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[Article]

Stream Fish Assemblages in Relation to Landscape Position and Local Habitat Variables

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Abstract.—The relative influence of local habitat variables and stream network position on fish assemblages was evaluated in this study of first-order through third-order streams within the Beaverkill–Willowemoc watershed in New York. We compared fish distribution and abundance over local and landscape scales by surveying 69 randomly selected tributaries within this 775-km^2 watershed. We used watershed-level metrics of stream link magnitude, branch link, confluence link, downstream link, and stream order to evaluate the importance of stream network position upon fish assemblages. Results of canonical correspondence analysis indicated that six factors significantly influenced fish species abundance in our study watershed. The proportion of fine substrate, canopy cover, in-stream vegetation, and water temperature were the four local habitat factors related to the abundance of fish species in this watershed; confluence link and stream order were the stream network position measures with the greatest influence on fish assemblages. Our results show that stream fish assemblages in the study watershed were influenced by a combination of small-scale habitat variables and stream position within a watershed network. The significance of confluence link relative to that of other link measures designed to evaluate stream network position has never been previously established in a direct comparison. The usefulness of confluence link to characterize fish assemblages is consistent with efforts to identify metrics that are relevant to both watershed network geomorphology and ecology.

Understanding fish–habitat relationships requires a comparison of fish assemblages over a range of spatial and temporal scales (Heggenes et al. 1999). Stream fish distributions are influenced by a variety of small-scale physical characteristics, as well as large-scale interactions (Bowlby and Roff 1986; Fausch 1988; Fausch et al. 1994). A newly developing landscape perspective calls for viewing streams as connected networks with a definable ‘‘network geometry’’ (Benda et al. 2004), instead of a linear hierarchy most commonly represented by stream order (Vannote et al. 1980). Although stream fish distributions are influenced by a variety of small-scale habitat features, the importance of stream network position is less established. Patterns in fish assemblages may be explained to some degree by landscape position characteristics inherent in stream network geometry. In this study, we incorporated landscape and local habitat factors in a single analysis to evaluate fish assemblages in a watershed network of streams.

Landscape position within a watershed influences fish assemblage patterns (Osborne and Wiley 1992; Fausch et al. 1994; Matthews and Robison 1998). Landscape attributes are often successful predictors of broad patterns of fish assemblages at large spatial extents but may fail under specific circumstances. For example, stream order (Strahler 1957) has been used to describe some variation in stream fish assemblages, and several authors have observed a strong association between stream order and fish species richness (Paller 1994; Fairchild et al. 1998). Exceptions to typical longitudinal patterns encompassed by stream order may occur at locations where small-scale habitat changes occur independently of stream order (McNeely 1986), or within small streams in close proximity to large assemblages of river species (Gorman 1986). Several additional metrics of stream position within a watershed network have been developed (Osborne and Wiley 1992; Nieman 1996; Fairchild et al. 1998), but these have never been evaluated together in one study to determine their relative influence upon fish assemblages.

As biotic and abiotic stream characteristics change from low-order headwater streams to high-order downstream locations, the distribution and abundance of fish species may also change (Matthews and Robison 1998; Peterson and Rabeni 2001). Use of measures that take into account the relative position of streams within a watershed could further define the extent to which fish assemblages are influenced by landscape position. Our overall objective was to determine the influence of local and landscape factors on fish abun-

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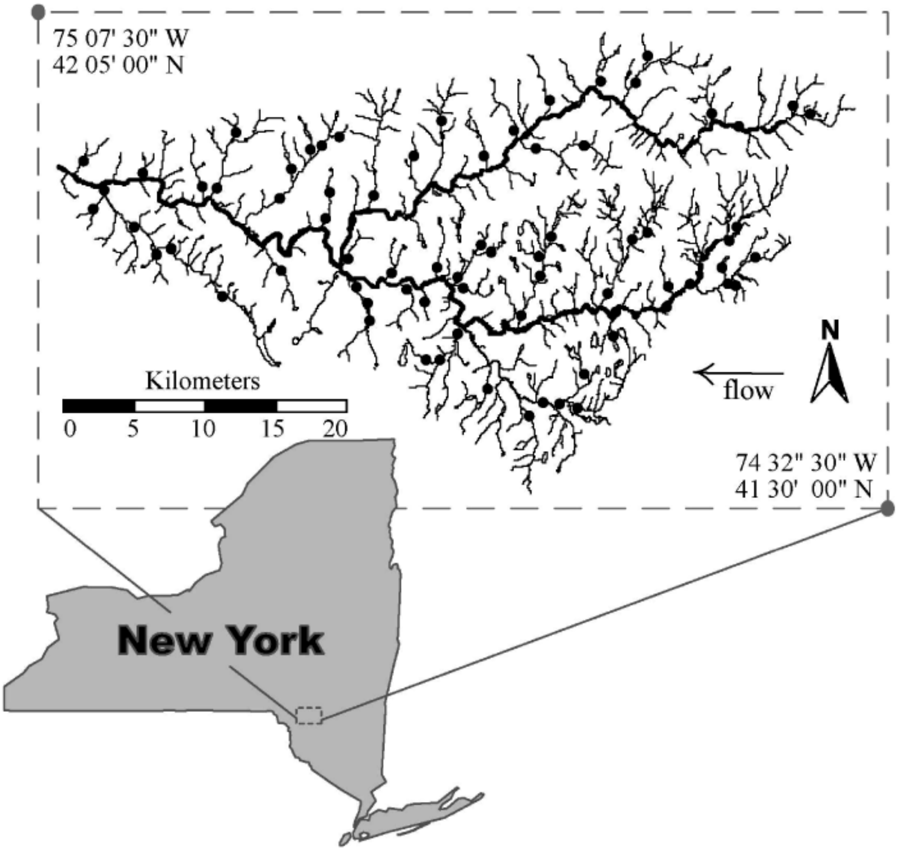


