*Ecology of Freshwater Fish 2012: 21: 597–608*
*Printed in Malaysia · All rights reserved*

ECOLOGY OF
FRESHWATER FISH

# Association of brook trout and *Oncorhynchus* spp. with large wood jams in a Lake Superior tributary in a northern old-growth watershed

**Arthur E. L. Morris[1]*, Lance R. Williams[2], P. Charles Goebel[1], Eugene C. Braig IV[3]**
[1]Ohio Agricultural Research and Development Center, School of Environment and Natural Resources, The Ohio State University, Wooster, OH, USA
[2]Department of Biology, University of Texas at Tyler, Tyler, TX, USA
[3]F.T. Stone Laboratory and Ohio Sea Grant College Program, The Ohio State University, Columbus, OH, USA

Accepted for publication May 22, 2012

Abstract – Wood in streams functions as fish habitat, but relationships between fish abundance (or size) and large wood in streams are not consistent. One possible reason for variable relationships between fish and wood in streams is that the association of fish with wood habitat may depend on ecological context such as large-scale geomorphology. We studied the relationship between salmonid assemblages and large wood jams (LWJ) in four settings that differed geomorphically at the scale of the stream corridor along a tributary to Lake Superior in old-growth conifer–hardwood forest in northern Michigan. The focal fish species of this study were brook trout (*Salvelinus fontinalis*), which were wild in the stream. Relocation efforts for coaster brook trout (an adfluvial life history variant of brook trout) were ongoing in the study stream. We measured fish abundance and length in pairs of pools of similar size and substrate, but varying in the presence of LWJ; this allowed us to evaluate associations of fish simply with the presence of LWJ rather than with other channel or flow-shaping functions of LWJ. The length of *Oncorhynchus* spp. and young introduced brook trout was not strongly correlated with LWJ presence; however, the presence of LWJ in pools was positively correlated with larger wild brook trout. We also found that the correspondence of LWJ with the abundance of salmonids appears to be moderated by the presence of alternative habitat in this relatively natural, old-growth forest stream.

Key words: brook trout; geomorphology; large wood; large wood jams; ecological restoration; geomorphology

## Introduction

Riparian forests contribute to ecosystems that span apparent terrestrial-aquatic boundaries. One way that riparian trees connect trans-stream ecosystems is by delivering wood to streams. Studies focused on large pieces of wood (LW: piece at least 10 cm in diameter and longer than 1 m) show that LW influences and is influenced by riverine landscapes that are variable at several scales (Gregory et al. 2003). One set of ecological functions provided by LW relates to its role as habitat for fish (Robinson et al. 2002; Benke & Wallace 2003; Steel et al. 2003). Wood in streams provides overhead cover, hiding cover, ambush cover, food resources and other functions that could benefit fish. As would be expected, salmonids and many other fish have been found to associate with LW (e.g., Dolloff & Warren 2003; Zalewski et al. 2003). For example, Sundbaum & Näslund (1998) showed that brown trout (*Salmo trutta*) in experimental channels with LW lost less mass over time and had heavier gut contents, lower swimming activity and lower aggression rates compared with counterparts in channels without LW. However, LW does not seem to always be the primary factor in habitat choices by trout in streams (e.g., Simondet 1997; Berg et al. 1998; Ford & Lonzarich 2000). This raises questions about associations between fish and LW in different environmental settings.

---

*Correspondence*: A. E. L. Morris, Ohio Agricultural Research and Development Center, School of Environment and Natural Resources, The Ohio State University, 1680 Madison Avenue, Wooster, OH 44691, USA. E-mail: arthur@utahopenlands.org
*Present address: Utah Open Lands Conservation Association, 2188 S. Highland Drive 203, Salt Lake City, UT 84106, USA

*Ecology of* FRESHWATER FISH

doi: 10.1111/j.1600-0633.2012.00581.x

The type, arrangement and ecological context of LW could affect its value as habitat for fish. LW aggregations (jams of more than two pieces, LWJ) may have a greater influence on fish populations than do single pieces of LW (Flebbe & Dolloff 1995; Flebbe 1999; Dolloff & Warren 2003). The physical structure and arrangement of LW in LWJ might also influence its function as fish habitat because LW arrangement influences the quality of cover, access to prey, shelter from high flows, etc. Large wood abundance and structure vary with geomorphic setting because geomorphic setting influences LW recruitment, transport and trapping functions of streams (Abbe 2000; Swanson 2003; Morris et al. 2007).

The functional importance of LW in streams could also change with stream context (i.e., the riparian and larger-scale environmental surroundings that influence the types of available structure and processes). It has been noted that the association of fish with LW is facultative where other habitat components can substitute for the direct functions of wood structure (Dolloff & Warren 2003). Stream channel features such as substrate, width, the arrangement of channel geomorphic units (e.g., frequency of pools) and primary pool-forming structures all relate to the provision of habitat components other than LW, and all have been found to correspond with relatively large-scale geomorphology in catchments (Montgomery et al. 2003; Swanson 2003; Morris et al. 2009). Therefore, relatively large-scale geomorphic setting may influence the role of LW as habitat for fish.

As part of a larger study, we investigated LW and stream channel characteristics in a tributary to Lake Superior in an old-growth forest in Northern Michigan, in which the stream corridor varied geomorphically on the order of 1 km of corridor length (Morris et al. 2007). We found differences corresponding to geomorphically defined segments in stream flow, substrate, channel morphology, and the abundance, size and arrangement of LW (Morris et al. 2007, 2009). In the old-growth forest context of our study, the structure of LW varied with geomorphic setting, providing the opportunity to test associations between LW and fish in a relatively anthropogenically unchanged forest system with varied stream environmental contexts and LW arrangements. We focused particularly on the relationships between salmonids and LWJ because a wild, reproducing population of eastern brook trout (*Salvelinus fontinalis*) was found in the study stream, restoration efforts for coaster brook trout were occurring, and both rainbow trout (*Oncorhynchus mykiss*) and coho salmon (*Oncorhynchus kisutch*) were reproducing in the lower reaches of the stream. We hypothesised that more and larger fish would be present in pools with LWJ compared with pools without LWJ in general because of the potential for LWJ to provide prey and complex cover. We anticipated, however, that fish associations with LWJ would vary between stream segments corresponding to different stream-corridor-scale geomorphology.

