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Relationships between trout habitat use and woody debris in two southern New England streams

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Abstract – In-stream habitat was measured and trout density was estimated in Merrick Brook (105 habitat units) and the Tankerhoosen River (135 habitat units), Connecticut to determine relationships between habitat use of brook trout *Salvelinus fontinalis* and brown trout *Salmo trutta* and woody debris. In each habitat unit, woody debris was inventoried, and length, width, depth, area, width : depth ratio and undercut bank area were estimated. Trout abundance was estimated by snorkeling. Multiple regression was used to test relationships between trout density and principal components describing habitat unit variables. In Merrick Brook, habitat unit size and shape explained most of the variability in density of brook trout ($<$130 and $\geq$130 mm) and brown trout ($<$150 mm) among habitat units, although principle components describing large woody debris or fine woody debris contributed significantly to variations in density of brook trout ($\geq$130 mm) and brown trout ($<$150 and $\geq$150 mm). In the Tankerhoosen River, fine woody debris explained most of the variability in density of brook trout ($<$130 and $\geq$130 mm), followed by habitat unit size and shape. Both large woody debris and fine woody debris contributed significantly to variations in density of brown trout ($\geq$150 mm). These results suggest that woody debris is an important component of wild trout habitat above that provided by habitat unit shape and size alone.

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Un resumen en español se incluye detrás del texto principal de este artículo.

Introduction

Woody debris is recognized as an important factor contributing to stream habitat and biological diversity. Large woody debris enhances aquatic habitat diversity in streams by creating hydraulic complexity (Sullivan et al. 1987), storing sediment (Megahan 1982; Nakamura & Swanson 1993) and fine organic matter (Bibly & Ward 1991), and creating off-channel habitat (Swanson et al. 1976; Bryant 1982; Beschta & Platts 1986). Woody debris contributes to biological diversity in streams by providing surface area for production of invertebrates (Benke et al. 1985), and cover for various life stages of fishes (Angermeier & Karr 1983; Crispin et al. 1993). Diverse hydrologic characteristics of flow-through channels are an important component of fish habitat (McMahon & Hartman 1989). Different fish species require unique habitat components, such as depth, cover and flow. Moreover, individual species of salmonids have evolved to utilize these diverse habitats throughout their life cycle. Large obstructions in streams, such as logs, rootwads and limbs increase the variation in water velocity, depth and cover, and thus help to provide necessary life-history habitat requirements (Sullivan et al. 1987).

Historically, woody debris has been removed from many North American streams because it was believed to inhibit logging, navigation and drainage (Angermeier & Karr 1983). Stream habitat improvements have been undertaken in many regions where streams lack large woody debris because of land use practices in the watershed, riparian zone clearing, or where direct removal of woody debris from streams was extensive. Habitat improvement for salmonids often consists of installation of logs, tree branches and deflector structures that mimic the effects of naturally occurring large woody debris (Angermeier & Karr 1983).

Forests in southern New England have secondary growth with a mixture of deciduous and coniferous species. Mature forests in this region are approximately 80–100 years old, although younger forests are also present. Consequently, many streams lack input of old, large woody debris that is characteristic of streams draining old-growth forests. Moreover, urbanization and development in rural areas has removed trees that may potentially contribute to the woody debris loading into streams. Habitat alterations, such as stream channelization and removal of riparian vegetation, frequently occur as urban development proceeds within a drainage basin (Scott et al. 1986). The objectives of this study were to: (1) determine the amount and size of woody debris occurring in two Connecticut streams; and (2) compare brook trout *Salvelinus fontinalis* and brown trout *Salmo trutta* use among habitat units with different amounts and sizes of large woody debris.

Materials and methods

Study sites

The study sites selected for this research included the Tankerhoosen River and Merrick Brook, Connecticut. Watershed areas for the Tankerhoosen River and Merrick Brook are 33.2 and 52.8 km^2, respectively. Mean annual stream flows have not been estimated for either stream, but discharge measured during routine fisheries surveys in summer was 0.11 m$^3 \cdot s^{-1}$ in the Tankerhoosen River and 0.12 m$^3 \cdot s^{-1}$ in Merrick Brook. Both streams drain hill-land and second growth mixed deciduous–coniferous forests and both streams support wild populations of brook trout and brown trout (Hagstrom et al. 1994, 1995). The section of the Tankerhoosen River chosen for this study is within the Belding Wild Trout Management Area and is approximately 1.5 km in length. Preliminary observations of the Tankerhoosen River indicated that it supported a large quantity of woody debris and a wide range of woody debris size classes. Types of woody debris present included single logs, rootwads, debris, vegetative cover and brush. The primary substrate types in the Tankerhoosen River are sand and gravel. The section of Merrick Brook chosen for this study begins in the Talbott State Wildlife Management Area and extends upstream approximately 1.5 km. Preliminary observations of Merrick Brook indicated that the stream supported a moderate quantity of woody debris. The primary substrate types in Merrick Brook are gravel and cobble.

Habitat measurements

Habitats within 1.5-km study reaches on each stream were classified into one of three habitat unit types (Hawkins et al. 1993): pools (deep, slow-water); glides (moderate depth and velocity); and riffles (shallow, highly turbulent water). Woody debris in each habitat unit of each stream was inventoried during early summer 1998. All pieces of woody debris that had a portion within the low-flow channel were counted and only the wetted portion of the woody debris was measured. Large woody debris was defined as being ≥ 5 cm in diameter and ≥ 50 cm long. For each piece of large woody debris, total length and three or more diameter measurements were recorded. Surface area was calculated (m^2) for each piece of large woody debris and the total surface area of large woody debris within a habitat unit was calculated as the sum of surface areas of all pieces.

