FISH ASSEMBLAGE STRUCTURE UNDER VARIABLE ENVIRONMENTAL CONDITIONS IN THE OUACHITA MOUNTAINS

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Abstract—Spatial and temporal variability of fish assemblages in Ouachita Mountain streams, Arkansas, were examined for association with stream size and flow variability. Fishes and habitat were sampled quarterly for four years at 12 sites (144 samples) in the Ouachita Mountains Ecosystem Management Research Project, Phase III watersheds. Detrended and Canonical Correspondence analyses were used to describe spatial and temporal patterns. Considerable spatial and temporal variability in fish assemblage structure was observed among sites. Across all sites and samples, assemblage variability was significantly associated with stream size and flow regime. The flow regime of the Little Glazypeau system differed from that of the Alum Fork system. Differences in flow regime were significantly associated with differences in fish assemblages across sites with trenchant differences noted between the Little Glazypeau and Alum Fork systems. The two systems are historically distinct and reflect large-scale differences in geomorphology, speciation, extinction, and dispersal.

INTRODUCTION

The Ouachita Mountains of Arkansas and Oklahoma contain a suite of river systems that ultimately drain into the Red and Arkansas River basins. The region supports a diverse fish fauna with several endemic species (Robison and Buchanan 1988). The implementation of the Ouachita Mountains Ecosystem Management Research Project (Phase III) by the USDA Forest Service provided us with the opportunity to study how environmental variability influences fish assemblage structure across a large spatial scale incorporating the four Phase III core watersheds.

Many factors affect the distribution and abundance of species, including interaction between the environment and population processes (Brown 1984). Determining environmental influences on distribution and abundance patterns is a difficult task because different spatial and temporal scales yield different types of information (Wiens and others 1986). Regardless, differences among species in distribution and abundance patterns within a region are, in part, due to individualistic responses to the environmental template. In streams, two complex environmental gradients appear to influence fish assemblages and habitat structure: stream size and hydrologic variability (Gorman and Karr 1978; Horwitz 1978; Poff and Ward 1989; Schlosser 1987; Sheldon 1968). Small, hydrologically dynamic streams in these Ouachita Mountain watersheds provide an ideal system to address questions concerning the effects of environmental variability on the distribution and abundance of fishes.

Our primary objective for this work was to examine how local fish assemblages change across the landscape and to see if these patterns were related to spatial and temporal variability in the environment. Specifically, we used multivariate direct and indirect gradient analyses to ask if patterns in fish assemblage structure were associated with stream size and variability in flow.

MATERIALS AND METHODS

Study Area and Species

The Ouachita Mountains of Arkansas and Oklahoma are characterized by strongly folded, uplifted sedimentary rock and pine-oak upland forest (Robison 1986). Our sample sites were located in two river systems (of the Red River drainage) that drain the eastern side of the uplift. Nine sites were located in the Alum Fork of the Saline River (hereafter Alum Fork) and three sites were in the Little Glazypeau system of the Ouachita River drainage (fig. 1). These are

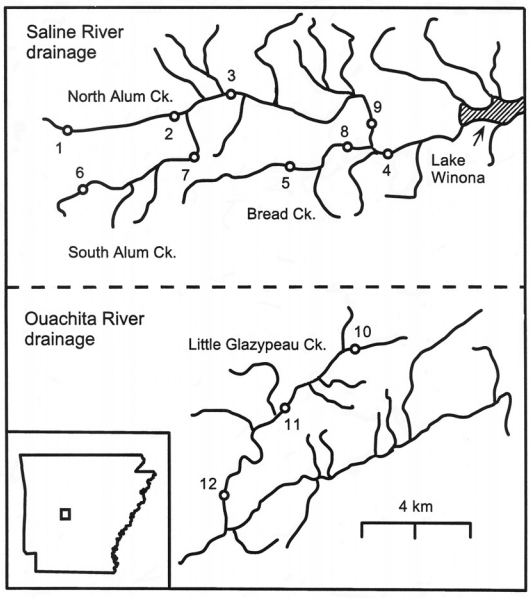

Figure 1—Map showing 12 sites in the Alum Fork and Little Glazypeau systems. Dashed line indicates that the geographic proximity of the two systems is not as shown.