FIGURE 1.—Map of the Beaverkill–Willowemoc watershed in New York State. Solid circles mark sample sites where fish populations were sampled in 2000 to assess landscape position and habitat variables.

dance and assemblage structure in streams within a 775-km^2 watershed. We were particularly interested in the extent to which stream network position influenced fish assemblages within this drainage system and which stream network position metric was most informative.

Methods

Study watershed.—The Beaverkill–Willowemoc watershed is located in the Catskill region of New York (Figure 1), about 193 km (120 mi) northwest of New York City. Our study area encompassed three subwatersheds: the upper Beaverkill, the Willowemoc, and the lower Beaverkill. The upper Beaverkill and the Willowemoc sub-basins drain into the lower Beaverkill, a major tributary of the East Branch Delaware River. The entire Beaverkill–Willowemoc watershed covers an area of approximately 775 km^2. The watershed is lightly populated, approximately one-third of the land being dedicated as state-owned forests. Streams within the Beaverkill–Willowemoc valley have predominantly steep-sided, narrow flood plains surrounded by forests predominated by birch *Betula* sp., maple *Acer* sp., beech *Fagus grandifolia*, and eastern hemlock *Tsuga canadensis*.

The study watershed has historically sustained a widely recognized trout fishery (Van Put 1996), but the fish assemblage has changed during the 20th century, particularly with regard to salmonids. Before European settlement, the brook trout *Salvelinus fontinalis* was the only salmonid native to this system. During the 1880s, both nonnative brown trout *Salmo trutta* and rainbow trout *Oncorhynchus mykiss* were introduced into the Beaverkill River (Van Put 1996). Both nonnative trout species are currently naturalized within the watershed and support active fisheries within the main stem (lower Beaverkill River), in addition to stocked brown trout and naturally produced warmwater fishes, including smallmouth bass *Micropterus dolomieu* and largemouth bass *M. salmoides*.

Site selection.—A stratified random sampling design was implemented to ensure a systematic and unbiased coverage of the watershed (i.e., we assumed that a weighting stratification based on stream order would randomly represent other environmental variables of interest). We followed Strahler (1957) in calculating stream orders for all stream segments (confluence to confluence) within the watershed except intermittent streams (U.S. Geological Survey 1:24,000 topographic maps). The watershed contained 204 first-order, 83 second-order, and 28 third-order stream segments, from which study sites were chosen. Sampling effort (n_h, or the number of sites to be sampled from each strata) was divided according to optimal sampling stratification (Levy and Lemeshow 1999) as follows:

$$n_h = \left(N_h \sigma_h \middle/ \sum_h N_h \sigma_h \right)(72); \qquad (1)$$

h = the different stream orders (h = 1, 2, 3),
N_h = the number of stream segments in each strata,
σ_h = the approximate variance in species response expected for each stream order,
72 = estimated number of sites that could be sampled over one season.

The number of species was expected to increase with stream order; therefore, variance in species abundance and species richness was also expected to increase with stream order ($\sigma_{1st} = 0.1$, $\sigma_{2nd} = 0.2$, $\sigma_{3rd} = 0.3$).

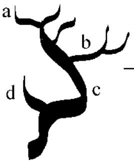
Stream segments were randomly selected before beginning fieldwork, at which time accessibility was assessed. In the event that access points to selected stream segments were unavailable, replacements were randomly selected from the same stream order strata. Inclement weather and high water conditions made it impractical to conduct surveys within three selected segments; therefore, 69 study sites were ultimately surveyed. A study site was selected to represent a particular stream segment such that it encompassed at least two mesohabitat units, which were defined within each site as either pools or riffles (the predominant mesohabitats in these streams). Study sites ranged in length from 32.0 to 73.3 m and ranged in area from 30 to 464 m^2.

A total of 32 first-order, 29 second-order, and 8 third-order stream sites were surveyed one time on randomly selected dates from June through September 2000 (Figure 1). Sites were surveyed in a random order to reduce seasonal biases. Small-scale physical habitat features were assessed on the same date as the biological surveys for all study sites, and all surveys were conducted during moderate to low flow conditions.

Biological surveys.—Fish abundance was estimated with three-pass depletion surveys via a battery-powered backpack electrofishing unit. Block nets were placed at the upstream and downstream ends of each study site during these surveys to maintain a temporarily closed system. Electrofishing surveys were conducted by a three-to-five-person crew, each carrying dip nets with 3-mm-diameter mesh. At least 10% of all fish captured for each species were weighed (0.1 g) and measured (total length; mm). Population estimates and electrofishing catchability coefficients were calculated using a Leslie Delury binomial model based on a binomial likelihood formulation, (P. J. Sullivan, Cornell University, personal communication).