Rootwads were classified separately from large woody debris because of their physical complexity. Rootwads were classified as either rootwads residing completely within the stream channel or as rootwads attached to the stream bank. The length of each rootwad was measured (m) along the longest wet axis.

Fine woody debris was classified by type: brush (single pieces of woody debris that failed to meet the large woody debris size criteria, usually in the form of branches or tree tops); debris (woody debris that also failed to meet the large woody debris size criteria; occurring as debris dams, etc.); fine roots (root systems that failed to meet the minimum 5 cm diameter of rootwads); and vegetative cover (instream portion of live vegetation growing along the stream bank). Length (m) and width (m) dimensions of fine woody debris types were measured to determine total area.

Other habitat features measured in each habitat unit were length, width, area, maximum depth, mean depth, width : depth ratio, dominant substrate type and undercut bank area. Stream measurements followed procedures outlined in McMahon et al. (1996). Habitat unit length was measured along the thalweg of the stream channel. Width (wetted) was measured at three or more equally spaced transects within each habitat unit and habitat unit mean width was calculated from these measurements. Depth was measured at five equally spaced intervals along each transect. These depth measurements were used to calculate habitat unit mean depth. Maximum depth was also measured for each habitat unit. The width : depth ratio of each habitat unit was calculated by dividing mean width by mean depth. Dominant substrate type for each habitat unit was visually classified and coded as sand (1), fine gravel (2), medium gravel (3), course gravel (4), very course gravel (5), small cobble (6), large cobble (7) and boulders (8) based on a classification system of Platts et al. (1983). Undercut banks were measured if they were within 30 cm of the water surface and the water below each undercut bank was at least 15 cm deep (following Hagstrom et al. 1995). Undercut bank area (m^2) was calculated by multiplying total undercut bank length by mean width determined from equally spaced undercut bank width measurements. Ratios of undercut bank area : area, brush area : area, debris area : area, fine root area : area, vegetative area : area, large woody debris area : area and rootwad length : length were calculated to express the relative coverage of these habitat types in each habitat unit.

Fish sampling

During the summer of 1998, data on abundance and sizes of each species of trout in all habitat units of each stream reach were collected using underwater snorkel observation techniques (Baltz et al. 1991; Dolloff et al. 1993; Flebbe & Dolloff 1995). Snorkeling was shown to be an effective technique for estimating abundance and size structure within habitat units of the Tankerhoosen River and Merrick Brook (Wildman 2000). Underwater observations followed procedures outlined by Dolloff et al. (1996). Snorkelers conducted observations during middle daylight hours under good visual conditions. Snorkelers began in a randomly selected habitat unit and proceeded systematically (every fifth habitat unit) upstream, being careful not to disturb fish. This technique enabled snorkelers to sample habitat units throughout the study reaches each day that the snorkeling survey was conducted. In each habitat unit the observer recorded the total number of trout of each species observed in the habitat unit and the length category of each fish encountered. All trout were classified as either substock- or stock-length following standard length categories provided in Anderson & Neumann (1996). Brook trout that were <130 mm (total length) were classified as substock-length, and brook trout ≥130 mm were classified as stock-length. Brown trout that were <150 mm (total length) were classified as substock-length, and brown trout ≥150 mm were classified as stock-length. For each habitat unit, trout abundance data were adjusted to density on a per area basis (number of trout/m^2).

Data analysis

Distributions of trout density and habitat data were assessed for univariate and bivariate normality, and transformations were performed to improve normality. In both streams, distributions of trout density and woody debris variables were most improved by a square-root transformation, and distributions of dominant substrate type were most improved by an inverse transformation. Distributions of habitat unit dimension measurements were best improved using a $\log_{10}$ transformation. A $\log_{10} X + 1$ transformation was used for undercut bank area : area ratio owing to the presence of zero values.

The relationships between trout density and habitat unit variables were examined in two ways. First, simple regression was used to determine correlations between trout density and each habitat unit variable. Owing to the large number of correlation tests being performed for each trout species and size group (14 habitat variables in Merrick Brook and 15 habitat variables in the Tankerhoosen River) the critical level of significance was based on a Bonferroni correction (adjusted level of significance: $P = 0.004$ in Merrick Brook, and $P = 0.003$ in the Tankerhoosen River).

Second, multiple regression (stepwise) was used to test relationships between trout density and principal components calculated from habitat unit variables. Intercorrelations between independent variables in multiple regression analysis can interfere with the interpretation of the selected regression model. Principle components analysis can be used to summarize patterns of intercorrelations among independent variables, and to determine coherent subgroups of variables that are uncorrelated (Tabachnick & Fidell 1989). Thus, in this case, principle components analysis was used to aid in the selection of uncorrelated variable subsets describing habitat. Principal components with eigenvalues greater than 1.0 were retained and rotated orthogonally (VARIMAX rotation) to improve the interpretability and scientific utility of the solution (Tabachnick & Fidell 1989). Stepwise multiple regression was used to test relationships between trout density and the factor scores generated by the principal component analysis.

Results

Merrick Brook

Trout abundance and habitat variables were measured in 105 habitat units in Merrick Brook (27 pools, 43 glides, and 35 riffles) (Table 1). Density of substock-length brook trout was significantly ($P < 0.004$) correlated with maximum depth, mean depth, width : depth, and dominant substrate type (Table 2). Density of stock-length brook trout was significantly correlated with several habitat variables that described habitat unit dimensions, dominant substrate type, and woody debris. Density of substock-length brown trout was significantly correlated with habitat unit width. Density of stock-length brown trout was significantly correlated with the majority of habitat unit variables (Table 2).