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clear water streams except during high precipitation events when dramatic increases in turbidity are evident. Because of the high gradient of these streams, riffle-pool development is strong. Pools ranged from a few to 50 m or more in length, and were usually separated by swift riffle habitats consisting of coarse substrate materials. These streams are characterized by high variability in the flow regime. Water levels can rise and fall very rapidly with heavy precipitation events and headwater reaches are intermittent, frequently drying to isolated pools during summer and autumn months. Thus, habitats and their corridors can grow, shrink, and change configuration rapidly (Taylor 1997).

Data Collection

From November 1995 through August 1998, we sampled fishes and measured environmental variables at the 12 sites (fig. 1) for a total of 144 samples. Samples for all years were taken in November, February, May, and August and were always completed within a three to four day time period under ambient conditions. At each site, we electrofished all habitat types within a 100 to 200-m stream reach (depending on stream size) that spanned at least two pool-riffle sequences. For stream fishes, the stream reach is a logical sample unit in a river system (Frissell and others 1986), and the effects of disturbance on assemblage level properties are measured most commonly at this scale (Matthews 1998). All sampling methods are biased and electrofishing is no exception. However, our system consisted of small, clear streams (first to third order) that were wadeable, and that could be sampled in a consistent manner each time. The same individual (CMT) always operated the backpack electroshocker and there were always two to three netters present to pick up stunned fishes. Thus, we are confident that we adequately assessed the composition of fish assemblages at a given site for each sample date. After sampling a site, all fishes were identified, counted, and returned to the stream alive.

After fish sampling and processing, we measured habitat variables along transects (perpendicular to stream flow) spaced at 10 to 15-m intervals along the sampled stream reach. The number of transects varied (eight to 12) depending on the length of the sampled stream reach. Transects were permanently marked and re-surveyed during each visit. At every other meter along transects, we measured current velocity, depth, and dominant substrate type. We categorized substrate following Taylor and Lienesch (1996a, 1996b) as bedrock, large boulder (> 300 mm), small boulder (150 to 300 mm), cobble (50 to 149 mm), gravel (3 to 49 mm), or sand (< 3 mm). We measured stream width at each transect as well as the presence/absence of aquatic macrophytes, algae, undercuts, and woody debris.

Data Treatment and Analyses

In order to summarize the fish assemblage data and quantify the effects of stream size and flow variability on fish assemblages, we performed three multivariate analyses. Detrended correspondence analysis (DCA) is an indirect ordination technique designed to summarize complex community data (Gauch 1982). We used DCA to qualitatively compare fish assemblages across space and time. Canonical correspondence analysis (CCA) is a multivariate direct gradient technique that is commonly used to explore the relationship between assemblages of organisms and the environment. The ordination axes (gradients in assemblage structure) are constrained by the suite of environmental variables being analyzed, thus maximizing the species-environment correlation (ter Braak 1986). All analyses were performed with PC-ORD software (McCune and Meford 1997).

The first CCA was designed to quantify the association between stream size and fish assemblage structure. To quantify stream size we first calculated the mean and maximum width, mean and maximum depth, and mean and maximum current velocity for each site/date. All environmental values were log-transformed before analysis. Our goal was to see if patterns in fish assemblage structure were associated with stream size variables. We used a Monte Carlo randomization procedure to determine if the relationship was significant (1000 permutations).

Next, we used CCA to identify patterns in assemblage structure that reflect variation through time in stream width, depth, and flow characteristics. We included coefficients of variation (CV) calculated for each site across sample dates for the following variables: mean and maximum width, mean and maximum depth, and mean and maximum current velocity. The species data used in this analysis included summed totals for each species at each site across the entire study period. We used a Monte Carlo randomization procedure to determine if the relationship between assemblage structure and flow variability was significant (1000 permutations). Multi-response permutation procedures (McCune and Meford 1997) were used to determine if there were assemblage-level differences between the Little Glazypeau system and the Alum Fork system with regard to the flow regime.

