbh about 60 cm. Most of the river is forested to the edge of the bankfull channel. The major source of mass mortality of riparian trees is windthrow. Seasonal precipitation can be heavy (800–900 mm precipitation, up to 7 m snowfall; Frelich 2002); however, the topography is not conducive to avalanches, landslides, or other forms of mass wasting except localized stream-bank failures. Fire is infrequent in these northern hardwood-conifer forests.

The substrate of the Little Carp River generally consists of loose cobble and gravel with rock-plane bedding in high-gradient and clay-lake plain sections. The mean bankfull channel of this river measures 9.6 m wide ($SE = 1.4$, $n = 12$). Floodplain development varies between sections of the river. Few records of streamflow exist for the Little Carp River. Goebel et al. (2003) reported discharge during annual floods ranging from $4.7 \text{ m}^3 \text{ s}^{-1}$ in the low gradient sections of the river to $9.4 \text{ m}^3 \text{ s}^{-1}$

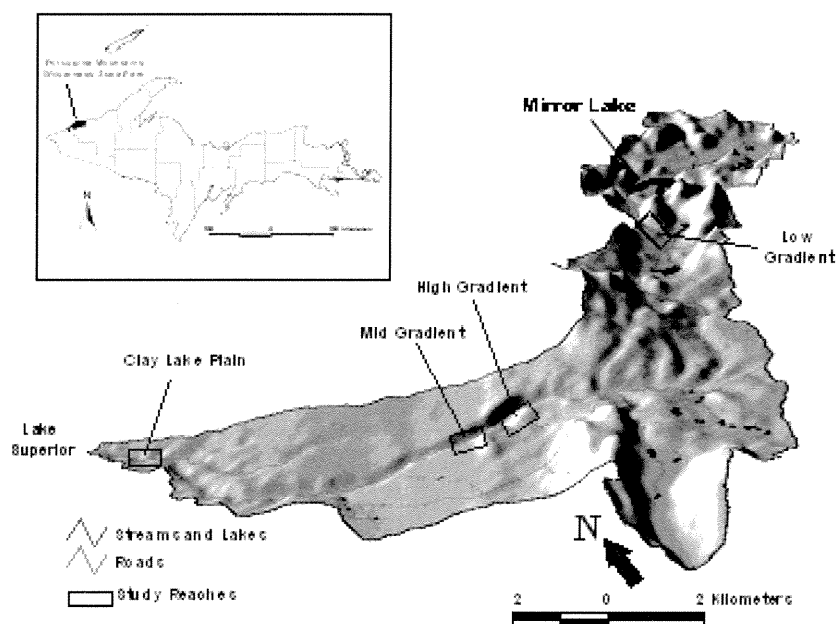


Figure 1. Geomorphic sections of the Little Carp River watershed, Upper Michigan.

in the lower, high gradient portions of the River. The discharge associated with 50-year flood events has been estimated to range between 17.5 and 38.1 m³ s⁻¹ (Goebel 2001). Most of these extreme events occur in the spring as dense snowpacks (ranging from 1 to 3 m thick) melt, often very rapidly (Goebel 2001).

Human influence to the shape or condition of the Little Carp River channel and surrounding forest is minimal. The most consistent human activity along the river consists of recreational hiking, camping, and fishing. Our observation is that fishing pressure along the river remains light but consistent during the summer. No timber harvesting or mining is known to have occurred along the Little Carp River.

More than 10 species of fish occur in the Little Carp River, including several species of dace (*Rhinichthys atratulus* Hermann; *Rhinichthys cataractae* Valenciennes; *Phoxinus eos* Cope), two species of sculpin (*Cottus bairdi* Girard; *Cottus cognatus* Richardson), brook trout, introduced rainbow trout (*Oncorhynchus mykiss* Walbaum) and coho salmon (USDA Forest Service, unpublished data). Historically, coaster brook trout reproduced in the Little Carp River. Currently brook trout occur in the river, although it is not known to what extent (if any) they demonstrate the anadromous lifestyles of coaster brook trout. Restoration efforts by the Michigan Division of Natural Resources currently include attempts to re-establish coaster brook trout in the Little Carp River. Approximately 20 000 to 30 000 3–5 inch brook trout from a strain of known coasters (Nipigon Lake strain) have been planted in the Little Carp River each year from 1999 to 2003. Less than 1 month prior to our study, 35 000 brook trout were released into the Little Carp