The first four principal components calculated from Merrick Brook habitat unit variables accounted for approximately 77% of the variation in the entire habitat unit variable data set (Table 3). Principal component 1 represented habitat unit shape (maximum and mean depth, width : depth ratio, undercut bank area : area ratio and rootwad length : length ratio), principal component 2 represented habitat unit size (habitat unit length, width and area), principal component 3 represented large woody debris (number of large woody debris pieces, large woody debris area : area ratio and debris area : area ratio), and principal component 4 represented fine woody debris (brush area : area ratio and fine root area : area ratio). Density of each species and size group of trout was significantly ($P < 0.05$) correlated with principal component 1 (shape) and 2 (size) (Table 4). Density of stock-length brook trout was also significantly correlated with principal component 3 (large woody debris) and density of stock-length brown trout was significantly correlated with principal components 3 (large woody debris) and 4 (fine woody debris) (Table 4).

In stepwise multiple regression models using the four principal components as independent variables, a larger amount of variation in trout density among habitat units was explained for stock-length trout than for substock-length trout (Table 5). Density of substock-length brook trout was significantly related to principal components 1 (shape) and 2 (size) ($R^2 = 0.11$; $P = 0.0033$); density of stock-length brook trout was significantly related to principal components 1–3 (large woody debris) ($R^2 = 0.41$; $P < 0.0001$). Density of substock-length brown trout was related to principal components 1, 2 and 4 (fine woody debris) ($R^2 = 0.17$; $P = 0.0002$); density of stock-length brown trout was significantly related to principal components 1–4 ($R^2 = 0.54$; $P < 0.0001$).

Table 1. Mean and range of trout density and habitat variables measured in habitat units in Merrick Brook ($N = 105$) and Tankerhoosen River ($N = 134$), Connecticut.

	Merrick Brook		Tankerhoosen River	
Habitat variable	Mean	Range	Mean	Range
Length (m)	13.1	2.4–46.0	10.7	1.3–43.0
Width (m)	4.7	1.9–11.0	4.1	0.9–7.6
Area (m^2)	67.0	9.0–302.1	47.9	4.4–274.3
Maximum depth (cm)	34.4	6.0–128.0	35.4	7.0–100.0
Mean depth (cm)	18.5	4.6–81.3	20.5	5.4–56.5
Width: depth	38.1	7.5–177.4	26.5	4.5–108.4
Dominant substrate	5.7	2–9	4.2	1–8
Undercut bank area : area	2.2	0–17.5	3.3	0–34.0
Brush area : area	0.01	0–0.09	0.02	0–0.91
Debris area : area	0.02	0–0.25	0.04	0–0.73
Fine root area : area	0.01	0–0.35	0.02	0–0.21
Vegetative area : area	–	–	0.01	0–0.34
Rootwad length : length	0.18	0–1.09	0.11	0–0.57
Large woody debris (*N*)	2.2	0–25	1.2	0–10
Large woody debris area : area	0.01	0–0.15	0.02	0–0.24
Brook trout density (*N*/m^2)				
Substock ($<$130 mm)	0.003	0–0.039	0.038	0–0.417
Stock ($\geq$130 mm)	0.011	0–0.145	0.015	0–0.305
Brown trout density (*N*/m^2)				
Substock ($<$150 mm)	0.114	0–0.653	0.125	0–0.641
Stock ($\geq$150 mm)	0.031	0–0.242	0.029	0–0.172

No vegetative cover was observed in Merrick Brook.

Table 2. Correlations (*r*) between brook trout and brown trout density [square root (number/m^2)] and habitat unit variables in Merrick Brook and the Tankerhoosen River, Connecticut.

	Brook trout				Brown trout			
	<130 mm		≥130 mm		<150 mm		≥150 mm	
Habitat variable	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*
Merrick Brook								
Log$_{10}$ length (m)	0.23	0.0201	0.47	<0.0001			0.45	<0.0001
Log$_{10}$ width (m)					−0.39	<0.0001	−0.19	0.0486
Log$_{10}$ area (m^2)			0.43	<0.0001	−0.26	0.0069	0.31	0.0012
Log$_{10}$ maximum depth (cm)	0.30	0.0016	0.59	<0.0001			0.70	<0.0001
Log$_{10}$ mean depth (cm)	0.32	0.0008	0.61	<0.0001			0.68	<0.0001
Log$_{10}$ width: depth	−0.32	0.0010	−0.51	<0.0001	−0.22	0.0244	−0.70	<0.0001
Inverse dominant substrate	0.36	0.0002	0.51	<0.0001			0.19	0.0483
Log$_{10}$ undercut bank area : area			0.30	0.0017			0.47	<0.0001
SQRT brush area : area			0.31	0.0012			0.28	0.0037
SQRT debris area : area			0.43	<0.0001			0.41	<0.0001
SQRT fine root area : area					0.21	0.0338	0.30	0.0020
SQRT rootwad length : length			0.36	0.0002			0.51	<0.0001
SQRT LWD (*N*)			0.49	<0.0001			0.39	<0.0001
SQRT LWD area : area			0.39	<0.0001			0.44	<0.0001
Tankerhoosen River								
Log$_{10}$ length (m)	0.27	0.0016	0.44	<0.0001			0.30	0.0005
Log$_{10}$ width (m)					−0.45	<0.0001		
Log$_{10}$ area (m^2)	0.26	0.0028	0.39	<0.0001	−0.26	0.0024	0.23	0.0088
Log$_{10}$ maximum depth (cm)	0.21	0.0166	0.45	<0.0001			0.55	<0.0001
Log$_{10}$ mean depth (cm)	0.22	0.0100	0.48	<0.0001			0.59	<0.0001
Log$_{10}$ width: depth			−0.36	<0.0001	−0.30	0.0004	− 0.52	<0.0001
Inverse dominant substrate							0.22	0.0101
Log$_{10}$ undercut bank area : area							0.36	<0.0001
SQRT brush area : area	0.38	<0.0001	0.37	<0.0001			0.20	0.0190
SQRT debris area : area							0.18	0.0340
SQRT vegetative area : area	0.32	0.0002	0.35	<0.0001				
SQRT fine root area : area			0.18	0.0412			0.21	0.0170
SQRT rootwad length : length	0.20	0.0194	0.36	<0.0001			0.32	0.0001
SQRT LWD (*N*)	0.18	0.0335	0.20	0.0197			0.31	0.0003
SQRT LWD area : area							0.29	0.0005

SQRT = square root, LWD = large woody debris.