Small-scale habitat surveys.—Average wetted width, bankfull stream width, and water depth were measured to the nearest 0.1 m at a minimum of three random locations within each mesohabitat unit. Other measurements within each mesohabitat unit included unit length, maximum water depth, water temperature, percent in-stream vegetation, percent in-stream shelter, percent canopy cover, and substrate composition. Percent in-stream vegetation was visually estimated as the percentage of stream bottom covered by submerged macrophytes and moss. Canopy cover was visually estimated as the percentage of the stream channel shaded by vegetation or land formations at midday during summer. The proportion of stream habitat with in-stream shelter and fine substrates (<2 mm in diameter) in each mesohabitat unit was visually estimated according to criteria modified from Simonson et al. (1994). Proportion of fine substrate (primarily silt, mud, and sand) was included in our analyses because of the importance of such substrates in other stream-fish studies (Heggenes 1988). Water conductivity, dissolved oxygen, current velocity, and pH were also measured at a subset of sites but were not incorporated in our analyses. Values for all environmental variables were proportionally weighted according to the area of each mesohabitat unit, then averaged over the entire study site such that

$$X_{\text{site}} = \sum A_i X_i \Big/ \sum A_i; \qquad (2)$$



Site	Stream order	Link	B-link	C-link	D-link
a	1	1	-1	4	2
b	2	2	1	2	5
c	3	5	0	1	6
d	1	1	1	1	6

FIGURE 2.—Hypothetical example of a stream network for delineating landscape position variables—stream order, link magnitude (link), branch link (B-link), confluence link (C-link), and downstream link (D-link)—for a simplified watershed.

X_{site} = value for the environmental variable for the entire study site
X_i = value of the environmental variable for the mesohabitat unit i
A_i = area of mesohabitat unit i.

Landscape position variables.—We used watershed-level metrics of stream link magnitude, branch link, confluence link, downstream link, and stream order to evaluate the importance of stream network position on fish assemblages (Figure 2). Stream order was assigned according to Strahler (1957). Stream link magnitude (link) is defined as the number of unbranched source streams upstream from a given segment in the drainage network (Shreve 1966). Branch link (B-link) is a function of the number of branches along a path to the right or left of the central axis or main stem (Nieman 1996). Confluence link (C-link) is the number of confluences downstream from each stream segment (Fairchild et al. 1998). Downstream link (D-link; Osborne and Wiley 1992), describes the upstream and downstream influences on a stream section within a drainage network and is calculated as the link magnitude of the next downstream confluence. Measures of these landscape-scale variables were assigned to each site using a U.S. Geological Survey 1:24,000 hydrology map (excluding intermittent streams). Further descriptions of the landscape-position variables, including the range of values for the study watershed, are provided in Table 1.

Statistical analysis.—We evaluated the number of species per site as a function of site area (m^2) to determine whether the survey area influenced species richness, defined as the total number of species per site. We also implemented a linear model to evaluate the total number of fish species per site as a function of the stream network position variables and evaluated correlations between all environmental variables.

Multivariate approaches can be applied to characterize differences in fish assemblages among sites influenced by a suite of environmental variables. Ordination techniques, such as canonical correspondence analysis (ter Braak 1986), have been used to examine species abundances with respect to other species, sites, and environmental variables (Lyons 1996; Peterson and Rabeni 2001). Canonical correspondence analysis (CCA) is a direct gradient ordination technique, in which species data can be directly related to a set of environmental variables (ter Braak 1986). This analysis combines correspondence analysis (reciprocal averaging)—an ordination technique that maximizes the correlation between species and environmental variables—with multiple regression techniques, such that the ordination axes are constrained to represent linear combinations of the explanatory variables.

The CANOCO 4.0 software program (ter Braak and Smilauer 1998) was used to perform CCA, which identifies a basis for community ordination by identifying patterns of variation in community composition best accounted for by a set of variables. The CCA finds synthetic gradients (ordination axes) from species abundance estimates and

TABLE 1.—Landscape position variable definitions and range of values for the 69 study sites in the Beaverkill–Willowemoc watershed, New York.

Landscape position variable	Author	Definition	Range of values
Stream order	Strahler (1957)	Order increases with the confluence of two equally ordered streams	1–3
Link magnitude	Shreve (1966)	Number of unbranched source streams upstream of a given segment in the drainage network	1–17
Branch link	Nieman (1996)	Number of branches along a path to the right (+) or left (−) of the central axis or main stem	−86 to +72
Confluence link	Fairchild et al. (1998)	Number of confluences downstream from each stream segment	2–65
Downstream link	Osborne and Wiley (1992)	Link magnitude of the next downstream confluence	2–208

environmental features by forming linear combinations of environmental variables that maximally separate species niches (ter Braak and Verdonschot 1995). Niche separation is expressed as the weighted variance of species centroids on a standardized gradient, each species centroid consisting of the weighted average of gradient values for sites at which the species occurs.

Environmental data were standardized to zero mean and unit variance to make them dimensionless and allow comparisons among canonical coefficients. Population estimates were converted into densities (number of fish/m^2) and were $\log_e(x + 1)$ transformed to stabilize variance. Three fish species were not included in these analyses because they were only present in one sample, and other rare species were down-weighted for the CCA analysis by methods described in ter Braak and Smilauer (1998).

The habitat preferences of different trout size-classes were evaluated by dividing each trout species into two size categories (1 = young of year and 2 = adult fish [age 1 and older]) based on length frequency histograms; these size-classes were then analyzed as distinct groups. The broader groupings (i.e., including both young-of-year and adults of each trout species) were included as supplements to the analysis; that is, these larger groups had no influence on the extraction of ordination axes but were added afterwards to the ordination diagrams to visually represent their relationship to environmental factors and other species (ter Braak and Smilauer 1998).