## Study area

The Little Carp River is almost entirely within one of the largest (13,000 ha) contiguous, old-growth, hard-

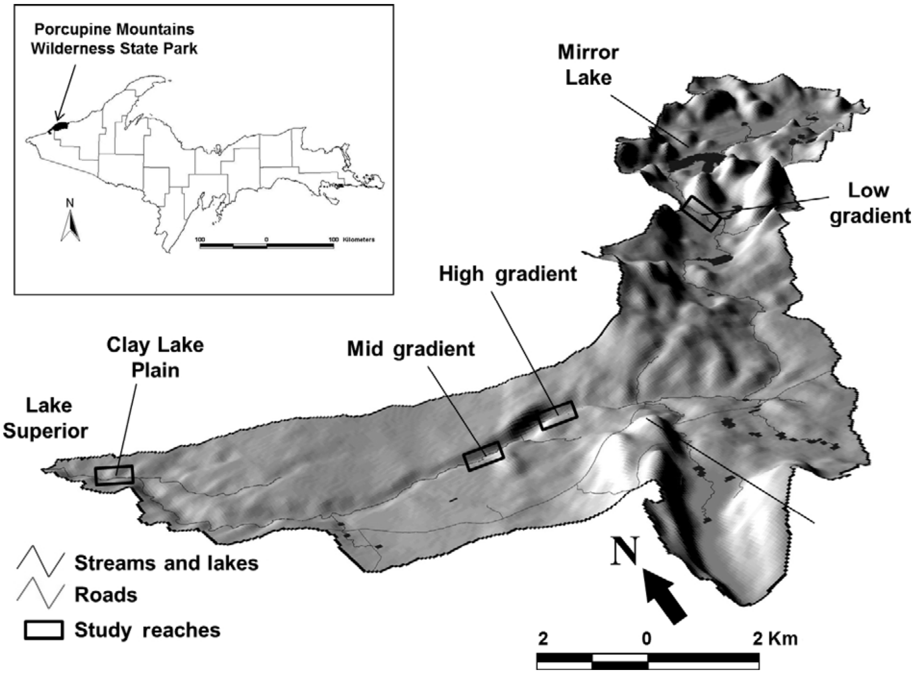

*Fig. 1.* Map of study areas on the Little Carp River.

wood–hemlock forests in the Lake States (Frelich 2002; Fig. 1). It flows through the Porcupine Mountains Wilderness State Park in Upper Michigan along the south shore of Lake Superior. The overstory forest of the Little Carp River consists primarily of eastern hemlock (*Tsuga canadensis*, (L.) Carr.), northern white cedar (*Thuja occidentalis*, L.), yellow birch (*Betula alleghaniensis*, Britt.) and sugar maple (*Acer saccharum*, Hook). Mean height of the tallest trees in the study area is roughly 25 m and mean diameter at breast height about 60 cm. Most of the river is forested to the edge of the bankfull channel. Bankfull channel ranges from about 5 m at the source (Mirror Lake) to approximately 20 m at the mouth. Few records of stream flow exist for the Little Carp River because no permanent stream gauges exist. Goebel et al. (2003) reported discharge during annual floods ranging from 4.7 $m^3 \cdot s^{-1}$ in the upper, low-gradient sections to 9.4 $m^3 \cdot s^{-1}$ in the lower, high-gradient portions. Discharge associated with 50-year flood events in the Little Carp River has been estimated to range from 17.5 to 38.1 $m^3 \cdot s^{-1}$ (Goebel et al. 2012). Direct human influences to the geomorphology of the river consist of minor changes incidental to recreational hiking and camping. Beaver (*Castor canadensis*) activity was apparent during our study, but no well-established beaver dams occurred in segments of stream that we studied.

Brook trout are wild in the Little Carp River. The study area included historical habitat for coaster brook trout, which were once common in the northern Great Lakes region but are now rare (Ridgway 2008; Schreiner et al. 2008). Thirty thousand brook trout from a strain known to exhibit coaster life histories in Lake Nipigon were stocked in the Little Carp River in 2003 and 40,000 in 2004, both at the same location at the head of the high-gradient geomorphic section. Stocked brook trout had clipped fins indicating the year of release. Several species of dace (*Rhinichthys atratulus*, Hermann; *Rhinichthys cataractae*, Valenciennes in Cuvier and Valenciennes; *Chrosomus eos*, Cope), sculpin (*Cottus* spp.), northern creek chub (*Semotilus atromaculatus*, Mitchill), central mudminnow (*Umbra limi*, Kirtland), introduced rainbow trout and coho salmon occur in the Little Carp River (Morris 2005). Both the rainbow trout and coho salmon are thought to be adfluvial, with populations in the Little Carp River consisting primarily of young fish that have not yet moved out to Lake Superior.

## Watershed and geomorphic settings

The Little Carp River begins at a lake and flows through a low-gradient valley, then descends steeply across a resistant lava inclusion and finally flows through the deep lacustrine remnants of the ancient lake before entering Lake Superior (Fig. 1). We identified one study segment of approximately 1 km or more in each of four distinct settings determined by stream-corridor geomorphology (Rosgen classification derived from Rosgen & Silvey 1996).

### *Low-gradient, bedrock controlled, parallel to mountain range (LRP)*

The upstream end of this stream segment is approximately 1 km downstream from its source (Mirror Lake). The stream here flows through an unconfined channel with gravel and cobble bedding in bedrock-controlled channels. Floodplains are relatively extensive. Large LWJ compared with the size of the stream channel are abundant here. Many pools in this section appear to have been formed by LWJ. Rosgen Classification: Type C3.

### *High-gradient, bedrock controlled, transverse to mountain range (HRT)*

The upstream end of this stream section is approximately 9 km from the source; the downstream end is the upstream end of the mid-gradient section. Valley constraint is high and floodplain development minimal. The LWJ occur in relatively low abundance and are primarily along channel margins. There are many sections of rock-plane bedding and step-pools. The rocky substrate appears to have formed most pools. All brook trout stocked in 2003 and 2004 were released from a bridge at the upstream end of this section. Rosgen Classification: Type A1.

### *Mid-gradient, bedrock controlled, transverse to mountain range (MRT)*

The upstream end of this stream section is 10 km from the source. The mid-gradient stream segment formed in the transition area between the high-gradient segment and the low-gradient clay-lake plain (CLP). Large wood and LWJ occur here in great abundance, with large amounts apparently contributed after transport through the adjacent upstream high-gradient section. Streambank failures are relatively frequent. Rock-plane bedding is rare in this section, and deep pools are relatively common. Many pools appear to have been formed and/or shaped by LW. Rosgen Classification: Type C3.

### *Clay-lake plain (CLP)*

The upstream end of this stream section occurs 16 km downstream from the source at Mirror Lake. The CLP segment has many plane-bed reaches, and channels tend to be incised through deep, ancient lacustrine sediment and flow through relatively wide floodplains. Streambank slope failures occur in many places. Large wood and LWJ are moderately abundant throughout the segment, compared with amounts in other study segments. The upstream end of the CLP is a waterfall thought to be impassable to adfluvial species such as coho salmon, rainbow trout and coaster brook trout. Rosgen Classification: Type F1.

## Methods

Within each segment, we identified and measured the length of each pool, noted the presence of all LWJ and the number of pieces of LW (pieces greater than 10 cm diameter and 1 m in length), and estimated the per cent of channel spanned by each LWJ (in 25% increments). We focused on pools that spanned the entire channel. We excluded pools with the largest LWJ (generally with more than 50 pieces and spanning the entire channel; several in each section) from this study because fish were not accessible for sampling under these complex structures.