Tankerhoosen River

Trout abundance and habitat variables were measured in 134 habitat units in the Tankerhoosen River (26 pools, 60 glides and 48 riffles) (Table 1). In the Tankerhoosen River, density of substock-length brook trout was significantly ($P < 0.003$) correlated with habitat unit length, area, brush area : area ratio and vegetative area : area ratio (Table 2). Density of stock-length brook trout was significantly correlated with variables describing habitat unit dimensions and brush area : area ratio, vegetative area : area ratio and rootwad length : length ratio. Density of substock-length brown trout was significantly correlated with habitat unit width, area and width : depth ratio. Density of stock-length brown trout was correlated with the majority of habitat unit variables.

The first five principal components calculated from Tankerhoosen River habitat unit variables accounted for approximately 74% of the variation in the entire habitat unit variable data set (Table 3). Principal component 1 represented habitat unit shape (width, maximum and mean depth, width : depth ratio and undercut bank area : area ratio), principal component 2 represented habitat unit size (length and area), principal component 3 represented large woody debris (number of large woody debris pieces, large woody debris area : area ratio and debris area : area ratio), and principal component 4 represented fine woody debris (brush area : area ratio and vegetative area : area ratio). In addition, principal component 5 (fine root area : area ratio) was identified, most likely owing to the larger amounts of fine root systems found in Tankerhoosen River compared to Merrick Brook.

Density of substock-length brook trout was significantly ($P < 0.05$) correlated with principal components 2 (size) and 4 (fine woody debris) (Table 4). Density of stock-length brook trout was

Table 3. Structure of rotated principal components calculated from the variables describing habitat units in Merrick Brook and the Tankerhoosen River, Connecticut.

	Principal components				
Variable	1 (Shape)	2 (Size)	3 (LWD)	4 (FWD)	5 (fine root)
Merrick Brook					
Log$_{10}$ length (m)		0.77			
Log$_{10}$ width (m)		0.65			
Log$_{10}$ area (m^2)		0.92			
Log$_{10}$ maximum depth (cm)	0.76				
Log$_{10}$ mean depth (cm)	0.78				
Log$_{10}$ width: depth	−0.91				
Log$_{10}$ undercut bank area : area	0.75				
SQRT brush area : area				0.70	
SQRT. debris area : area			0.73		
SQRT fine root area : area				0.77	
SQRT rootwad length : length	0.71				
SQRT LWD (*N*)			0.81		
SQRT LWD area : area			0.85		
% of variance explained	44.6	16.0	8.6	7.7	
Tankerhoosen River					
Log$_{10}$ length (m)		0.84			
Log$_{10}$ width (m)	0.63				
Log$_{10}$ area (m^2)		0.96			
Log$_{10}$ maximum depth (cm)	0.69				
Log$_{10}$ mean depth (cm)	0.75				
Log$_{10}$ width: depth	−0.97				
SQRT brush area : area				0.85	
Log$_{10}$ undercut bank area : area	−0.63				
SQRT vegetative area : area				0.85	
SQRT debris area : area			0.61		
SQRT fine root area : area					0.82
SQRT LWD (*N*)			0.87		
SQRT LWD area : area			0.91		
% of variance explained	31.7	15.1	10.8	9.2	7.6

Only factor loadings with an absolute value of 0.6 or greater are shown. SQRT = square root, LWD = large woody debris, FWD = fine woody debris.

significantly correlated with principal components 1 (shape), 2 and 4. Density of substock-length brown trout was significantly correlated with principal components 1 and 2. Density of stock-length brown trout was significantly correlated with principal components 1–3 (large woody debris). Trout density was not correlated to principal component 5.

In stepwise regression models using the four principal components as independent variables, a larger amount of variation in trout density was explained for stock-length trout than for

Table 4. Correlations (*r*) between brook trout and brown trout density [square root (number/m^2)] and principal components in Merrick Brook and Tankerhoosen River, Connecticut.

Principal component	Brook trout				Brown trout			
	<130 mm		≥130 mm		<150 mm		≥150 mm	
	r	*P*	*r*	*P*	*r*	*P*	*r*	*P*
Merrick Brook								
1 (Shape)	0.25	0.0099	0.38	<0.0001	0.24	0.0121	0.63	<0.0001
2 (Size)	0.21	0.0331	0.41	<0.0001	−0.29	0.0023	0.20	0.0460
3 (Large woody debris)			0.30	0.0018			0.22	0.0221
4 (Fine woody debris)							0.23	0.0163
Tankerhoosen River								
1 (Shape)			−0.33	<0.0001	−0.32	0.0002	−0.51	<0.0001
2 (Size)	0.22	0.0118	0.37	<0.0001	−0.28	0.0011	0.19	0.0275
3 (large woody debris)							0.24	0.0047
4 (fine woody debris)	0.41	<0.0001	0.43	<0.0001				

LWD = large woody debris, FWD = fine woody debris. Structure of principal components is listed in Table 3.

Table 5. Results of stepwise multiple regression analysis between brook trout and brown trout density [square root (number/m^2)] and rotated principal components of habitat unit variables in Merrick Brook, Connecticut.