River from an access bridge approximately 10 km from the mouth of the river in the high-gradient section. Since 1999, all brook trout have been released from that point with the exception of one year when 20 000 were carried by hand in buckets and released approximately 3 km upstream from the mouth in the clay lake plain section. Newly stocked fish in 2003 had their right pectoral fins clipped, allowing differentiation from other brook trout. Brook trout stocked in previous years had other fins clipped. We refer to brook trout as resident brook trout if they have no fin clips or fins other than right-pectoral fins clipped.

Study design

We designated four zones with similar large-scale geomorphic characteristics (hereafter referred to as geomorphic sections) along the Little Carp River (Fig. 1, Table 1), and measured the characteristics of nine LWJ within each section using a standard monitoring program adapted from Washington State's Timber-Fish-Wildlife program for monitoring large wood in streams (Schuett-Hames et al., 1999). For the purposes of this study, LWJ was an aggregation of wood with at least one piece exceeding 1 m in length and 10 cm in diameter. We randomly selected three LWJ for fish surveys from each of the four geomorphic settings. Each selected LWJ formed the midpoint of a study reach (i.e., 3 reaches per section for a total of 12 reaches). We divided each reach into three channel geomorphic units relative to the LWJ: upstream (US), downstream (DS), and directly at the jam (J). The jam unit lay immediately adjacent to the LWJ for the width of the LWJ as determined by wood in the LWJ and the pool formed by the LWJ. Upstream and downstream units began at

Table 1. Characteristics of the study sections examined along the Little Carp River, Upper Michigan

Geomorphic setting	Valley gradient ¹	Valley constraint ²	Channel bedding ³
Clay-lake Plain	2%	Moderate	Rock-plane
Mid-gradient	3%	Low	Cobble/gravel
High-gradient	5%	High	Rock-plane
Low-gradient	1%	Moderate	Gravel/cobble

¹Valley gradient measured from a 1:64,000 topographic map. ²Valley constraint was classified visually, based on relative distance from the stream channel to the nearest large terraces or valley walls. ³Channel substrate was classified visually based on apparent predominance of substrate material.

the edges of the LWJ or the pool clearly formed by the LWJ and continued for a distance approximately two bankfull channel widths or halfway to the next LWJ, depending on the proximity of other LWJ. For example, if the upstream edge of the focal LWJ was only 10 m away from the downstream edge of the nearest upstream LWJ, we sampled approximately 5 m upstream from the edge of the focal LWJ. At each of the jams where the fish assemblage was sampled, we also noted the length of the associated pool, and whether riffles or pools occurred immediately adjacent upstream and downstream. Fish surveys were conducted by single-pass electrofishing (Smith-Root model LR-24) during the week of 20–24 October 2003. We typically started our sample at a natural barrier downstream of the LWJ (e.g., riffle) and proceeded upstream to include the area of the LWJ up to the next adjacent natural barrier. Captured fish were identified, measured, and released after surveying the portion of the reach where they were collected. Juvenile rainbow trout and coho salmon were grouped, as were dace and sculpin species for ease in tallying and because our primary focus was brook trout. Brook trout stocked in 2003 might have associated with jams differently than trout that had resided in the river for a longer period of time, so we evaluated newly stocked brook trout (right pectoral fin clipped; 2003) separately from “resident” brook trout and other salmonids that had other or no fins clipped.