We compared the abundance of fish in pools with and without LWJ. To do this, we chose pools so that each study segment contained ten for sampling: five containing LWJ and five similar pools without LWJ. We chose five pools with LWJ across the range of pool surface areas in each segment. We then selected one pool without LWJ to match size, depth, flow and substrate as closely as possible for each pool with LWJ in each study segment. Where more than one pool existed that was an appropriate choice, we randomly selected one to study. We assumed that paired pools (one with LWJ and the other without) represented similarities in major features affecting fish in the pools as well as possible under field conditions. We isolated pools with upstream and downstream block nets and conducted fish surveys by triple-pass electrofishing (Smith-Root model LR-24). We surveyed all pools during the period from 30 June to 5 July 2004 and then again during the period from 12 October to 20 October 2004. We surveyed all pools in one geomorphic segment before moving to another segment for logistical reasons. A large tree fell after June in one pool in the CLP that we had sampled. In October, we chose a similar nearby pool to sample as a replacement for the pool in which the tree fell. Weather conditions remained fairly constant during the weeks of sampling; there were no unusual shifts in temperature, and rainfall near the time of sampling did not substantially change water clarity or level during each sampling season. We measured canopy cover during fish sampling in early summer using a spherical densiometer while standing at the approximate centre of each pool.

All captured fish were identified and measured. We evaluated newly stocked brook trout (right pectoral fin clipped, year 2003; left ventral fin clipped, year 2004) separately from apparently wild-born brook trout (fins not clipped: 'wild') and from each other because of the possibility that newly stocked, naïve fish would choose habitat differently than established fish. Rainbow trout and coho salmon were grouped (referred to hereafter as *Oncorhynchus* spp.) for ease in tallying and because of our focus on brook trout.

The abundance of fish captured in a pool was standardised by dividing fish counts by pool surface area (hereafter catch-per-unit-area is termed 'abundance' for simplicity). Fish length was averaged for species by pool. When the lengths of several species of fish were averaged for a pool, mean length was computed as the average length weighted by species abundance (e.g., the length of *Oncorhynchus* spp. in a pool is the mean length of rainbow trout and coho salmon).

### Data analysis

To compare fish between pools with and without LWJ, we computed two simple metrics – relative abundance (RA) and relative length (RL). Each metric represented fish in pools with LWJ relative to fish in pools without LWJ. RA and RL were used as the basis for statistically evaluating differences between pools with and without LWJ (comparing RA and RL to target values using one-sample *t*-tests) and differences in associations with LWJ corresponding to stream segment and season (with mixed-model analysis of variance).

Relative abundance between pairs of similar pools was calculated using Eq. (1)

$$\mathrm{RA} = A_{\mathrm{LWJ}}/(A_{\mathrm{NOT}} + A_{\mathrm{LWJ}}) \tag{1}$$

where $A_{\mathrm{LWJ}}$ is the abundance of fish in a pool with LWJ and $A_{\mathrm{NOT}}$ is the abundance of fish in a matched pool without LWJ. RA values of 0.5 indicated the same number of fish in the pool with LWJ as in the pool without LWJ. More fish in pools with LWJ would result in RA values >0.5. RA was computed for each assemblage separately. RA was only computed if the target species occurred in at least one pool of a matched pair (otherwise division by zero would have occurred).

To compare fish lengths between paired pools, we first computed the RL between pairs of similar pools using Eq. (2)

$$\mathrm{RL} = L_{\mathrm{LWJ}}/L_{\mathrm{NOT}} \tag{2}$$

where $L_{\mathrm{LWJ}}$ is the mean length of fish in a pool with LWJ and $L_{\mathrm{NOT}}$ is the mean length of fish in a matching pool without LWJ. RL of 1.0 indicated equivalent mean lengths between similar pools. RL values exceeding 1.0 indicated longer fish in pools with LWJ compared with pools without LWJ. RL values were computed for each assemblage separately. RL was only computed if the target fish occurred in both pools of a matched pair.

To test overall associations of fish with LWJ in pools, we considered paired pools the experimental units for one-sample *t*-tests after averaging RA and RL values by season ($n = 20$; i.e., four segments, with five pool pairs in each). We evaluated RA and RL across all segments, comparing RA to 0.5 (null hypothesis: RA = 0.5) and RL to 1.0 (null hypothesis: RL = 1.0), or those values adjusted for transformations of the data (Minitab v. 14.0, Minitab, Inc., State College, PA, USA). RA of wild brook trout was transformed by log(RA + 1), to meet assumptions of normality. RL of year 2003 brook trout were transformed by log(log(RL + 1)) and RL of wild brook trout by log(RL) to normalise data. The RL of year 2004 brook trout could not be normalised through transformations, so we analysed these data using a nonparametric sign test (Minitab v 14.0). No other exceptions were necessary for parametric analysis.

To test patterns of variability in RA or RL associated with geomorphic setting and season, we used mixed-model analysis of variance (ANOVA; Proc Mixed, SAS v 9.1; SAS Institute, Cary, NC, USA). Variance was estimated with restricted maximum likelihood (REML), and geomorphic setting was considered a fixed classification factor. We considered paired pools the experimental units, nested within geomorphic setting. Paired pools were treated as random samples from choices available in the designated geomorphic sections of the Little Carp River. We considered pairs as a random factor because our choice of pools to study was meant to reflect all possible pairs, and the types of pools we studied would not necessarily be studied again if the study were repeated (Bennington & Thayne 1994). Season (June or October) was considered a fixed classification factor applied to paired pools and was evaluated as if it had been applied to subsamples of the experimental unit (compare with factor relationships described in Bergerud 1996). We used the Kenward–Rogers method for error structure (SAS command: DDFM = KR) in mixed-model ANOVA. The only transformations needed to meet the assumptions of ANOVA were: RA data of wild brook trout were log(RA + 1) transformed, and RL data of wild brook trout and year 2004 brook trout were log(log(RL + 1)) transformed. RL of year 2003 brook trout required analysis with the non-parametric Kruskal-Wallis test. Geomorphic sections were considered in ANOVA only if the target fish assemblage occurred there. Only four wild brook trout and 1 year 2003 brook trout were located in the CLP geomorphic section, so this section was excluded from the ANOVA for wild brook trout and year 2003 assemblages.

Finally, we evaluated potential relationships between LWJ characteristics and wild brook trout RA and RL using linear multiple regression (Minitab 14.0). We performed regression analysis with mean RA and RL of wild brook trout, averaged by season. Predictor variables were the number of pieces of LW in the LWJ, the total volume of LW in the LWJ and proportion of the channel spanned by the LWJ. Data did not require transformation to adequately meet assumptions for regression analysis. This evaluation did not evaluate the full range of variability in LWJ characteristics because of the limited number of LWJ that were sampled for this study; it simply suggests LWJ characteristics that were most strongly correlated with wild brook trout abundance and length from within the range of LWJ that were sampled.

## Results

### Pools and LWJ

We observed considerable variation in the characteristics of pools and LWJ among the different geomorphic settings. Each study segment contained about the same number of pools (31–41), but the length of pools, the length of step-pools (usually rock-plane bedded), forest canopy cover, and the number and span of LWJ varied considerably among sections (Table 1). The LWJ that we sampled spanned 25–100% of the active channel, but – unlike some of the largest LWJ in the stream – were not so complex that they could not be effectively sampled.