The following small-scale variables were included in the CCA: water temperature, in-stream cover, percent in-stream shelter, mean depth, mean width, maximum depth, percent in-stream vegetation, percent fine substrate, and percent canopy cover. Landscape position variables incorporated in the analysis were stream order, link, B-link, C-link, and D-link. A forward selection procedure identified the variables that described the greatest amount of variation not accounted for by previously selected variables (ter Braak and Smilauer 1998), where environmental and landscape variables were ordered by their ability to account for the variance in species abundance data. Subsequently, the most important variable was then tested for significance (defined as $P < 0.05$) in 1,000 Monte Carlo simulations before inclusion in the model. Remaining variables were ordered by their importance in accounting for additional variance in the species data, and this procedure was repeated for each variable included in the model.

We applied CCA to identify predictors that best accounted for the variance in species assemblages for all 69 sites and to determine species that tended to occur at similar locations. The statistical significance of the relationship between species abundances and the entire set of environmental variables were tested using Monte Carlo permutation tests at $\alpha = 0.05$. To do this, we used two test statistics, one based on the first canonical eigenvalue and another based on the sum of all canonical eigenvalues (ter Braak and Smilauer 1998).

Results

We collected 9,273 individual fish throughout the watershed during this study, representing 26 species, 3 of which were collected only at single sites (Table 2). Slimy sculpin were the most widely distributed species (52 out of 69 sites) and accounted for about 60% of the total number of fish captured. The next most abundant species were young-of-year (age-0) brook trout (9.7%, 53 sites) and blacknose dace (9.4%, 32 sites). When quantified according to density (number/m^2), slimy sculpin made up the majority of the total catch, followed by age-0 brook trout, age-1 and older (adult) brook trout, adult brown trout, blacknose dace, and age-0 brown trout (Table 2). The maximum population estimate for all species at a given site was 1,051 (mean = 181), and electrofishing catchability for all sites averaged 60%.

Our analyses showed that species richness increased with stream order ($P = 0.01$, $r^2 = 0.095$) and D-link ($P = 0.01$, $r^2 = 0.086$) and decreased with C-link ($P = 0.01$, $r^2 = 0.094$); no other environmental variables were significantly related to species richness. No significant relationship was found between species richness and survey area ($P = 0.44$). Positive correlations were found between link magnitude and stream order ($r = 0.76$), percent pool and percent fine substrate ($r = 0.54$), C-link and B-link ($r = 0.39$), percent in-stream shelter and percent pool ($r = 0.36$). Link magnitude and percent canopy were negatively correlated ($r = -0.36$).

The forward selection procedure for the CCA resulted in the retention of six variables as significant contributors to variation in the ordination: percent fine substrate, stream order, C-link, percent canopy cover, water temperature, and percent in-stream vegetation. The CCA produced four axes that together accounted for 24.2% of the total variance in fish species abundances among sites (Table 3). Eigenvalues, which range between 0 and 1, measure the importance of each axis. The first

TABLE 2.—Abundance and relative composition of fish captured at 69 study sites in the Beaverkill–Willowemoc watershed, New York, 2000.

Code	Species	Total number caught	Number of sites present	Percent catch	
				By number	By area
SS	Slimy sculpin *Cottus cognatus*	5,583	52	60.2	34.1
STYY	Brook trout, age 0 *Salvelinus fontinalis*	900	53	9.7	25.0
BND	Eastern blacknose dace *Rhinichthys atratulus*	871	32	9.4	4.9
STAD	Brook trout, adult[a]	512	49	5.5	14.1
BTYY	Brown trout, age 0 *Salmo trutta*	388	37	4.2	3.4
LND	Longnose dace *Rhinichthys cataractae*	311	27	3.4	1.9
BTAD	Brown trout, adult[a]	193	31	2.1	10.5
RTYY	Rainbow trout, age 0 *Oncorhynchus mykiss*	101	8	1.1	2.8
TD	Tessellated darter *Etheostoma olmstedi*	74	6	0.8	0.4
CSH	Common shiner *Luxilus cornutus*	67	6	0.7	0.5
WS	White sucker *Catostomus commersoni*	53	11	0.6	0.3
AME	American eel *Anguilla rostrata*	37	10	0.4	0.2
CC	Creek chub *Semotilus atromaculatus*	41	4	0.4	0.3
RTAD	Rainbow trout, adult[a]	29	11	0.3	0.7
CLM	Cutlip minnow *Exoglossum maxillingua*	30	5	0.3	0.2
LAM	Sea lamprey (ammocoete) *Petromyzon marinus*	31	4	0.3	0.2
MT	Margined madtom *Norurus insignis*	23	4	0.3	0.1
BB	Brown bullhead *Ameiurus nebulosus*	11	4	0.1	0.1
PS	Pumpkinseed *Lepomis gibbosus*	8	3	0.1	0.1
LMB	Largemouth bass *Micropterus salmoides*	2	2	0	0
Cyp. spp.	Cyprinidae spp. (unknown)[b]	3	1	0	0
PKL	Chain pickerel[b] *Esox niger*	2	1	0	0
SMB	Smallmouth bass[b] *Micropterus dolomieu*	4	1	0	0
Total		9,273			

[a] Adult = age 1 and older fish.