Data analysis

We used principal components analysis (PCA) to quantify the relationship between LWJ and geomorphic setting and determine the influence of large-scale geomorphology on LWJ characteristics using the data from all nine of the LWJ characterized in each geomorphic section (36 jams total). Variables used in the PCA included valley gradient (%), valley constraint (high, medium, or low), distance to nearest downstream LWJ (m), distance to nearest upstream LWJ (m), volume of large wood in the LWJ (m^3), number of large wood pieces in the LWJ, number of large wood pieces contacting the water, proportion of the bankfull channel spanned by the LWJ (%), and the proportion of conifer pieces in the LWJ (%). We performed PCA after general data relativization,

and also computed broken-stick eigenvalues to test for significance (broken-stick eigenvalues greater than one indicate significant gradients; PC-ORD 3.01, MJM Software Design, Gleneden Beach, OR, USA). We calculated Pearson correlation coefficients to measure the correlation between environmental variables and factor scores with MINITAB software (Minitab Inc. Rel 14, State College, PA, USA).

We compared differences in the abundance and length of salmonids (rainbow trout/coho salmon, resident brook trout, and newly stocked brook trout) and the abundance of non-salmonids relative to LWJ using one-way ANOVA. We calculated abundance as the number of fish per meter of each stream portion sampled, a metric we considered appropriate because wetted channel widths remained relatively constant between reaches we sampled (approximately 7 m). Locations within sampled reaches relative to LWJ (US, DS, J) formed the independent variable. We included abundance data from above and below LWJ in ANOVA rather than just grouping data into two locations (away from LWJ and at LWJ) because we believed that there could be association of fish with LWJ related to flow direction. Reaches were only included for analysis if fish were captured there (some species of fish were not caught in some reaches, e.g., rainbow trout/coho salmon did not occur in any reaches upstream from the clay-lake plain geomorphic section). We also used a one-way ANOVA to test for differences in the length of brook trout between geomorphic settings, using a Tukey’s mean comparison test to differentiate between groups if ANOVA indicated an overall significance between groups. We conducted ANOVA using PROC GLM with SAS software (V8, SAS institute, Cary, NC, USA). Abundance data for resident brook trout was transformed by dividing the data by 10 then computing the arcsine of the double square root. All other abundance data was square root transformed, while length data did not require transformation to meet the assumption of normality for parametric statistical evaluation.

We used multiple regression to relate the length and proportion of resident salmonids (resident brook trout with rainbow trout and coho salmon, and resident brook trout alone) occurring at LWJ to the characteristics of the LWJ and geomorphic

setting. We used as environmental variables the LWJ and geomorphic characteristics shown to be most related along the first two (significant) PCA axes. We computed the proportion of fish at LWJ by dividing the abundance at the LWJ by the total abundance (at and away from the LWJ). To account for sampling effort, we adjusted total abundance for the proportional length of sampled portions of the reach upstream and downstream (US and DS). We adjusted total abundance for the relative length of portions of the reach by first calculating abundance (number m^{-1}) for the US and DS portions, then multiplying abundance by the ratio of away-from-LWJ lengths, which yielded a representation of the abundance of fish away from LWJ:

$$A_{\text{away}} = A_{\text{US}} \cdot (D_{\text{US}} / (D_{\text{US}} + D_{\text{DS}})) + A_{\text{DS}} \cdot (D_{\text{DS}} / (D_{\text{US}} + D_{\text{DS}})) \quad (1)$$

where A represents abundance (number m^{-1}) and D is the length of the portion of the reach (m). Subscripts indicate the portion of the reach: "away" indicates the combined portions not at LWJ, and DS and US indicate positions relative to LWJ as explained previously. By computing relative abundances in this way, we standardized data to the portions of streams sampled at LWJ, so if fish were distributed in equal numbers throughout the sampled reaches, the proportion at LWJ and away from LWJ would be equal (e.g., 0.5 at LWJ and 0.5 away from LWJ). Mean length and proportion were approximately normally distributed so did not require transformation. We used SAS General Linear Model (GLM) type 3 mean square errors and p -values to select the smallest subset of independent LWJ and geomorphic setting variables to explain the variability in the dependent fish variable (abundance, length or proportion at jams). The best model was considered the one that explained the most variability (had the highest correlation coefficient) while at the same time showed the most change when any single term was removed, and had the lowest overall p -value. Because it was possible that differences in the abundance of salmonids could reflect the recent stocking of brook trout in the high-gradient section, we also included the distance from the point of release to the section as an explanatory variable in our original model.