### Fish

Brook trout occurred primarily in geomorphic segments other than the CLP, while *Oncorhynchus* spp. occurred only in the CLP segment. Young wild brook trout were mainly found far upstream above barriers to *Oncorhynchus* spp. and above where brook trout had been stocked. Only one adult coho salmon was found in the studied pools. We captured four wild brook trout (no clipped fins) in the CLP study segment, but only one of those was captured in October, suggesting that most or all of the sampled wild brook trout in the CLP segment were not displaying coaster life histories (coaster brook trout move into tributaries to spawn in the fall). Of the stocked brook trout from Lake Nipigon coaster strain, we captured only one (an individual stocked in 2003) in the CLP. All other stocked brook trout were found in the high-gradient geomorphic section close to where they had been stocked or just downstream in the furthest upstream reaches of the mid-gradient geomorphic section. Only wild brook trout (including most juvenile wild brook trout) were found in the LRP geomorphic section (furthest upstream study section). Nonsalmonids in general occurred throughout all geomorphic sections.

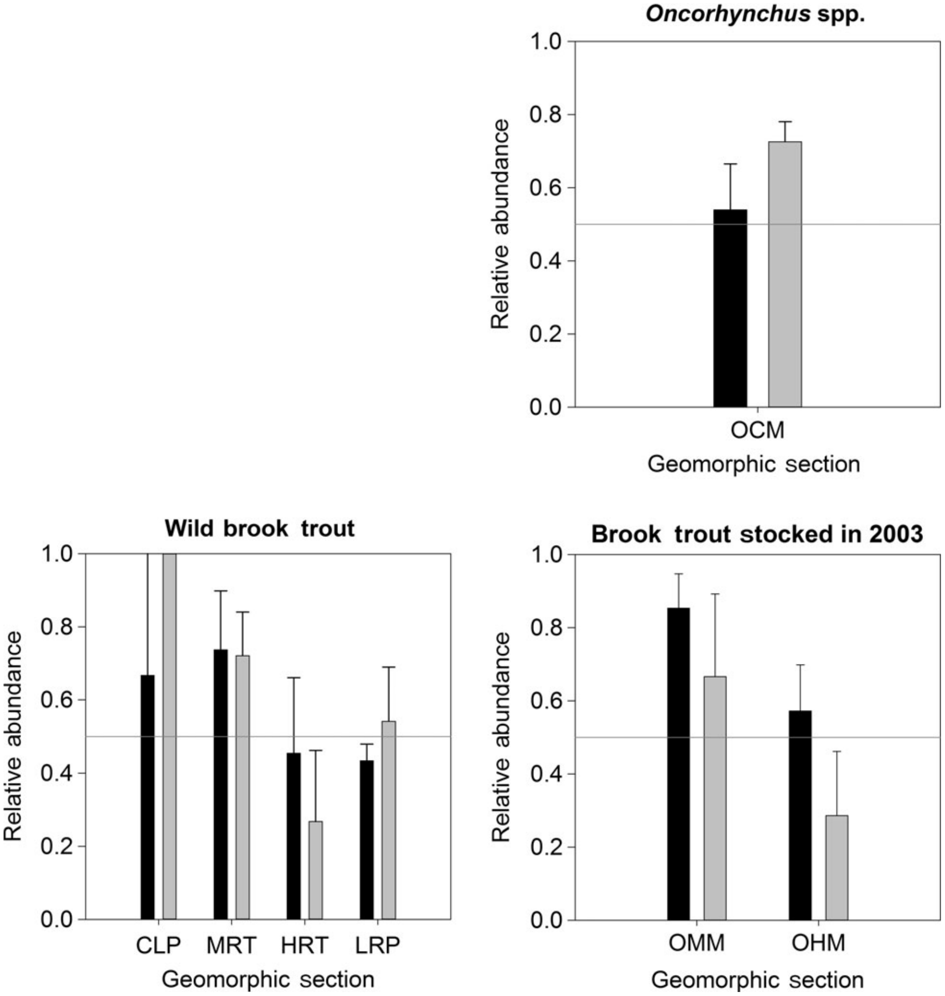

*Fig. 2.* Relative abundance (RA) of fish in study segments. Error bars represent standard error. Black bars represent June/July sampling; grey bars represent October sampling. RA of 0.5 indicates equal numbers of fish in matched pools with and without large wood jams (LWJ), while RA >0.5 indicates greater density of fish in pools with LWJ. For wild brook trout, the grey bar that reaches one represents a single brook trout that was found in a pool with LWJ (RA = 1.0).

Table 1. Pool characteristics of study sections (± standard deviation).

| | Clay-lake plain | Mid-gradient | High gradient | Low gradient |
|---|---|---|---|---|
| Total section length (m) | 2991 | 1568 | 1388 | 851 |
| Bankfull channel width (m) | 18.3 ± 4.0 | 10.1 ± 2.2 | 13.4 ± 2.7 | 5.0 ± 1.8 |
| Active channel width (m) | 7.2 ± 1.7 | 5.2 ± 1.4 | 6.5 ± 1.4 | 3.7 ± 1.4 |
| Number of pools | 34 | 31 | 37 | 41 |
| Number of pools containing LWJ | 12 | 23 | 9 | 21 |
| % Of pools adjacent to a pool containing LWJ | 69% | 93% | 43% | 67% |
| Mean length of pools spanning the entire channel (m)[†] | 23 ± 15 | 14 ± 8 | 14 ± 8 | 8 ± 8 |
| % Of total section length in pools spanning entire channel[†] | 14% | 16% | 25% | 29% |
| Mean length of step-pools (m)[‡] | 83 ± 87 | 18 | 50 ± 25 | none |
| % Of total section length in step-pools[‡] | 20% | 1% | 29% | 0% |
| % Of channel spanned by LWJ in pools | 42 ± 41% | 82 ± 30% | 39 ± 40% | 83 ± 29% |
| % Forest canopy cover over stream[§] | 44 ± 28% | 67 ± 20% | 65 ± 17% | 82 ± 22% |

LWJ, large wood jams.

†Not counting step-pools.

‡Most step-pool channel geomorphic units contained primarily rock-plane bedding; this measure is proxy for rock-plane substrate.

§Measured in June at the centre of the 10 pools per geomorphic section that we surveyed for fish.