Principal component	Partial Slope	r^2	Model P	Model R^2	Model Intercept
Brook trout <130 mm					
1 (Shape)	0.012	0.06			
2 (Size)	0.010	0.05			
Model			0.0033	0.11	0.018
Brook trout ≥130 mm					
2 (Size)	0.037	0.17			
1 (Shape)	0.035	0.15			
3 (LWD)	0.027	0.09			
Model			<0.0001	0.41	0.050
Brown trout <150 mm					
2 (Size)	− 0.039	0.08			
1 (Shape)	0.032	0.06			
4 (FWD)	0.022	0.03			
Model			0.0002	0.17	0.312
Brown trout ≥150 mm					
1 (Shape)	0.078	0.39			
3 (LWD)	0.028	0.06			
4 (FWD)	0.029	0.05			
2 (Size)	0.024	0.04			
Model			<0.0001	0.54	0.127

LWD = large woody debris, FWD = fine woody debris. Structure of principal components is listed in Table 3.

substock-length trout (Table 5). Density of substock-length brook was related to principal components 4 (fine woody debris) and 2 (size) ($R^2 = 0.21$; $P < 0.0001$); density of stock-length brook trout was related to principal components 4, 2 (size) and 1 (shape) ($R^2 = 0.43$; $P < 0.0001$). Density of substock-length brown trout was related to principal components 1 and 2 ($R^2 = 0.18$; $P < 0.0001$); density of stock-length brown trout was related to principal components 1–4 ($R^2 = 0.38$; $P < 0.0001$).

Discussion

In most cases, the greatest amount of variation in density of brook trout and brown trout among habitat units was explained by variables describing habitat unit dimensions (shape and size), although woody debris variables also significantly contributed to the variation in trout density among habitat units. For substock- and stock-length brook trout and stock-length brown trout, density increased with increasing size of habitat units in both streams. However, density of substock-length brown trout increased with decreasing size of habitat units in both streams. When habitat unit shape was a significant contributor to trout density, density increased with increasing habitat unit depth and decreasing width : depth ratio. This indicated that trout density was greatest in deep, narrow habitat units.

Factor loadings of habitat variables in the rotated component matrix indicated that rootwad length : length ratio, undercut bank area : area ratio, depth and width : depth ratio were strongly correlated to principal component 1 (shape) in Merrick Brook. In most cases, where one or more rootwads was present in a habitat unit, the rootwads were attached to the stream bank possibly resulting in increased bank stability. This stability may lead to undercutting of stream banks and decreased width : depth ratios. Because rootwad length : length ratio was combined with other habitat unit shape variables in principal component 1, the amount of variation in trout density attributed to rootwads alone in Merrick Brook could not be explained. However, rootwads attached to the stream bank may have influenced habitat unit shape and provided cover, thus providing an important habitat function. In the Tankerhoosen River, percent undercut bank area : area ratio and width : depth ratio also loaded heavily on principle component 1 describing habitat unit shape, but rootwad length : length ratio did not. Thus, it appeared that root wads were not contributing to habitat unit shape in the Tankerhoosen River as much as in Merrick Brook.

In the Tankerhoosen River, habitat unit shape may be linked more to drainage basin factors than on Merrick Brook, where rootwads attached to the stream bank may be a stronger factor influencing habitat unit shape. Lanka et al. (1987) studied the relationships between geomorphology, stream habitat and trout standing stock in small Rocky Mountain streams and found high canonical correlations between geomorphic variates (reach elevation, stream order, basin area, channel slope and others) and stream habitat variables (channel width, velocity, average depth, width : depth ratio and substrate) indicating that stream habitat was a function of geologic processes within the drainage basins. They were able to improve a regression model between trout standing stock and stream habitat variables by including geomorphic variables. Most of the stream variables used by Lanka et al. (1987) were included in principal component 1 (shape), and to a lesser extent in principal component 2 (size). Lanka et al. (1987) concluded that the relationship between drainage basin geomorphology and trout standing stock was the result of a functional link between features of a drainage basin and stream habitat. If this functional link between drainage basin and habitat unit shape exists on Merrick Brook and the Tankerhoosen River, then

Table 6. Results of stepwise multiple regression analysis between brook trout and brown trout density [square root (number/m^2)] and rotated principal components of habitat unit variables in the Tankerhoosen River, Connecticut.

Principal component	Partial Slope	r^2	Model P	Model R^2	Model Intercept
Brook trout $<$130 mm					
4 (FWD)	0.060	0.16			
2 (Size)	0.032	0.05			
Model			<0.0001	0.21	0.127
Brook trout $\geq$130 mm					
4 (FWD)	0.046	0.18			
2 (Size)	0.040	0.14			
1 (Shape)	-0.036	0.11			
Model			<0.0001	0.43	0.062
Brown trout $<$150 mm					
2 (Size)	-0.046	0.10			
1 (Shape)	-0.053	0.08			
Model			<0.0001	0.18	0.314
Brown trout $\geq$150 mm					
1 (Shape)	-0.063	0.26			
3 (LWD)	0.030	0.06			
2 (Size)	0.024	0.04			
4 (FWD)	0.019	0.02			
Model			<0.0001	0.38	0.117

LWD = large woody debris, FWD = fine woody debris. Structure of principal components is listed in Table 3.

the relationships between trout density and woody debris on the two streams may be affected differently. Habitat unit variables grouped by the principal component analysis into principal component 1 (shape) for each stream may be the result of a link between drainage basin factors and stream habitat.

The principle component describing fine woody debris contributed to most of the variability in density of brook trout among habitat units in the Tankerhoosen River (Table 6). Fine woody debris was more prevalent in the Tankerhoosen River than in Merrick Brook. Because the Tankerhoosen River is smaller than Merrick Brook, peak velocities may be lower resulting in more fine woody debris being retained in the Tankerhoosen River. Fine woody debris has been shown to provide refuge from predators and current (Culp et al. 1996). Culp et al. (1996) found a significant increase in rainbow trout *Oncorhynchus mykiss* abundance at treatment sites with fine woody debris additions when compared to untreated sites.