Results

Characteristics of large wood jams by geomorphic setting

Large wood jams in the Little Carp River differed in size and position, varying generally with the larger-scale geomorphology of the river corridor. The first two principal components accounted for 51% of the variance in jam characteristics, and exceeded broken-stick eigenvalues, indicating a significant gradient along each axis (Fig. 2). The first principal component related most strongly with percent of channel spanned by the LWJ ($r=0.79$, $p<0.001$), valley gradient ($r=-0.61$, $p<0.001$), valley constraint (high constraint $r=-0.66$, low constraint $r=0.85$, $p<0.001$ for both), and the number of pool forming pieces in the LWJ ($r=0.60$, $p<0.001$). The second principal component related most strongly with volume of wood in the LWJ ($r=-0.57$, $p<0.001$) and the number of pieces in the LWJ ($r=-0.55$, $p=0.001$).

Fish assemblages by geomorphic setting

Trout were the dominant species numerically throughout the reaches we electrofished, except in

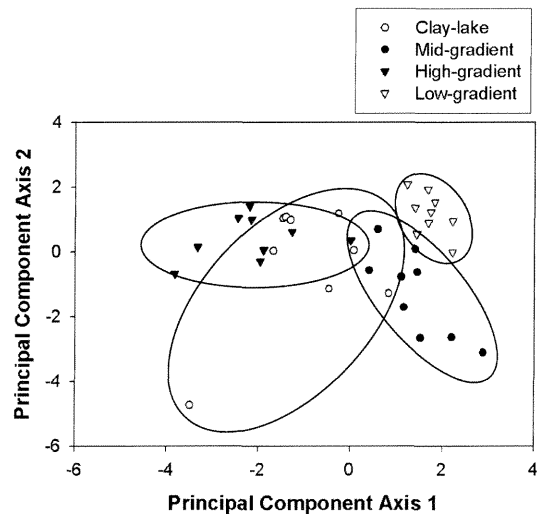


Figure 2. Principal components analysis (PCA) of large wood jams (LWJ) based on LWJ and geomorphic characteristics in different geomorphic settings of the Little Carp River watershed, Upper Michigan. Ellipses were drawn to highlight groups.

two reaches of the low-gradient section (Table 2). In the clay lake plain section (less than 3 km from the river's mouth) juvenile rainbow trout (steelhead) and coho salmon were the most numerous species. We found and captured only one brook trout during our electrofishing surveys in the clay-lake plain (and it was at a LWJ). No rainbow trout or coho salmon were observed in geomorphic sections other than the clay-lake plain. In the mid and high-gradient sections (8–12 km from the mouth) both wild-born (unclipped fins) and stocked brook trout were collected more frequently than any other species. We did not find newly stocked brook trout downstream in the clay-lake plain or upstream in the low-gradient section. In the high-gradient section we captured 6 resident brook trout, all away from LWJ. Ten of the resident brook trout we captured in the mid-gradient section, and three captured in the high-gradient section appeared to have fin clips other than right pectoral; all other resident brook trout were wild-born. In the low gradient section, which was the furthest upstream (20 km from the mouth), wild-born brook trout comprised the only population of trout and were less abundant than dace in two reaches we sampled in that section (Table 2).

Salmonid and non-salmonid abundance and length near LWJ habitat

Although there appeared to be greater salmonid (resident brook trout, rainbow trout/coho salmon) and non-salmonid fish abundance near LWJ (Figs. 3 and 4, Tables 3 and 4) these associations

tended to be highly variable. The abundance of resident brook trout, newly stocked brook trout, rainbow trout/coho salmon and non-salmonids did not differ overall between portions of reaches relative to LWJ when all reaches were considered together (all p -values > 0.10 , 1-way ANOVA).

Lengths of resident brook trout also did not differ between portions of reaches relative to LWJ ($p = 0.75$), nor did the lengths of rainbow trout/coho salmon ($p = 0.31$). The length of resident brook trout did vary, however, with geomorphic section ($p < 0.01$): smaller resident brook trout occurred in the low-gradient section, but we observed no difference in resident brook trout size among other sections (Fig. 5). Fish stocked in 2003 comprised a single size class (approximately 102 mm), thus size differences relative to LWJ did not exist between portions of stream away from or at LWJ ($p = 0.40$) or between the two geomorphic sections (high and mid gradient) where newly stocked brook trout occurred ($p = 0.67$).