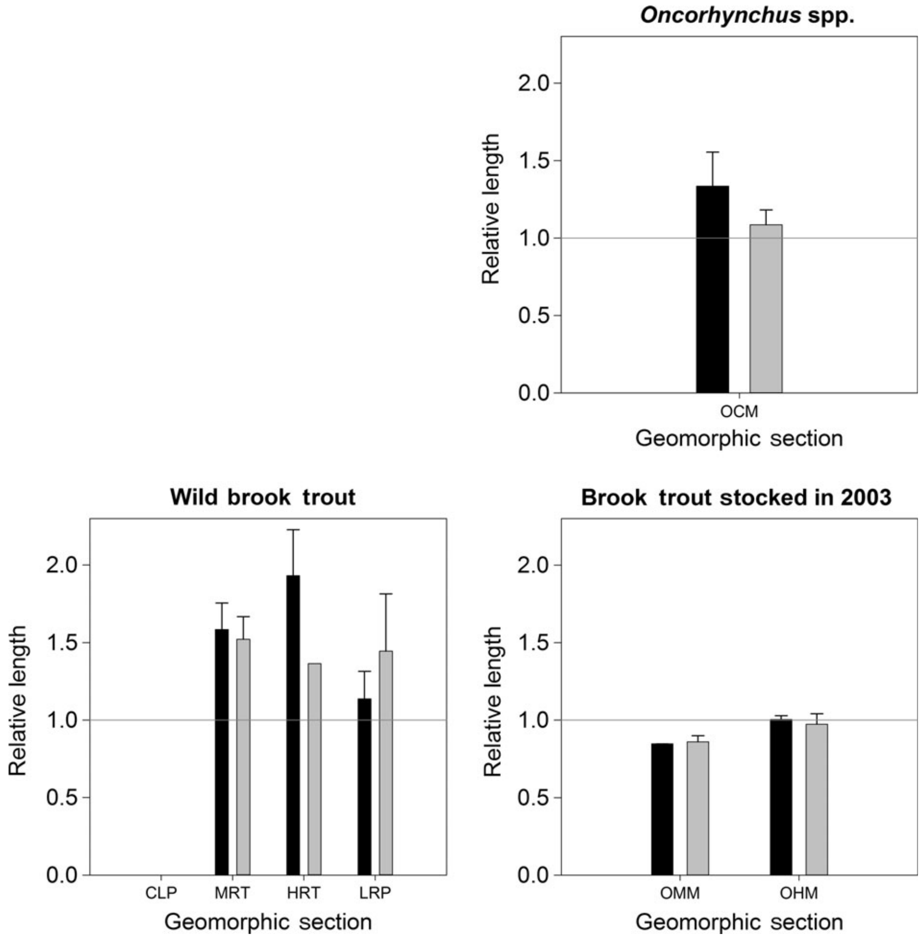

*Fig. 3.* Relative length (RL) of fish in study segments. Error bars represent standard error. Black bars represent June/July sampling; grey bars represent October sampling. RL of 1.0 indicates equal lengths of fish in matched pools with and without large wood jams (LWJ), while RL >1.0 indicates longer fish in pools with LWJ.

### Fish associations with LWJ

Overall, mean abundance of most fish was greater in pools with LWJ compared with pools without LWJ in general (mean RA > 0.5: Fig. 2); however, for pools included in the statistical analysis, variability in fish abundance between pools with and without LWJ was high enough that means were not considered statistically different for most assemblages (wild brook trout: $P = 0.69$; stocked brook trout year 2003: $P = 0.79$; year 2004: $P = 0.26$; Table 2). *Oncorhynchus* spp. abundance in pools with LWJ compared with pools without LWJ was significant at $P = 0.02$. Repeated t-tests in our analysis raised the possibility that a nonsystematic difference would appear statistically significant. A small sample size for *Oncorhynchus* ($n = 5$ paired pools) and high variability in abundances (0.76 ± 0.78 fish per m$^2$ without LWJ; 0.34 ± 0.26 fish per m$^2$ with LWJ; mean ± 95% confidence interval) exacerbate the uncertainty. We conclude that observed differences in *Oncorhynchus* abundance are suggestive, but not strong.

With regard to length, longer wild brook trout clearly occurred in pools with LWJ compared with pools without LWJ ($P = 0.004$) when all geomorphic settings were considered. Brook trout were 1.42 ± 0.28 times longer in pools with LWJ than in pools without LWJ, which translates to an actual difference of 33 ± 20 mm reflected in the statistical analysis. When lengths in all pools were averaged by presence of LWJ regardless of whether or not both pools in each matched pair contained fish (several additional pools, including those in the CLP section), the difference was 39 mm in the spring (131 ± 20 mm with LWJ, 92 ± 20mm without LWJ) and 38 mm in the fall (138 ± 35 mm with LWJ, 100 ± 19 mm without LWJ). There is a high probability that RL did not differ from 1.0 among all pools for stocked brook trout (year 2003: $P = 0.22$; year 2004: $P = 0.45$). Lengths of *Oncorhynchus* spp. were not different between fish at pools with LWJ compared with pools without LWJ ($P = 0.09$) using $\alpha$-value = 0.05; however, the probability that observed differences were nonrandom (i.e., that the

Table 2. Fish abundance and lengths in pools of the Little Carp River.

| Assemblage | Mean no. fish caught no. (SD, *n*[†]) | Mean length[‡] mm (SD, *n*) | Mean[§] abundance[¶] in pools with LWJ no. per $m^2$ (SD, *n*[**]) | Mean[§] abundance[¶] in pools without LWJ no. per $m^2$ (SD, *n*[**]) | Mean[§] length in pools with LWJ mm (SD, *n*[**]) | Mean[§] length in pools without LWJ mm (SD, *n*[**]) |
|---|---|---|---|---|---|---|
| Wild brook trout | 2.10 (2.55, 80) | 112.49 (48.80, 55) | 0.06 (0.08, 18) | 0.08 (0.08, 18) | 127 (37, 13) | 96 (25, 1 3) |
| Year 2003 brook trout | 1.73 (1.77, 40)[††] | 145.47 (15.73, 29) | 0.02 (0.02, 11) | 0.04 (0.05, 11) | 150 (9, 7) | 142 (11, 7) |
| Year 2004 brook trout | 48.90 (83.87, 20)[‡‡] | 96.57 (6.93, 17) | 0.80 (1.45, 10) | 0.91 (1.32, 10) | 95 (2, 7) | 100 (9, 7) |
| *Oncorhynchus* sp. | 51.00 (46.94, 20)[§§] | 58.63 (21.60, 20) | 0.34 (0.21, 5) | 0.76 (0.63, 5) | 55 (5, 5) | 62 (3, 5) |

LWJ, large wood jams.

[†] Forty pools were sampled: five pools with LWJ and five pools without LWJ in each of four stream segments. Sampling occurred once in the spring and once in the fall (80 sampling episodes in pools total).

[††] Brook trout stocked in 2003 only were found in the MRT and HRT segments, so pools in the CLP and LRP segments were excluded from the count means (20 pools excluded for each season in this column).

[‡‡] Brook trout stocked in 2004 were only found in the MRT and HRT segments in the fall (they were stocked after the spring sampling), so pools in the CLP and LRP segments and all pools from the spring were excluded from the count means (20 pools excluded for the fall; 40 pools excluded for the spring in this column).

[§§] Oncorhynchus species were only found in the CLP segments, so pools in all other segments were excluded from the count means (30 pools excluded each season for this column). Of the total *Oncorhynchus* individuals caught, the majority were parr: 668 parr of 705 individuals in the spring and 294 parr of 314 individuals in the fall.

[‡] Mean length includes lengths only for pools where fish were present.

[§] Spring and fall data averaged together for each pool.

[¶] Abundance (no. per $m^2$) was calculated by dividing the number of individuals caught per pool by the surface area of the pool.

[**] In mean abundance and length for pools with and without LWJ, *n* represents the number of pool pairs from which data were used for computation of RA (relative abundance) or RL (relative length). Although 20 pool pairs were surveyed for all species (40 pools each season), RA was computed only if target fish were present in at least one pool of a pair and RL was computed only if target fish were present simultaneously in both pools of a pair.