[b] Not included in analysis.

ordination axis accounted for 14.4% of the variance of the species data, whereas the second axis accounted for 4.9% of this variance; we did not attempt to interpret the third and fourth ordination axes (Table 3). The entire ordination accounted for more variation than expected by chance (Monte Carlo permutation tests, $N = 1000$, $P = 0.001$), indicating a significant relationship between species abundance and the environmental variables.

The Monte Carlo permutation tests indicated that the following factors were important in constructing CCA ordination axis one: percent fine substrate, percent in-stream vegetation, percent canopy cover, and water temperature (Table 3). Percent fine substrate, percent in-stream vegetation, and water temperature were positively correlated with the first ordination axis, whereas canopy cover was negatively correlated. C-link and stream order were the two factors important to CCA ordination axis two. C-link was positively correlated with the second ordination axis, and stream order showed a negative correlation.

TABLE 3.—Canonical correspondence analysis summary statistics for the Beaverkill–Willowemoc watershed, New York. Total inertia was 1.721.

Statistic	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	0.248	0.084	0.057	0.027
Species–environment correlation	0.788	0.548	0.572	0.470
Cumulative percentage variance				
Explained by species only	14.4	19.3	22.6	24.2
Explained by species + environmental variables	58.0	77.6	90.8	97.1
Interset correlations with axes				
Stream order	0.117	−0.121	0.522	−0.118
Water temperature	0.375	−0.038	−0.009	−0.120
Canopy cover (%)	−0.286	0.025	0.078	0.238
In-stream vegetation (%)	0.347	0.102	0.012	−0.121
Fine substrate (%)	0.553	0.088	−0.005	0.304
Confluence link	−0.026	0.449	0.278	−0.039

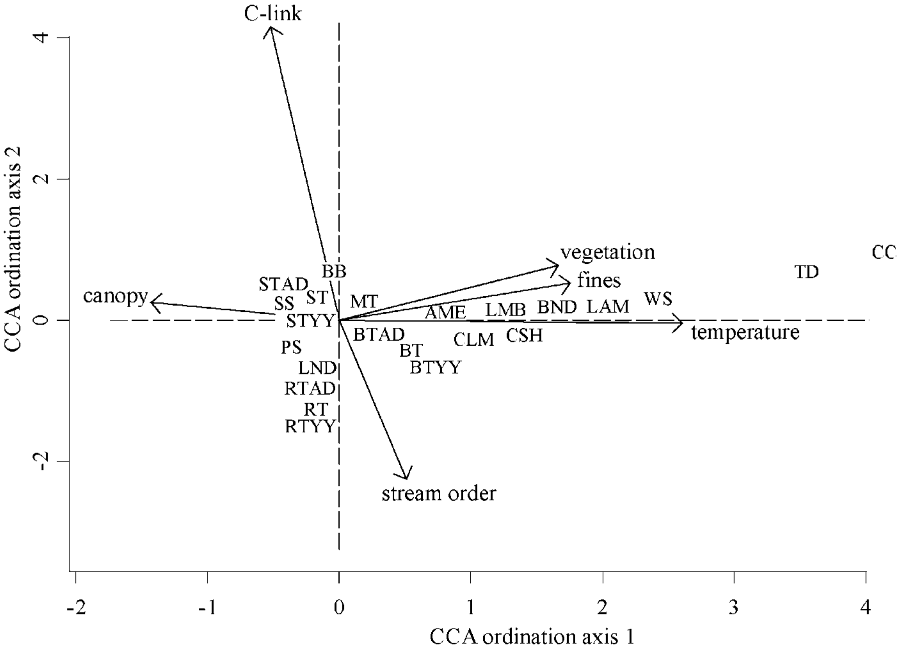


FIGURE 3.—Canonical correspondence analysis (CCA) diagram for 69 random sites for which six environmental variables were examined in the Beaverkill–Willowemoc watershed, New York, in 2000. Abbreviations are as follows: AME = American eel, BB = brown bullhead, BND = blacknose dace, BT = all brown trout, BTAD = adult brown trout (age 1 and older), BTYY = age-0 brown trout, CC = creek chub, CLM = cutlip minnow, CSH = common shiner, LAM = sea lamprey ammocoete, LMB = largemouth bass, LND = longnose dace, MT = madtom, PS = pumpkinseed, RT = all rainbow trout, RTAD = adult rainbow trout, RTYY = age-0 rainbow trout, SS = slimy sculpin, ST = all brook trout, STAD = adult brook trout, STYY = age-0 brook trout, TD = tessellated darter, and WS = white sucker.

The plot of the species scores on the ordination diagram (Figure 3) indicates their relationship with the CCA ordination axes with the reduced number of environmental variables. Two main gradients were apparent from the CCA. One separates assemblages based on small-scale environmental variables: canopy cover, percent fine substrate, in-stream vegetation, and water temperature. The other major gradient includes two landscape position variables: stream order and C-link. Slimy sculpins and brook trout were most abundant in streams with high percentage canopy cover, low percent fine substrate, and low water temperatures. Longnose dace, pumpkinseeds, and rainbow trout (age 0 and adult) exhibited similar preferences to brook trout (age 0 and adult) with regard to water temperature, in-stream vegetation, and fine substrate. Brown bullheads also showed similar tendencies, but were more tolerant of higher temperatures, percent vegetation, and percent fine substrate. The optima for rainbow trout, longnosed dace, pumpkinseeds, and margined madtoms fell in the centroid of canopy cover, in-stream vegetation, water temperature, and percent fine substrate gradients.