In multiple regression models using principal components describing habitat units, large woody debris contributed to variation in density of stock-length brook trout and brown trout among habitat units, but not to variation in density of sub-stock-length brook and brown trout. Lewis (1969) found that cover was the most important factor influencing density of brown trout in a Montana stream. Flebbe & Dolloff (1995) found that in Appalachian streams, brook trout and brown trout were always found in habitat units that contained large woody debris. In a study of over 900 Connecticut streams, Hagstrom et al. (1997) found that channel morphometry and cover were important influences on the abundance of older brown trout. The value of cover is probably related to a fish's security and the photo-negative response of trout causing them to seek out areas with overhead cover (Gibson & Keenleyside 1966).

The percentage of variance in trout density among habitat units explained by the variables measured in this study varied considerably among species and size groups of trout, and most relationships were moderate. Factors other than those investigated in this study, such as redd densities, local stream temperature, angler harvest, tree shading, experimental scale and local water velocities may also have caused differences in trout densities among habitat units in Merrick Brook and the Tankerhoosen River. Beard & Carline (1991) found that redd densities in stream reaches accounted for 53–56% of the variation in catches of age-0 and older brown trout, suggesting that trout expressed site fidelity to spawning areas. Variability in temperature between habitat units may have been present thereby creating cold-water thermal refuges that may have attracted and congregated trout. If this was the case in the streams in this study, then high, localized trout densities resulting from spawning site fidelity or thermal refuges may have confounded results. In the absence of redd and habitat unit temperature data, spatial variation in trout density was assessed by plotting density along a longitudinal profile of each river; no localized patterns of higher densities within specific habitat units or stream reaches were on either stream. Thus, possible influences of redd densities or localized thermal refuges on trout density was not detected.

The Tankerhoosen River is subject to catch-and-release regulations; however, angler harvest of adult wild trout in Merrick Brook was estimated to be 37.5% in 1996 (Hagstrom et al. 1997). A plot of trout density in relation to stream access areas in Merrick Brook revealed no trends in decreasing densities in proximity to access areas. Thus, angler harvest did not appear to be an important factor influencing results.

Shading and canopy cover may contribute to variations in density among habitat units or stream reaches. Although Merrick Brook had consistently closed canopy throughout the study reach, the Tankerhoosen River had a section (approximately 250 m in length) that lacked canopy. Keith et al. (1998) found that the value of canopy and shading over a stream may be species or age-class dependent. Age-0 chinook salmon *O. tshawytscha* demonstrated a preference for shaded sections of an artificial channel (Meehan et al. 1987). However, the initial carrying capacity of experimental channels in British Columbia for coho salmon *O. kisutch* fry was less with shade added; the young coho salmon appeared to avoid areas of dense shade. No localized patterns of higher densities within stream reaches on either stream was observed, indicating that if a relationship existed between trout density and overhead canopy in this study, it went unexplained.

Another factor that may have contributed to the level of significance observed in our study was the scale of the experimental unit. Although the habitat unit scale (i.e. pool, riffle, glide) is valuable for describing localized habitat, it does not account for habitat connectivity and trout habitat use within a larger stream reach. The habitat unit scale may have been too small to detect density variations within and among reaches of streams that may be used during diel or other periodic movements for routine activities. Trout may use a variety of habitat units during a 24-h period, providing there is acceptable access to and from each habitat unit. Bunnell et al. (1998) found that large brown trout moved greater distances than small brown trout in a southern Appalachian river, and that hourly movement patterns differed seasonally. Brown trout exhibited the greatest total distance moved and the largest diel range during the fall, possibly associated with a spawning migration. They found that during summer, significant movements did not occur and that most brown trout exhibited restricted diel movements within a single riffle-pool or run-pool sequence. The magnitude of diel movements by riverine fish such as brown trout may be a function of the size of the habitat which provides adequate feeding and resting sites (Bunnell et al. 1998).

Velocity measurements were not included in this study, primarily because we were concentrating on structural habitat variables. However, velocity and changes in velocity, have been shown to be important factors influencing trout habitat use (Fausch 1984; Heggenes 1988; Heggenes & Saltveit 1990). In the present study, some variation in trout density owing to the current velocity may have been accounted for by velocity-related habitat variables such as habitat unit width, depth, dominant substrate type, and woody debris. We recommend that future studies investigating trout habitat use should include water velocity measurements.

Interactions of trout with other species might contribute to habitat use beyond the effects of physical habitat variables alone. In a Swedish study, Naaslund et al. (1998) found that brown trout living under intense pressure from other species remained in riffle habitats throughout their life cycle, although those under moderate pressures from other species used slow-flowing habitats. Large brown trout were found in all three habitat unit types in Merrick Brook and in the Tankerhoosen River, suggesting that brown trout habitat use was not influenced by other species. DeWald & Wilzbach (1992) found that microhabitat location and vertical distribution of brook trout within experimental stream channels shifted in the presence of hatchery-raised brown trout, although emigration from stream channels by brook trout was small. Correlations between brook trout density and brown trout density, when present, were positive in Merrick Brook and the Tankerhoosen River, indicating that if competitive or predatory interactions between the two species were present, they were not distinguishable.

Another factor affecting the relationships between habitat and trout density may have been the method used to sample trout. Snorkel surveys have gained acceptance as a valid sampling technique to estimate salmonid density (Zubik & Fraley 1988), size structure (Thurow & Schill 1996; Mullner et al. 1998) and habitat use (Flebbe & Dolloff 1995). Although some of the habitat units snorkeled during this study were fairly shallow; the water was generally deep enough to submerge a mask in the shallowest conditions. In a separate study, Wildman (2000) found that snorkeling was an effective sampling technique for estimating abundance and size structure in the Tankerhoosen River and Merrick Brook; however, correlations between abundance estimated by snorkeling and electrofishing were generally stronger for large trout compared to small trout. Some regression equations that predicted electrofishing depletion estimates from snorkel counts were significantly improved with the addition of independent variables describing large woody debris. Thus, in this study, habitat units with woody debris may have had more trout than actually counted by snorkeling.