Table 3. Results of ANOVA comparing RA among geomorphic settings and seasons in the Little Carp River.

| Assemblage[†] | Factor | Num DF | Den DF | *F* | *P* |
|---|---|---|---|---|---|
| *Oncorhynchus* Spp. | Geomorphology | na | – | – | – |
| | Season | 1 | 4 | 2.12 | 0.22 |
| | Interaction | na | – | – | – |
| Wild brook trout | Geomorphology | 3 | 14 | 2.38 | 0.11 |
| | Season | 1 | 13 | 2.91 | 0.11 |
| | Interaction | 3 | 12 | 2.64 | 0.10 |
| Year 2003 brook trout | Geomorphology[‡] | 1 | 8.4 | 3.53 | 0.10 |
| | Season | 1 | 7.05 | 5.36 | 0.05 |
| | Interaction | 1 | 7.05 | 0.44 | 0.53 |

RA, relative abundance.

[†] Year 2004 brook trout RA data could not be transformed for parametric analysis. Results of a Kruskal–Wallis test on the effects of geomorphology are given in the text.

[‡] Years 2003 and 2004 brook trout occurred almost exclusively in the mid- and high-gradient sections, so only mid- and high-gradient geomorphic sections were included in ANOVA for these assemblages shown in Tables 3 and 4.

Table 4. Results of ANOVA comparing RL among geomorphic settings and seasons in the Little Carp River.

| Assemblage[†] | Factor | Num DF | Den DF | *F* | *P* |
|---|---|---|---|---|---|
| *Oncorhynchus* Spp. | Geomorphology | na | – | – | – |
| | Season | 1 | 8 | 1.09 | 0.33 |
| | Interaction | na | – | – | – |
| Wild brook trout | Geomorphology[‡] | 2 | 10.4 | 2.38 | 0.33 |
| | Season | 1 | 6.03 | 0.00 | 0.98 |
| | Interaction | 2 | 5.92 | 0.73 | 0.52 |
| Year 2004 brook trout | Geomorphology | 1 | 5 | 1.95 | 0.22 |
| | Season | na | – | – | – |
| | Interaction | na | – | – | – |

CLP, clay-lake plain; RL, relative length.

[†] Year 2003 brook trout data did not allow parametric analysis. Results from Kruskal–Wallis tests of the effects of geomorphology by season are given in the text.

[‡] Wild brook trout did not occur simultaneously in both pools of pairs in the CLP geomorphic section, so RL data from the CLP geomorphic section were not included in ANOVA for this assemblage.

null hypotheses should have been rejected) was higher than for other stocked brook trout assemblages.

## Differences in fish association with LWJ by geomorphic setting or season

With regard to differences between stream segments, it appeared that the abundance of wild brook trout and year 2003 brook trout in pools with and without LWJ differed between segments (Fig. 2); however, this was only significant at $P = 0.11$ (wild brook trout) and $P = 0.10$ (year 2003 brook trout; Table 3), evidencing substantial difference with fairly high variability. Wild brook trout appeared to be more abundant in pools with LWJ than without LWJ in the CLP and MRT sections, similarly abundant in both types of pools in the LRP and less abundant in pools with LWJ in the HRT (Fig. 2). Differences varied somewhat by season, with relatively more abundant wild brook trout in pools of the HRT section in the spring compared with the fall (this is reflected in the interaction term of the ANOVA, $P = 0.10$; Table 3). Year 2003 brook trout appeared to be more abundant in pools with LWJ in the MRT segment than in the HRT segment. RA for year 2003 brook trout appeared to shift with season, so that by October relatively fewer of these fish were found in pools with LWJ. The RA data for brook trout stocked in 2004 could not be transformed for parametric analysis. Results of a Kruskal–Wallis test on the effects of geomorphology on year 2004 brook trout indicate no difference in the RA of year 2004 brook trout between geomorphic segments ($H = 1.84$, $P = 0.17$).

Although longer brook trout generally occurred in pools with LWJ, geomorphic setting (study segment) or season did not appear to correspond with differences in the length of salmonids in pools with and without LWJ ($P = 0.22$ to $0.98$; Table 4; Fig. 3b). The RL data for brook trout stocked in 2003 did not allow parametric analysis. Results from Kruskal–Wallis test comparing year 2003 RL between geomorphic settings are as follows: June – $H = 3.43$, $P = 0.06$; and October – $H = 2.4$, $P = 0.12$; in June, relatively shorter year 2003 brook trout were found in pools with LWJ compared with pools without LWJ in the MRT segment, while lengths were essentially equivalent in the HRT segment.

### Wild brook trout with LWJ characteristics

Relative abundance of wild brook trout corresponded most strongly with the number of pieces of LW per LWJ ($P = 0.01$, adjusted $r^2 = 0.31$); this weak relationship was largely attributed to the contribution of fish that occurred in three pools with LWJ consisting of more than 20 pieces. RL of wild brook trout corresponded most strongly with the volume of LW per LWJ ($P = 0.02$, adjusted $r^2 = 0.31$). Proportion of channel spanned by LWJ did not explain a significant amount of variability in the RA of wild brook trout ($P = 0.49$, adjusted $r^2 = 0.00$) or in the RL of wild brook trout ($P = 0.56$, adjusted $r^2 = 0.00$), nor did it improve predictive ability when included with other explanatory variables (LWJ pieces and/or volume) in linear regression models. The volume of LW and the number of pieces of LW together did not improve the regression model for wild brook trout RA or RL. The volume of LW per LWJ alone predicted wild brook trout RA less well than did the number of pieces of LW (adjusted $r^2 = 26.2$, $P = 0.02$). The number of pieces of LW per LWJ alone was not useful for predicting wild brook trout length (adjusted $r^2 = -0.35$, $P = 0.35$).

## Discussion

The presence of LWJ corresponded strongly with the length of wild brook trout in the Little Carp River overall (when all stream segments were considered for both seasons together). Larger wild brook trout occurred in pools with LWJ compared with pools without LWJ in all geomorphic settings. The positive association we measured for the length of wild brook trout with the presence of LWJ in the Little Carp River suggests that LWJ functioned directly to influence habitat choice of individuals from this wild fish population. We infer that LWJ provided habitat function(s) attractive to larger wild brook trout, a conclusion in keeping with other studies that have also reported positive responses of brook trout to pools containing LW (Riley & Fausch 1995; Neumann & Wildman 2002) and a stronger relationship between larger individuals of salmonid assemblages and LWJ than between smaller individuals of the assemblage and LWJ (Angermeier & Karr 1984; Dolloff & Reeves 1990; Binns 1994; Neumann & Wildman 2002).

With regard to overall abundance (without regard for stream segment or season), contrary to our expectations, no fish assemblage in this study showed clear differences in abundance between pools with and without LWJ. It appears that the functions of LWJ in pools were not uniquely strong enough to order general patterns of fish abundance for the assemblages we evaluated. Other studies have found that the presence of LW corresponds to greater fish densities in reaches and streams, in some cases varying by season (e.g., Fausch & Northcote 1992; Roni & Quinn 2001). Our research focused on LWJ as a habitat component specifically in pools, as part of untangling the functions of LW in streams. LWJ provides cover and supports both aquatic and terrestrial prey; however, cover and prey can also be provided by other structure or simply by pooled water itself. Berg et al. (1998) found that fish used deep water more than any other cover type, including wood. Flebbe (1999) also found that pools were more important than wood for fish. Warren & Kraft (2003) found that the effects of wood removal on fish populations were limited when pool habitat remained after wood removal. They suggested that habitat complexity provided by large boulders and other structure limited the influence of woody debris on brook trout (Warren & Kraft 2003). Nagayama et al. (2009) found that all size classes of Masu salmon (*Oncorhynchus masou*) were more abundant in flowing water habitats where LW was artificially placed than in similar habitats where LW was not placed, attributing much of the positive effects of LW to its pool-forming function. Our study adds to other studies by further elucidating patterns of fish abundance and length specifically associated with LWJ in individual pools. Further research could focus on investigating associations between LWJ and fish in other ecoregional or geomorphic contexts.