Factors influencing salmonid association with LWJ

Eight explanatory variables were examined for correlation with the mean proportion and length of salmonids (brook trout, rainbow trout, and coho salmon together) that occurred at LWJ habitat ($n = 12$; Table 5). Variability in the proportion of resident salmonids (rainbow trout/coho salmon and resident brook trout) occurring at LWJ most reflected high valley constraint and total wood volume combined with the number of pieces of wood in LWJ ($r^2 = 0.74$, $p = 0.04$). By

Table 2. Counts of fish captured in different geomorphic sections of the Little Carp River, Upper Michigan

Species	Section of the Little Carp River			
	Clay-lake plain	Mid-gradient	High-gradient	Low-gradient
<i>Salvelinus fontinalis</i>	1	168	367	33
<i>Oncorhynchus mykiss</i> ¹	192	0	0	0
<i>Oncorhynchus kisutch</i>	3	0	0	0
<i>Semotilus atromaculatus</i>	1	0	0	5
<i>Rhinichthys atratulus</i> , <i>Rhinichthys cataractae</i> , <i>Phoxinus eos</i> ¹	24	8	13	56
<i>Umbra limi</i>	0	1	0	4
<i>Cottus bairdi</i> , <i>Cottus cognatus</i> ¹	12	10	10	0

¹We did not differentiate some similar species for ease in tallying and because our focus was primarily on brook trout. Juvenile rainbow trout and coho salmon were grouped, as were dace and sculpin species.

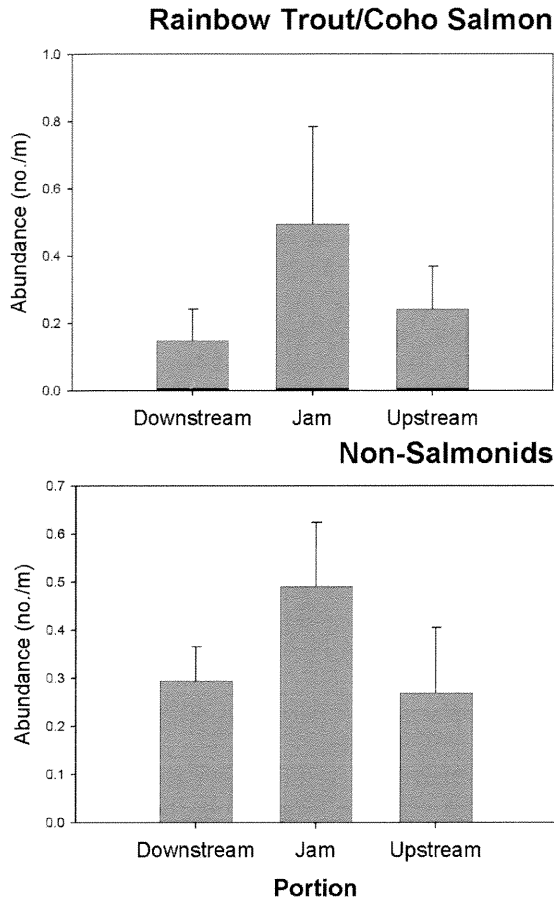


Figure 3. Relative abundance (± 1 SE) of fish other than brook trout relative to large wood jams (LWJ) in the Little Carp River watershed, Upper Michigan. Abundance represents the number of captured fish divided by the length of stream sampled.

comparison, the best regression model for the proportion of resident brook trout occurring at jams explained 89% of the variability in terms of valley gradient and the percent of channel spanned by LWJ ($p < 0.01$). Variability in the length of resident brook trout occurring at LWJ was best explained by valley gradient alone ($r^2 = 0.81$, $p = 0.01$).