The same species groupings reflected tendencies in relation to two landscape position variables: stream order and C-link. Brook trout, slimy sculpin, brown bullheads, and margined madtoms were found near the centroid of the landscape position gradient, showing a slight tendency to be associated with first-order and second-order streams with many downstream confluences. Other fishes were most abundant in second-order streams, except for white suckers, tessellated darters, and creek chub, which were found almost exclusively in third-order streams with low C-links.

Although we found a distinct separation among the three trout species, only slight differences were found in the location of species optima for all three age-0 and adult trout comparisons within species. Differences between age-0 and adult trout were more pronounced along the landscape position gradient. Adults of all three trout species were more often found in high ordered streams with lower C-links than their age-0 counterparts.

Discussion

Landscape position within a watershed stream network was a significant factor influencing fish species abundance in our study watershed. Specifically, confluence link and stream order were the significant stream network position measures identified in our analysis. The significance of confluence link, compared with other link measures designed to evaluate stream network position, has never been previously established in a direct comparison of these measures. The usefulness of confluence link in characterizing fish assemblages is an important insight consistent with efforts to identify metrics relevant to both watershed network geomorphology and ecology (Benda et al. 2004).

The presence of particular species at locations within their potential geographical range is influenced by both historical and biogeographic conditions, such as prior colonization opportunities that define the regional species pool, and contemporary local factors, such as small-scale habitat conditions (Jackson et al. 2001). Given the complexity of large stream networks, accounting for even a small proportion of overall variation in an entire fish community is valuable in identifying a subset of key variables that influence species abundance (Gauch 1982; ter Braak 1986; Palmer 1993). Using the forward selection procedure of the CCA, we were able identify six variables that significantly influenced the abundance of 23 fish species at 69 stream locations within the study watershed. Significant variables correlated with local species abundance in this study included C-link, stream order, water temperature, percent canopy cover, percent in-stream vegetation, and percent fine substrate. The CCA specifically identified two stream network position variables (i.e., C-link and stream order) that significantly influenced fish abundance, highlighting the influence of landscape position variables upon fish assemblages.

Our results support the use of C-link—rather than other stream link measures—as a landscape position measure influencing fish assemblages. Fairchild et al. (1998) found a similar result in a CCA ordination of fish communities within a southeastern Pennsylvania watershed: C-link and link magnitude, the only landscape position variables evaluated, accounted for 13.5% of the variation in species composition among sites. The utility of C-link is also supported by the relevance of stream confluences to geomorphological processes within streams that are likely to influence ecological processes (Benda et al. 2004). C-link was likely most informative because of its ability to distinguish between small adventitious streams that connect with larger or main-stem streams (Gorman 1986) and streams of a similar size located farther upstream. It is important to recognize, however, that maximum C-link values are influenced by the size of a study watershed; therefore, absolute C-link values can only be used to compare locations within, rather than between, watersheds.

Our results should not be interpreted to mean that the significant variables identified by the CCA ‘‘predicted’’ 24% of the variability in fish abundance, or that other unknown variables would explain the remaining 76% variability. This misunderstands the use of CCA in this (or any) study, and we do not suggest using results from CCA to predict fish abundance. Instead, we have identified six key variables that significantly influence fish abundance within this watershed. Our results have identified significant structure in a complex, comprehensive dataset, and our unique contribution is that we have identified confluence link as a key component of that structure. This approach is consistent with the use of ordination techniques in community ecology. For example, in a comprehensive recent review of this subject, McCune and Grace (2002) noted that ‘‘r^2 values are commonly called the percentage of variance ‘explained’, but ‘represented’ is a more appropriate word.’’ McCune and Grace (2002) further noted that no fixed answer can be given to the question, ‘‘What is a ‘good’ r^2?’’, and they provide a CCA example for stream fauna in which the total species-environment r^2 (for two axes) was 15% but nevertheless provided useful insight regarding the influence of pollution on stream biota. Similarly, we have rejected the hypothesis that confluence link (and five other variables) did not influence fish abundance in our study watershed.

Other link measures did not have a significant influence on fish abundance in our study. By contrast, Osborne and Wiley (1992) found a significant relationship between D-link and fish species richness in a central Illinois watershed, and Nieman (1996) found a similar result using B-link; however, neither study evaluated the significance of C-link. Given the perspective that landscape position within stream network is best determined from a measure incorporating some aspect of network geometry (Benda et al. 2004), we consider both B-link and D-link as flawed measures that have limited utility. B-link is limited by only providing information about how the watershed differs on one side or the other of a main-stem branch. D-link incorporates information downstream from a given stream segment but is limited by an inability to distinguish between stream locations that are often quite different (e.g., compare sites c and d in Figure 2).

Although fish assemblages are clearly influenced at small scales by local biotic and abiotic factors, factors operating at larger scales are less evident (Jackson et al. 2001). Recent studies have increasingly evaluated streams at a landscape scale and as components within complex watersheds, rather than simply as independent entities (Richards et al. 1996). The most prominent landscape position species-environment gradient found in our study distinguished between sites closely connected to larger main-stem waters (predominated by tessellated darters, white suckers, margined madtoms, cutlip minnows, common shiners, and creek chub) and those located farther upstream in the watershed (predominated by slimy sculpin and brook trout).