The results of this study suggest that in Merrick Brook and the Tankerhoosen River, large woody debris and fine woody debris contributed significantly to wild trout habitat above and beyond that provided by habitat unit shape and size alone, and in Merrick Brook, habitat unit shape and a form of large woody debris (rootwads) may be implicitly linked. Because both of these streams would be considered non-degraded compared to many southern New England streams, the relationship between trout density and woody debris may be stronger in streams with degraded or poor habitat, where woody debris may act to compensate for poor channel shape and form. Both of these streams drain secondary-growth forests and the recruitment of woody debris to the stream channel should increase as the forest continues to mature. This benefit to habitat can only be realised if steps are taken to ensure that woody debris recruitment to stream channels continues.

Resumen

1. Con el fin de determinar relaciones entre el uso de habitat por *Salvelinus fontinalis* y *Salmo trutta* y restos de Madera, estimamos densidades de truchas junto a medidas de habitat en dos rios de Cunnecticut (USA): Merrick Brook (105 unidades de habitat) y Tankerhoosen (135 unidades de habitat). En cada unidad de habitat, inventariamos los restos de Madera y ademas estimamos la longitud, anchura, profundidad, proporción anchura-profundidad y area colateral. La abundancia de truchas fue estimada por buceo. Utilizamos regresiones multiples para analizar las relaciones entre la densidad de truchas y los components principales que describen las variables de unidad de habitat.
2. En Merrick brook, el tamaño y la forma de las unidades de habitat explicaron la mayor parte de la variabilidad en la densidad de *Salvelinus* <130 y >130 mm y de *S. trutta* truchas <150 mm, entre unidades de habitat, aunque los components principales describieron que tanto restos de madera pequeños como grandes contribuyeron tambien significativamente a las variaciones en la densidad de *Salvelinus* <130 mm y de *S. trutta* <150 y >150 mm. En el rio Tankerhoosen, restos de madera delgados explicaron la mayor parte de la variabilidad en la densidad de *Salvelinus* <130 y >130 mm seguido por el tamaño y la forma de la unidad de habitat. Tambien los restos de madera tanto delgados como gruesos contribuyeron significativamente a las variaciones en densidad de *S. trutta* >150 mm.
3. Estos resultados sugieren que los restos de madera son un componente importante del habitat de truchas por encima del tamaño y la forma del habitat.

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References

Anderson, R.O. & Neumann, R.M. 1996. Length, weight, and associated structural indices. In: Murphy B.R. & Willis, D.W. eds. Fisheries techniques, 2nd edn. Bethesda, Maryland: American Fisheries Society, pp. 447–482

Angermeier, P.L. & Karr, J.R. 1983. Relationships between woody debris and fish habitat in a small warmwater stream. Transactions of the American Fisheries Society 113: 716–726.

Baltz, D.M., Vondracek, B., Brown, L.R. & Moyle, P.B. 1991. Seasonal changes in microhabitat selection by rainbow trout in a small stream. Transactions of the American Fisheries Society 120: 166–176.

Beard, T.D. Jr & Carline, R.F. 1991. Influence of spawning and other stream habitat features on spatial variability of wild brown trout. Transactions of the American Fisheries Society 120: 711–722.

Benke, A.C., Henry, R.L., III, Gillespie, D.M. & Hunter, R.J. 1985. Importance of snag habitat for animal production in southeastern streams. Fisheries (Bethesda) 10(5): 8–13.

Beschta, R.L. & Platts, W.S. 1986. Morphological features of small streams: significance and function. Water Resources Bulletin 22: 369–379.

Bibly, R.E. & Ward, J.W. 1991. Characteristics and function of large woody debris in streams draining old-growth, clear-cut, and second-growth forests in southwestern Washington. Canadian Journal of Fisheries and Aquatic Sciences 48: 2499–2508.

Bryant, M.D. 1982. Organic debris in salmonid habitat in southeast Alaska: measurement and effects. In: Armantrout N.B., ed. Acquisition and utilization of aquatic habitat inventory information. Western Division, Bethesda, Maryland: American Fisheries Society. pp. 62–73.

Bunnell, D.B., Jr, Isely, J.J., Burrell, K.H. & Van Lear, D.H. 1998. Diel movement of brown trout in a Southern Appalachian river. Transactions of the American Fisheries Society 127: 630–636.

Crispin, V., House, R. & Roberts, D. 1993. Changes in instream habitat, large woody debris, and salmon habitat after the reconstructing of a coastal Oregon stream. North American Journal of Fisheries Management 13: 96–102.

Culp, J.M., Scrimgeour, G.J. & Townsend, G.D. 1996. Simulated fine woody debris accumulations in a stream increase rainbow trout fry abundance. Transactions of the American Fisheries Society 125: 472–479.

DeWald, L. & Wilzbach, M.A. 1992. Interactions between native brook trout and hatchery brown trout: effects on habitat use, feeding, and growth. Transactions of the American Fisheries Society 121: 287–296.

Dolloff, C.A., Hankin, D.G. & Reeves, G.H. 1993. Basinwide estimation of habitat and fish populations in streams. USDA Forest Service. General Technical Report SE-83.

Dolloff, C.A., Kershner, J. & Thurow, R. 1996. Underwater observation. In: B.R. Murphy & Willis, D.W., eds. Fisheries Techniques, 2nd edn. Bethesda, Maryland: American Fisheries Society. pp. 533–554.