Discussion

Large wood jams in this relatively undisturbed river associated with an old-growth landscape of the northern Lake States differed structurally with geomorphic setting. We found that large wood

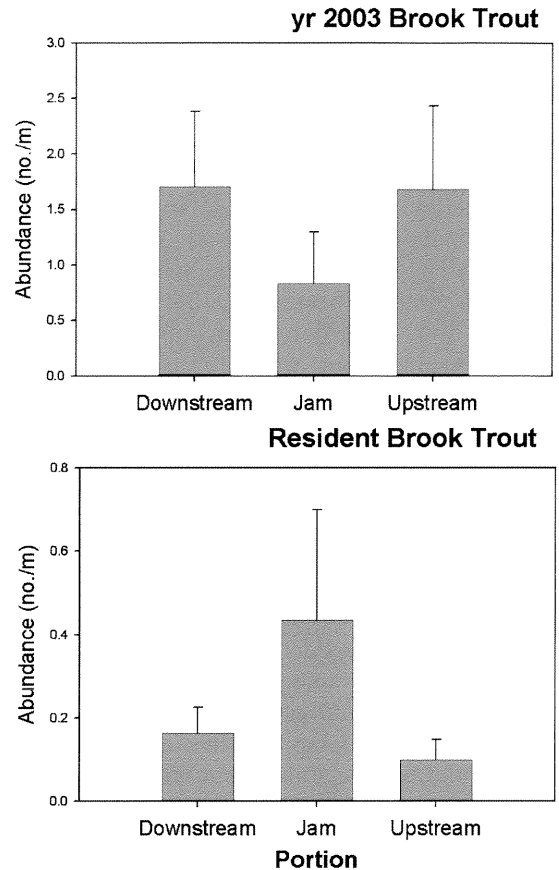


Figure 4. Brook trout abundance (± 1 SE) relative to large wood jams (LWJ) in the Little Carp River watershed, Upper Michigan. Abundance represents the number of captured fish divided by the length of stream sampled. See text for explanation of resident versus stocked brook trout.

jams that spanned more of the channel and had a higher number of pieces in contact with the water occurred in lower gradient sections which tended to have lower valley constraint, higher sinuosity, and smaller channel bed materials than the higher gradient sections of the river. Within recognizably different geomorphic settings, structural characteristics of LWJ also varied considerably.

When all study reaches were considered together, neither the abundance nor length of salmonids or nonsalmonids corresponded significantly with portions of stream at LWJ compared to portions away from LWJ. This is surprising, given the common understanding that LWJ benefit salmonids and seems to represent preferred habitat for many species of fish (Dolloff & Warren, 2003).

Table 3. Mean (± 1 SE) brook trout abundance (number per m) and mean (± 1 SE, n) length (mm) by geomorphic section and stream portion (DS, J, US; see text for explanation) associated with large wood jams (LWJ) of the Little Carp River, Upper Michigan. For abundance data, $n = 3$; n = number of reaches

	Geomorphic Section											
	Clay-lake			Mid-gradient			High-gradient			Low-gradient		
	DS	J	US	DS	J	US	DS	J	US	DS	J	US
<i>Abundance</i>												
Stocked in 2003	–	–	–	1.78 (1.02)	0.97 (0.58)	0.78 (0.40)	5.02 (0.87)	2.36 (1.59)	5.94 (0.26)	–	–	–
Resident	–	0.01 (0.01)	–	0.16 (0.12)	1.18 (1.04)	–	0.13 (0.13)	–	0.10 (0.10)	0.37 (0.12)	0.54 (0.07)	0.37 (0.03)
<i>Length</i>												
Stocked in 2003	–	–	–	103 (4.2)	96 (4.2)	103 (3.2)	101 (2.3)	101 (2.3)	102 (2.3)	–	–	–
Resident	–	127 (0.1)	–	119 (17.2)	147 (9.2)	–	142 (0.1)	–	127 (0.1)	66 (5.3)	80 (13.3)	87 (6.3)

The lack of statistically significant association of salmonids with large wood in the Little Carp River agrees, however, with findings from other studies (Berg et al., 1998; Ford & Lonzarich, 2000; Du-Bois et al., 2001; Warren & Kraft 2003), and most likely reflects variability related to environmental factors of the stream landscape.