We hypothesised that geomorphic setting might influence stream environments and/or typical LWJ in such a way that fish would associate differently with the presence of LWJ in different geomorphic settings. Brook trout was the only assemblage for which abundance was arguably associated with LWJ in pools differently between geomorphic settings in this study. Sampling suggested that for brook trout, fewer fish associated with LWJ in the HRT segment than in other geomorphic settings although LWJ was least abundant in the HRT segment. Large-scale structure has been shown to predict fish distributions in other studies (Lanka et al. 1987; Kocovsky & Carline 2006; Nislow & Lowe 2006); however, this study is the first of which we are aware that considers the predictability of fish abundance and length by LWJ in pools of different stream-corridor-scale geomorphologies in an old-growth forest setting of the eastern USA. To the extent that the results of this study can be generalised to other locations, they suggest that in an anthropogenically unaltered forest, the abundance of brook trout and other fish associated with LWJ is quite variable. It appears, however, that where flows are highest and substrate includes substantial rock with step-pools, brook trout use alternative habitat to LWJ. In areas where flow rates are moderate, substrates tend to not be massive rock (as in the MRT and CLP study segments), and LWJ are relatively large, more brook trout appear to select pools with LWJ than pools without LWJ. It appears that brook trout and other sampled fish favour habitat with good structure, but not necessarily LWJ when other structure is available.

We found a significant but weak relationship between the abundance of wild brook trout and the number of pieces of LW in LWJ that we sampled, with more individuals occurring at LWJ with more pieces. However, as noted, this relationship was due largely to the contribution of a few large LWJ. It appears that LWJ with <20 pieces were not consistently selected by brook trout over pools without LWJ in the Little Carp River. We also found a significant but weak positive relationship between the length of wild brook trout and the volume of wood in the LWJ. It appeared that the size of LWJ pieces was more important for predicting longer brook trout in pools with LWJ than was the number of pieces of LW in the LWJ. However, we excluded the largest LWJ from this study because of the difficulty of sampling fish in them. The results we report are only for the limited number of LWJ we sampled, within the range of LWJ that were possible to effectively sample.

Other studies have reported correspondence between the size of LWJ and fish abundance. Flebbe & Dolloff (1995) reported finding brook trout, rainbow trout and brown trout most frequently in pools with more than four or five pieces of LW. Flebbe (1999) also reported that brook trout and rainbow trout occupied a greater proportion of pools with two or more pieces of LW than pools with one piece or no LW. We found it interesting that the amount of channel spanned by LWJ was not effective at predicting either the abundance or length of wild brook trout relative to similar pools without LWJ. The function of LWJ structure of the size that we studied in pools in the old-growth context of the Little Carp River appears to be limited by the presence of other habitat structure of pools. However, as in previous studies, the size of pieces and complexity of LWJ appear to influence wild brook trout assemblages. It follows that stream-corridor factors that correspond to some degree with wild brook trout abundance and size in pools with LWJ are those that influence the number of pieces of LW and the size of pieces of LW in LWJ in pools. Further assessment of the role of LWJ and geomorphic context remains to be carried out.

## Implications

Stream and forest managers may consider placing LWJ where favoured by stream-corridor-scale geomorphology, with the recognition that LWJ are only one component of many competing fish-habitat structures found in anthropogenically unaltered streams. In keeping with the findings of this study, restoration of natural-type LWJ to pools in geomorphically defined settings would be advanced for brook trout in settings with moderate flows and relatively small-grained substrates or substrates that were not massive rock, such as the MRT and CLP segments in the Little Carp River. Contrarily, installation of geomorphically appropriate LWJ in pools with abundant structure (e.g., in settings with high flows and rocky substrates with step-pools (such as the HRT segment in the Little Carp River) would not generally be expected to positively affect brook trout as much as it would in other settings with less inherent structure.

In the Little Carp River, larger wild brook trout were found everywhere in conjunction with LWJ in pools that we sampled, but this effect was not clearly observed for rainbow trout or introduced young brook trout. LWJ appear to be desired habitat at least for larger brook trout. Assuming that conditions in the Little Carp River represent desired restoration objectives for other streams, monitoring abundance and size of one fish assemblage alone cannot be expected to fully represent the effects of LWJ restoration on all assemblages.

## Acknowledgements

Financial support for this study was provided by a grant from the USDA National Research Initiative Program, USDA Forest Service, and the Ohio Agricultural Research and Development Center (OARDC), The Ohio State University. We thank John Pagel and Jerry Edde of the USDA Forest Service, Adam Beichler and Rebekah Andrus for help with fish sampling, and Hannah Earick for laboratory assistance. Additional thanks to Robert Moeder, Bruce and Kelly Watt, and Herb and Joanne Marutz for field support. We also wish to thank Marie Semko-Duncan and Rachel Rowe who provided laboratory assistance and helped refine the content of the manuscript, and Bert Bishop of OARDC and Susan Durham of Utah State University who provided statistical consultation.

## References

Abbe, T.B. 2000. Patterns, mechanics and geomorphic effects of wood debris accumulations in a forest river system. Seattle, Washington: Ph.D. dissertation, University of Washington.

Angermeier, P.L. & Karr, J.R. 1984. Relationships between woody debris and fish habitat in a small warmwater stream. Transactions of the American Fisheries Society 113: 716–726.

Benke, A.C. & Wallace, J.B. 2003. Influence of wood on invertebrate communities in streams and rivers. In: Gregory, S.V., Boyer, K.L. & Gurnell, A.M., eds. The ecology and management of wood in world rivers. Bethesda, MD: American Fisheries Society, Symposium 37, pp. 149–177.

Bennington, C.C. & Thayne, W.V. 1994. Use and misuse of mixed model analysis of variance in ecological studies. Ecology 75: 717–722.

Berg, N., Carlson, A. & Azuma, D. 1998. Function and dynamics of woody debris in stream reaches in the central Sierra Nevada, California. Canadian Journal of Fisheries and Aquatic Science 55: 1807–1820.

Bergerud, W.A. 1996. Displaying factor relationships in experiments. The American Statistician 50: 228–233.

Binns, N.A. 1994. Long-term responses of trout and macrohabitats to habitat management in a Wyoming headwater stream. North American Journal of Fisheries Management 14: 87–98.

Dolloff, C.A. & Reeves, G.H. 1990. Microhabitat partitioning among stream-dwelling juvenile coho salmon, *Oncorhynchus kisutch*, and dolly varden, *Salvelinus malma*. Canadian Journal of Fisheries and Aquatic Sciences 47: 2297–2306.