Fausch, K.D. 1984. Profitable stream positions for salmonids relating specific growth rate to net energy gain. Canadian Journal of Zoology 62: 441–451.

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.

Gibson, R.J. & Keenleyside, M.H.A. 1966. Responses to light of young Atlantic salmon, *Salmo salar*, and brook trout, *Salvelinus fontinalis*. Journal of the Fisheries Research Board of Canada 23: 1007–1024.

Hagstrom, N.T., Humphreys, M. & Hyatt, W.A. 1994. A survey of Connecticut streams and rivers – lower Thames River, Pawcatuck River, and Eastern Coastal Drainages. Federal Aid in Sport Fish Restoration Progress Report

F-66-R-6. Connecticut Department of Environmental Protection, Hartford.

Hagstrom, N.T., Humphreys, M. & Hyatt, W.A. 1995. A Survey of Connecticut Streams and Rivers – Upper Thames River Drainage. Federal Aid in Sport Fish Restoration Progress Report F-66-R-7. Connecticut Department of Environmental Protection, Hartford.

Hagstrom, N.T., Humphreys, M. & Hyatt, W.A. 1997. A Survey of Connecticut Streams and Rivers – Statewide Summary. Federal Aid in Sport Fish Restoration Progress Report F-66-R-Final Report. Connecticut Department of Environmental Protection, Hartford.

Hawkins, C.P. & 10 Co-authors. 1993. A hierarchical approach to classifying stream habitat features. Fisheries 18: 3–12.

Heggenes, J. 1988. Effects of short-term flow fluctuations on displacement of, and habitat use by, brown trout in a small stream. Transactions of the American Fisheries Society 117: 336–344.

Heggenes, J. & Saltveit, S.J. 1990. Seasonal and spatial microhabitat selection and segregation in young Atlantic salmon, *Salmo salar* L. & brown trout, *Salmo trutta* L., in a Norwegian River. Journal of Fish Biology 36: 707–720.

Keith, R.M., Bjornn, T.C., Meehan, W.R., Hetrick, N.J. & Brusven, M.A. 1998. Response of juvenile salmonids to riparian and instream cover modifications in small streams flowing through second-growth forests of Southeast Alaska. Transactions of the American Fisheries Society 127: 889–907.

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.

Lewis, S.L. 1969. Physical factors influencing fish populations in pools of a trout stream. Transactions of the American Fisheries Society 98: 14–22.

McMahon, T.E. & Hartman, G.F. 1989. Influence of cover complexity and current velocity on winter habitat use by juvenile coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 46: 1551–1557.

McMahon, T.E., Zale, A.V. & Orth, D.J. 1996. Aquatic habitat measurements. In: Murphy, B.R. & Willis, D.W., eds. Fisheries techniques, 2nd edn. Bethesda, Maryland: American Fisheries Society, pp. 83–120.

Meehan, W.R., Brusven, M.A. & Ward, J.F. 1987. Effects of artificial shading on distribution and abundance of juvenile chinook salmon (*Onchorhynchus tshawytscha*). Great Basin Naturalist 47: 22–31.

Megahan, W.F. 1982. Channel sediment storage behind obstructions in forested drainage basins draining the granitic bedrock of the Idaho Batholith. In: Swanson, et al., eds. Sediment budgets and routing in forested drainage basins. USDA Forest Service, Pacific Northwest Forest and Range Experiment Station PNW-141. pp. 114–142.

Mullner, S.A., Hubert, W.A. & Wesche, T.A. 1998. Snorkeling as an alternative to depletion electrofishing for estimating abundance and length-class frequencies of trout in small streams. North American Journal of Fisheries Management 18: 947–953.

Naaslund, I., Degerman, E. & Nordwall, F. 1998. Brown trout (*Salmo trutta*) habitat use and life history in Swedish streams: possible effects of biotic interactions. Canadian Journal of Fisheries and Aquatic Sciences 55: 1034–1042.

Nakamura, T. & Swanson, F.J. 1993. Effects of coarse woody debris on morphology and sediment storage of a mountain stream system in western Oregon. Earth Surface Processes and Landforms 18: 43–61.

Platts, W.S., Megahan, W.F. & Minshall, G.W. 1983. Methods for evaluating stream, riparian, and biotic conditions. USDA Forest Service. General Technical Report INT-138.

Scott, J.B., Steward, C.R. & Stober, Q.J. 1986. Effects of urban development on fish population dynamics in Kelsey Creek. Washington. Transactions of the American Fisheries Society 115: 555–567.

Sullivan, K., Lisle, T.E., Dolloff, C.A., Grant, G.E. & Reid, L.M. 1987. Stream channels: the link between forests and fishes, pp. 39–97In: Salo, E.O. & Cundy, T.W., eds. Streamside management: forestry and fishery interactions. University of Washington, Seattle.

Swanson, F.J., Lienkaemper, G.W. & Sedell, J.R. 1976. History, physical effects, and management implications of large organic debris in western Oregon streams. USDA Forest Service. General Technical Report PNW-69.

Tabachnick, B.G. & Fidell, L.S. 1989. Using Multivariate Statistics, 2nd edn. New York: Harper/Collins Publishers Inc.

Thurow, R.F. & Schill, D.J. 1996. Comparison of day snorkeling, night snorkeling, and electrofishing to estimate bull trout abundance and size structure in a second-order Idaho stream. North American Journal of Fisheries Management 16: 314–323.

Wildman, T.L. 2000. Relationship between density of wild brook and brown trout in two connecticut streams, and a comparison between trout sampling methods. MSc Thesis, University of Connecticut, Storrs.

Zubik, R.J. & Fraley, J.J. 1988. Comparison of snorkel and mark-recapture estimates for trout populations in large streams. North American Journal of Fisheries Management 8: 58–62.