Geomorphic and LWJ characteristics explained most of the variability in the proportion of salmonids occurring at LWJ, suggesting that structural characteristics of the LWJ (which varied significantly among geomorphic settings) and the availability of geomorphically influenced habitat influenced the function of LWJ as fish habitat. Regression analyses indicated that variability in

the proportion of resident salmonids at LWJ was best explained by a combination of geomorphic setting (high valley constraint) and LWJ characteristics (number of pieces of wood, wood volume in the LWJ). The results of the PCA suggest that LWJ characteristics such as the number of pool forming pieces also corresponded with large-scale geomorphic characteristics (e.g., valley constraint). We tested for the effects of LWJ in and out of the water by considering in the regression the number of pieces in the jam in contact with the water and the percent of channel spanned by the jams. The number of pool forming pieces did not explain a substantial amount of variability in salmonid abundance or length at jams. However, the percent of the channel spanned by LWJ and valley gradient were related significantly to the proportion of resident brook trout occurring at LWJ. We conclude that the size and volume of LWJ influence fish in ways other than just contacting the water (such as by creating high-flow refuges, or affecting temperature or prey abundance; Dolloff & Warren, 2003) or that these factors correlated with other habitat variables influencing fish abundance (Richmond & Fausch, 1995; Zalewski et al., 2003). Wondzell & Bisson (2003) suggested that many studies have not shown increased biodiversity near large wood in rivers because the functional role of wood depends on a variety of factors (such as the presence of other structure) whose total effect

Table 4. Mean (± 1 SE) combined rainbow trout and coho salmon fingerling abundance (per m) and length (mm) by stream portion associated with large wood jams (LWJ) of the clay lake plain geomorphic section of the Little Carp River, Upper Michigan

	Stream Portion		
	DS	J	US
Abundance	0.59 (0.25)	1.98 (0.63)	0.97 (0.05)
Length	82 (3)	88 (1)	80 (5)

For all reported values, $n = 3$ reaches. Rainbow trout and coho salmon did not occur in any geomorphic section other than the clay-lake plain.

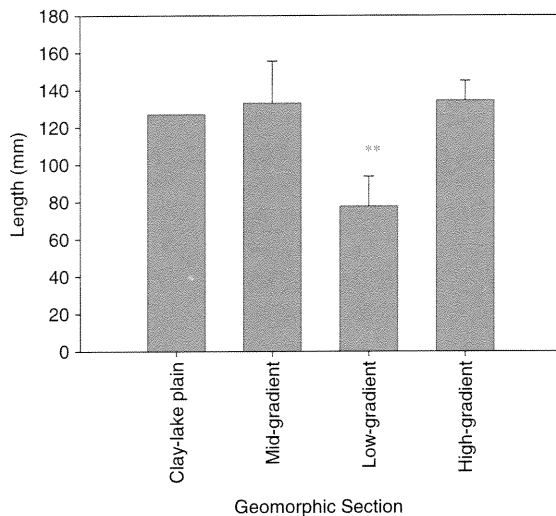


Figure 5. Length of resident brook trout (± 1 SD) in geomorphic sections of the Little Carp River. For clay-lake plain $n=1$, mid-gradient $n=4$, high-gradient $n=2$, and low-gradient $n=9$. ** indicates significance at $\alpha < 0.01$.

determines biodiversity, not just the presence of large wood. The correlation of salmonid proportions at LWJ with a combination of geomorphic and LWJ characteristics suggests that other factors in addition to LWJ may also influence the relative abundance of brook trout at LWJ in the Little Carp River. In relatively undisturbed systems like the Little Carp River ecosystem, high habitat diversity may mean that functions of LWJ which affect their correlation with fish abundance will be relatively less significant than in less complex systems.

We found that resident brook trout length at LWJ was also correlated with stream valley gradient, measured at the scale of geomorphic sections. Smaller resident brook trout occurred more often in the low-gradient upper reaches of the Little Carp River than in the middle sections, possibly because lower flows and complex habitats in the low gradient section favored wild reproduction and the survival of small fish. Resident brook trout in the high and mid-gradient sections have also faced annually repeated competition from thousands of stocked brook trout of around 100 mm length, which might have contributed to excluding smaller brook trout. Rainbow and coho were relatively even-sized because they represented a small segment of the population (most adults

appear to have migrated to Lake Superior). Further study could examine resident brook trout reproduction and competition to determine reasons why lengths varied more between sections than relative to LWJ as well as why longer brook trout occurred where they did.