Tributaries joining with larger rivers, such as those in the lower Beaverkill subwatershed, are closer to more diverse sources of colonizing fish species than are tributaries farther upstream in the watershed (Osborne and Wiley 1992). Adventitious streams, defined as streams at least three stream orders smaller than streams into which they flow, are located closer to a more diverse species pool (Gorman 1986) than similar-sized streams with larger C-link values. Small streams also often require recolonization following harsh winter or summer conditions, and the density of source populations can also affect movement and recolonization rates (Sheldon and Meffe 1995). Note that only one site, upper Mongaup Creek, was located in close proximity to a lake, and it therefore was the only study site in close proximity to a source of species associated with warm lake conditions. Three species found solely at that site were therefore excluded from the CCA. This raises a caution that landscape position influences associated with stream network branching patterns might be reduced in a study watershed encompassing numerous lake and stream connections because of the likely influence of lakes as source populations.

Other interactions between species and stream characteristics may contribute to differences among assemblages, highlighting the need to evaluate both small-scale and large-scale features when examining fish community composition. For example, habitat-use and landscape preferences of fishes may change with ontogeny (Schlosser 1995); we found that age-0 brown and rainbow trout were more abundant in streams with lower C-link and higher stream order than were their adult counterparts. Additionally, body size and mobility may influence the location of fishes with a stream landscape (Minns 1995). Some fishes found within our study system, such as tessellated darters and slimy sculpin, typically live in very short stream sections and may complete their entire life within a single habitat unit (Hill and Grossman 1987). This contrasts with observations of highly mobile fishes, such as American eel, sea lamprey, and trout species.

The results from the CCA analysis corroborate other studies focusing on small-scale environmental factors that influence fish abundance. The influence of temperature on stream fish distributions has been well documented (Symons et al. 1976; Drake and Taylor 1996; Taniguchi et al. 1998). Canopy cover was also a significant predictor of fish species abundance in the study watershed. The presence of extensive canopy cover was important for certain species, such as brook and rainbow trout, but areas of open canopy were associated with species such as the tessellated darter and creek chub. Although shade and temperature are probably correlates because canopy cover can shade a stream, such correlated variables can still influence species abundance in different ways. For example, a stream location with extensive canopy cover probably has an intact riparian area that provides many other stream habitat functions (Gregory et al. 1991). A particular strength of CCA is its ability to detect independent effects of such highly correlated variables, and the arrangement of species and habitat variables in CCA diagrams are not greatly influenced by strong correlations (Palmer 1993).

The percentage of fine substrates (<2 mm in diameter) also significantly influenced fish assemblage composition in the study watershed, separating species that prefer complex habitats with gravel or cobble substrates (e.g., brook trout and slimy sculpin) from other fishes. By contrast, we found that brown bullheads and margined madtoms showed no preference, and therefore tend to be generalists with regard to substrate. Submerged macrophytes provide underwater structure and offer shelter and foraging habitat for fishes in a manner similar to complex substrates. Several species were found in streams with a large percentage of in-stream vegetation, particularly creek chub, white suckers, tessellated darters, largemouth bass, sea lamprey, blacknose dace, common shiners, and cutlip minnows.

Local habitat variables such as substrate composition or canopy cover are easy to assess and provide information regarding other important stream habitat factors. For example, fines are more likely to accumulate at low-gradient stream locations seldom influenced by high-energy flow events, which cannot be determined as readily as substrate composition. Similarly, abundant canopy cover often indicates that the riparian area is relatively intact, which can influence factors such as stream temperature, nutrient availability, and particulate terrestrial inputs (Gregory et al. 1991). This CCA analysis supports the contention that such surrogate habitat measures can be valuable in conducting rapid assessments designed to evaluate fish assemblages.

Several small-scale variables measured in this study often vary throughout a day, season, or year (i.e., temperature, pool depth, in-stream vegetation, and canopy cover). By contrast, the landscape position variables incorporated in these analyses remain consistent through time. Temperature was the only significant variable from our analyses that varied extensively over short periods. Because summer 2000 was relatively cool and wet in the study watershed, temperature conditions may have been less influential during our field collections than would have occurred during warmer years.

Our results indicate that stream fish assemblages are significantly influenced by a combination of both local and landscape features associated with stream network position. A significant proportion of the variation in stream fish abundance within the study watershed was accounted for by a small number of easily-obtained habitat variables and stream network position variables that can be obtained from standard topographic maps. Most of the significant small-scale variables are unlikely to change from year to year, and stream network position remains constant, thereby providing a landscape framework from which to evaluate fish assemblages.

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References

Benda, L., N. L. Poff, D. Miller, T. Dunne, G. Reeves, G. Pess, and M. Pollock. 2004. The network dynamics hypothesis: how channel networks structure riverine habitats. Bioscience 54:413–427.

Bowlby, J. N., and J. C. Roff. 1986. Trout biomass and habitat relationships in southern Ontario, Canada, streams. Transactions of the American Fisheries Society 115:503–514.

Drake, M. T., and W. W. Taylor. 1996. Influencing of spring and summer water temperature on brook char, *Salvelinus fontinalis*, growth and age structure in the Ford River, Michigan. Environmental Biology of Fishes 45:41–51.

Fairchild, G. W., R. J. Horwitz, D. A. Nieman, M. R. Boyer, and D. F. Knorr. 1998. Spatial variation and historical change in fish assemblages of the Schuylkill River drainage, southeast Pennsylvania. American Midland Naturalist 139:282–295.

Fausch, K. D. 1988. Tests of competition between native and introduced salmonids in streams: what have we learned? Canadian Journal of Fisheries and Aquatic Sciences 45:2238–2246.