Dolloff, C.A. & Warren, M.L. Jr 2003. Fish relationships large wood in small streams. In: Gregory, S.V., Boyer, K.L. & Gurnell, A.M., eds. The ecology and management of wood in world rivers. Bethesda, MD: American Fisheries Society, Symposium 37, pp. 179–193.

Fausch, K.D. & Northcote, T.G. 1992. Large woody debris and salmonid habitat in a small coastal British Columbia stream. Canadian Journal of Fisheries and Aquatic Sciences 49: 682–693.

Flebbe, P.A. 1999. Trout use of woody debris and habitat in Wine Spring Creek, North Carolina. Forest Ecology and Management 114: 367–376.

Flebbe, P.A. & Dolloff, C.A. 1995. Trout use of woody debris and habitat in Appalachian wilderness streams of North Carolina. North American Journal of Fisheries Management 15: 579–590.

Ford, J.E. & Lonzarich, D.G. 2000. Over-winter survival and habitat use by juvenile coho salmon (*Oncorhynchus kisutch*) in two Lake Superior tributaries. Journal of Great Lake Research 26: 94–101.

Frelich, L.E. 2002. Forest dynamics and disturbance regimes. Cambridge, UK: Cambridge University Press.

Goebel, P.C., Pregitzer, K.S. & Palik, B.J. 2003. Geomorphic influences on large wood dam loadings, particulate organic matter and dissolved organic matter in an old-growth northern hardwood watershed. Journal of Freshwater Ecology 18: 479–490.

Goebel, P.C., Pregitzer, K.S. & Palik, B.J. 2012. Influence of flooding and landform properties on riparian plant communities in an old-growth northern hardwood watershed. Wetlands, DOI: 10.1007/s13157-012-0300-1.

Gregory, S.V., Boyer, K.L. & Gurnell, A.M. editors. 2003. The ecology and management of wood in world rivers. Bethesda, MD: American Fisheries Society, Symposium 37.

Kocovsky, P.M. & Carline, R.F. 2006. Influence of landscape-scale factors in limiting brook trout populations in Pennsylvania streams. Transactions of the American Fisheries Society 135: 76–88.

Lanka, R.P., Hubert, W.A. & Wesche, T.A. 1987. Relations of geomorphology to stream habitat and trout standing stock in small Rocky Mountain streams. Transactions of the American Fisheries Society 116: 21–28.

Montgomery, D.R., Collins, B.D., Buffington, J.M. & Abbe, T. B. 2003. Geomorphic Effects of Wood in Rivers. In: Gregory, S.V., Boyer, K.L. & Gurnell, A.M., eds. The ecology and management of wood in world rivers. Bethesda, MD: American Fisheries Society, Symposium 37, pp. 21–47.

Morris, A.E.L. 2005. Influence of stream corridor geomorphology on large wood jams and associated fish assemblages in Upper Michigan. Columbus, OH: Ph.D dissertation, The Ohio State University.

Morris, A.E.L., Goebel, P.C. & Palik, B.J. 2007. Geomorphic and riparian forest influences on characteristics of large wood and large-wood jams in old-growth and second-growth forests in Northern Michigan, USA. Earth Surface Processes and Landforms 32: 1131–1153.

Morris, A.E.L., Goebel, P.C. & Palik, B.J. 2009. Spatial distribution of large wood jams in streams related to stream-valley geomorphology and forest age in northern Michigan. River Research and Applications, DOI: 10.1002/rra.1297.

Nagayama, S., Kawaguchi, Y., Nakano, D. & Nakamura, F. 2009. Summer microhabitat partitioning by different size classes of masu salmon (*Oncorhynchus masou*) in habitats formed by large wood in a large lowland river. Canadian Journal of Fisheries and Aquatic Sciences. 66: 42–51.

Neumann, R.M. & Wildman, T.L. 2002. Relationship between trout habitat use and woody debris in two southern New England streams. Ecology of Freshwater Fish 11: 240–250.

Nislow, K.H. & Lowe, W.H. 2006. Influences of logging history and riparian forest characteristics on macroinvertebrates and brook trout (*Salvelinus fontinalis*) in headwater streams (New Hampshire, U.S.A.). Freshwater Biology 51: 388–397.

Ridgway, M.S. 2008. A roadmap for coasters: landscapes, life histories, and the conservation of brook trout. Transactions of the American Fisheries Society 137: 1179–1191.

Riley, S.C. & Fausch, K.D. 1995. Trout population response to habitat enhancement in six northern Colorado streams. Canadian Journal of Fisheries and Aquatic Science 52: 34–53.

Robinson, C.T., Tockner, K. & Ward, J.V. 2002. The fauna of dynamic riverine landscapes. Freshwater Biology 47: 661–677.

Roni, P. & Quinn, T.P. 2001. Density and size of juvenile salmonids in response to placement of large woody debris in western Oregon and Washington streams. Canadian Journal of Fisheries and Aquatic Sciences 58: 282–292.

Rosgen, D.L. & Silvey, H.L. 1996. Applied river morphology. Pagosa Springs, CO: Wildland Hydrology Books.

Schreiner, D.R., Cullis, K.I., Donofrio, M.C., Fischer, G.J., Hewitt, L., Mumford, K.G., Pratt, D.M., Quinlan, H.R. & Scott, S.J. 2008. Management perspectives on coaster brook trout rehabilitation in the Lake Superior basin. North American Journal of Fisheries Management 28: 1350–1364.

Simondet, J.A. 1997. Seasonal and diel response to habitat complexity by an allopatric population of coastal cutthroat trout. In: Hall, J.D., Bisson, P.A. & Gresswell, R.E., eds. Sea-run cutthroat trout: biology, management and future conservation. Oregon Chapter, Corvallis, Oregon: American Fisheries Society, p. 179.

Steel, E.A., Richards, W.H. & Kelsey, K.A. 2003. Wood and wildlife: benefits of river wood terrestrial and aquatic vertebrates. In: Gregory, S.V., Boyer, K.L. & Gurnell, A.M., eds. The ecology and management of wood in world rivers. Bethesda, MD: American Fisheries Society, Symposium 37, pp. 235–247.

Sundbaum, K. & Näslund, I. 1998. Effects of woody debris on the growth and behavior of brown trout in experimental stream channels. Canadian Journal of Zoology 76: 56–61.

Swanson, F.J. 2003. Wood in rivers: a landscape perspective. In: Gregory, S.V., Boyer, K.L. & Gurnell, A.M., eds. The ecology and management of wood in world rivers. Bethesda, MD: American Fisheries Society, Symposium 37, pp. 291–313.

Warren, D.R. & Kraft, C.E. 2003. Brook trout (*Salvelinus fontinalis*) response to wood removal from high-gradient streams of the Adirondack Mountains (N.Y., U.S.A.). Canadian Journal of Fisheries and Aquatic Sciences 60: 379–389.

Zalewski, M., Lapinska, M. & Bayley, P.B. 2003. Fish relationships with wood in large rivers. In: Gregory, S.V., Boyer, K.L. & Gurnell, A.M., eds. The ecology and management of wood in world rivers. Bethesda, MD: American Fisheries Society, Symposium 37, pp. 195–211.

## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Data used for pool matching.