There are other factors that could have influenced the occurrence of salmonids near LWJ, including the fact that brook trout spawn in the fall and travel to spawning areas during this time of year (Josephson & Youngs, 1996). Three of the larger resident brook trout we captured were spawning, and so might have moved away from LWJ to find or utilize spawning areas. Although spawning might have drawn brook trout away from LWJ, brook trout have been shown to maintain high levels of movement throughout the year (Gowan & Fausch, 1996). Consequently, associations of brook trout with LWJ may be dynamic throughout the year, and perhaps strongest in the spring during high flows (Warren & Kraft, 2003). The large number of new brook trout planted at the upstream end of the high-gradient section could have also induced behavioral changes in resident brook trout as newly stocked fish saturated available habitat in the high-gradient section where LWJ were less common. Even though the timing and design of this study limit the generalization of its results, the data show that the role of LWJ in the Little Carp River does not seem to be as an unequivocal focus of salmonid abundance across all settings.

The association of brook trout and other fish with large wood in streams in the Lake States should be explored further by sampling a larger set of LWJ to represent more completely the spatial and temporal scales of variability for factors similar to those we measured. Our results confirm, however, that association of young salmonids with LWJ is not always apparent, and that the association of brook trout with LWJ, when it occurs, corresponds with a few physical characteristics of LWJ and setting that are related to larger-scale geomorphology.

Implications for stream restoration

If emulating an old-growth system is the desired goal for large wood addition to streams, attention should be given to the correlation of LWJ with

Table 5. Characteristics of large wood jams surveyed for fish in the Little Carp River, Upper Michigan

Section	Jam	km to 2003 Fish Release ²	m to nearest downstream jam	m to nearest upstream jam	% BFC spanned ²	Vol. (m ³) ²	No. of pool form pieces ²	No. of pieces ²	% Conifer pieces ²	Proportion of all salmonids at LWJ ³	Proportion of salmonids excluding year 2003 brook trout at LWJ	Proportion of resident brook trout at LWJ
Clay-lake	1	7	20	190	20	7.94	1	12	83	0.70	0.70	—
	2	7	70	70	20	17.55	4	47	66	0.77	0.77	—
	3	7	70	0	100	10.94	3	10	80	0.54	0.54	1.00
Mid-gradient	1	1	30	20	80	0.28	4	1	100	0.99	0.98	0.98
	2	1	60	70	50	28.62	9	111	55	0.38	0.00	0.00
	3	1	20	50	100	65.78	21	133	61	0.51	1.00	1.00
High-gradient	1	0	10	90	2	2.33	3	12	67	0.07	—	—
	2	0	90	50	6	4.65	0	20	45	0.17	0.00	0.00
	3	0	50	20	3	3.68	4	25	40	0.47	—	—
Low-gradient	1	7	10	70	100	1.63	6	11	36	0.67	0.67	0.67
	2	7	20	20	90	1.12	3	7	0	0.55	0.55	0.55
	3	7	10	60	100	3.44	14	24	33	0.63	0.63	0.63

¹Valley gradient and valley constraint are shown in Table 1.²Used as independent variable in regression analysis along with valley gradient and constraint.³Salmonids: rainbow trout, juvenile coho salmon, resident brook trout, and brook trout planted in 2003.

larger scale geomorphology of the reference river. Our results suggest that restoring LWJ to streams should not be expected to influence habitat selection by salmonids the same way in all areas. Further work is needed to ascertain geomorphic factors that are most correlated with fish use of LWJ in a variety of settings, as well as the structure and function of LWJ in different settings. However, the ordering of LWJ along environmental gradients and the association of fish with LWJ that we observed correlated with variables representing geomorphology of the river corridor. When evaluating reference streams, the restoration practitioner should therefore consider not only the mean amount, size, or type of wood in LWJ, but also the distribution and form of those LWJ relative to recognizable geomorphology like valley gradient and constraint.

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