Fausch, K. D., N. Shigeru, and K. Ishigaki. 1994. Distribution of two congeneric charrs in streams of Hokkaido Island, Japan: considering multiple factors across scales. Oecologia (Berlin) 100:1–12.

Gauch, H. G. 1982. Multivariate analysis in community ecology. Cambridge University Press, New York.

Gorman, O. T. 1986. Assemblage organization of stream fishes: the effects of rivers on adventitious streams. American Naturalist 128:611–616.

Gregory, S. V., F. J. Swanson, W. A. McKee, and K. W. Cummins. 1991. Ecosystem perspectives of riparian zones. Bioscience 41:540–551.

Heggenes, J. 1988. Substrate preferences of brown trout fry (*Salmo trutta*) in artificial stream channels. Canadian Journal of Fisheries and Aquatic Sciences 45:1801–1806.

Heggenes, J., J. L. Bagliniere, and R. A. Cunjak. 1999. Spatial niche variability for young Atlantic salmon (*Salmo salar*) and brown trout (*S. trutta*) in heterogeneous streams. Ecology of Freshwater Fish 8:1–21.

Hill, J., and G. D. Grossman. 1987. Home range estimates for three North American stream fishes. Copeia 1987:376–380.

Jackson, D. A., P. R. Peres Neto, and J. D. Olden. 2001. What controls who is where in freshwater fish assemblages: the roles of biotic, abiotic, and spatial factors. Canadian Journal of Fisheries and Aquatic Sciences 58:157–170.

Levy, P. S., and S. Lemeshow. 1999. Sampling of population methods and applications. Wiley, New York.

Lyons, J. 1996. Patterns in the species distribution of fish assemblages among Wisconsin streams. Environmental Biology of Fishes 45:329–341.

Matthews, W. J., and H. W. Robison. 1998. Influence of drainage connectivity, drainage area, and regional species richness on fishes of the interior highlands in Arkansas. American Midland Naturalist 139:1–19.

McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon.

McNeely, D. L. 1986. Longitudinal patterns in the fish assemblages of an Ozark, USA stream. Southwestern Naturalist 31:375–380.

Minns, C. K. 1995. Allometry of home range size in lake and river fishes. Canadian Journal of Fisheries and Aquatic Sciences 52:1499–1508.

Nieman, D. A. 1996. Perspectives on the recent status of redfin pickerel in the Schuylkill River basin of southeast Pennsylvania. Pages 1–27 *in* R. Soderberg, editor. Warmwater workshop proceedings: esocid management and culture. American Fisheries Society, Northeast Division, Mansfield, Pennsylvania.

Osborne, L. L., and M. J. Wiley. 1992. Influence of tributary spatial position on the structure of warmwater fish assemblages. Canadian Journal of Fisheries and Aquatic Sciences 49:671–681.

Paller, M. H. 1994. Relationships between fish assemblage structure and stream order in South Carolina coastal plain streams. Transactions of the American Fisheries Society 123:150–161.

Palmer, M. W. 1993. Putting things in even better order: the advantages of canonical correspondence analysis. Ecology 74:2215–2230.

Peterson, J. T., and C. F. Rabeni. 2001. The relation of fish assemblages to channel units in an Ozark stream. Transactions of the American Fisheries Society 130:911–926.

Richards, C., L. B. Johnson, and G. E. Host. 1996. Landscape-scale influences on stream habitats and biota. Canadian Journal of Fisheries and Aquatic Sciences 53(Supplement 1):295–311.

Schlosser, I. J. 1995. Critical landscape attributes that influence fish population dynamics in headwaters streams. Hydrobiologia 303:71–81.

Sheldon, A. L., and G. K. Meffe. 1995. Short-term recolonization by fishes of experimentally defaunated pools of a coastal plain stream. Copeia 1995:828–837.

Shreve, R. L. 1966. Statistical law of stream numbers. Journal of Geology 74:1737.

Simonson, T. D., J. Lyons, and P. D. Kenehl. 1994. Guidelines for evaluating fish habitat in Wisconsin streams. U.S. Forest Service, General Technical Report NC 164,.

Strahler, A. N. 1957. Quantitative analysis of watershed geomorphology. Transactions, American Geophysical Union 38:913–920.

Symons, P. E. K., J. L. Metcalfe, and G. D. Harding. 1976. Upper lethal and preferred temperatures of the slimy sculpin *Cottus cognatus*. Journal of the Fisheries Research Board of Canada 33:180–183.

Taniguchi, Y., F. J. Rahel, D. C. Novinger, and K. G. Gerow. 1998. Temperature mediation of competitive interactions among three fish species that replace each other along longitudinal stream gradients. Canadian Journal of Fisheries and Aquatic Sciences 55:1894–1901.

ter Braak, C. J. F. 1986. Canonical correspondence analysis: a new eigenvalue technique for multivariate direct gradient analysis. Ecology 65:1167–1179.

ter Braak, C. J. F., and P. F. M. Verdonschot. 1995. Canonical correspondence analysis and related multivariate methods in aquatic ecology. Aquatic Sciences 57:255–289.

ter Braak, C. J. F., and P. Smilauer. 1998. CANOCO reference manual and user's guide to CANOCO for Windows: software for canonical community ordination, version 4. Microcomputer Power, Ithaca, New York.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130–137.

Van Put, E. 1996. The Beaverkill. Lyons & Burford, New York.