RESULTS AND DISCUSSION

We collected a total of 30 fish species (and numerous individuals of a hybrid sunfish, *Lepomis sp.*) from the 12 sites. Species were taxonomically distributed across six families and functionally distributed across six trophic groups (Allan 1995). We present species relative abundances and distributional information in table 1 and summary environmental data in table 2.

Species varied greatly in their overall relative abundances and in their distribution across sites (table 1). At the coarsest level, five species were collected only from the Little Glazypeau system, and six species were collected only in the Alum Fork system. Large-scale historic differences in geomorphology, speciation, extinction, and dispersal account for the non-shared components of the assemblages. Both systems drain into the Red River, but are isolated by long distances of lowland, big river habitat. The effectiveness of isolation is demonstrated by the evolution of one endemic form (*Noturus lachneri*, Alum Fork system) and several species that occur in one system but not the other. Within a given drainage abundances and occurrences were also highly variable across space and time, reflecting the different ecological conditions that occur spatially and temporally. These patterns are exemplified in the following indirect and direct gradient analyses.

Table 1—Species, species acronyms, species occurrences in the two drainage systems, total number of localities occupied (occurrence) by species, and overall relative abundances of species

Species	Acronym	Little Glazypeau	Alum Fork	Occurrence	Relative abundance
Ameiurus natalis (Lesueur)	AMENAT	X	X	7	< 0.01
Aphredoderus sayanus (Gilliams)	APHSAY	X	X	9	0.01
Campostoma anomalum (Rafinesque)	CAMANO	X	X	11	0.18
Chaenobryttus gulosus (Cuvier)	LEPGUL		X	1	< 0.01
Erimyzon oblongus (Mitchill)	ERIOBL	X	X	12	0.04
Esox americanus Gmelin	ESOAME	X	X	10	0.01
Etheostoma blennioides Rafinesque	ETHBLE	X	X	3	< 0.01
Etheostoma collettei Birdsong & Knapp	ETHCOL		X	6	0.07
Etheostoma radiosum (Hubbs & Black)	ETHRAD	X		3	0.05
Etheostoma whipplei (Girard)	ETHWHI		X	9	0.09
Fundulus catenatus (Storer)	FUNCAT	X		2	0.01
Fundulus olivaceous (Storer)	FUNOLI	X	X	10	0.05
Hypentelium nigricans (Lesuer)	HYPNIG	X	X	3	< 0.01
Ichthyomyzon gagei Hubbs and Trautman	ICHGAG		X	3	< 0.01
Labidesthes sicculus (Cope)	LABSIC	X	X	6	0.01
Lepomis cyanellus Rafinesque	LEPCYA	X	X	12	0.07
Lepomis hybrid	LEPHYB	X	X	5	< 0.01
Lepomis macrochirus Rafinesque	LEPMAC	X	X	8	0.01
Lepomis megalotis (Rafinesque)	LEPMEG	X	X	11	0.19
Lythrurus umbratilis (Girard)	LYTUMB	X	X	10	0.07
Luxilus chrysocephalus Rafinesque	LUXCHR	X		3	0.01
Micropterus dolomieu Lacepede	MICDOL	X		1	< 0.01
Micropterus punctulatus (Rafinesque)	MICPUN	X	X	6	< 0.01
Micropterus salmoides (Lacepede)	MICSAL	X	X	5	< 0.01
Notropis boops Gibert	NOTBOO	X	X	7	0.02
Notropis ortenburgeri Hubbs	NOTORT		X	3	0.01
Noturus nocturnus Jordan & Gilbert	NOTNOC	X		1	< 0.01
Noturus lachneri Taylor	NOTLAC		X	7	0.05
Percina caprodes (Rafinesque)	PERCAP	X	X	5	0.01
Pimephales notatus (Rafinesque)	PIMNOT	X	X	5	0.02
Semotilus atromaculatus Mitchill	SEMATR	X	X	9	0.04

Table 2—Substrate characteristics (percent composition of point estimates), mean stream width, mean stream depth, and mean stream current speed for the 12 sites

	Substrate								
Sites	Sand	Gravel	Cobble	Small boulder	Large boulder	Bed-rock	Mean width	Mean depth	Mean current speed
1	0	30	25	15	10	20	2.6	16.7	0.07
2	0	0	43	36	14	7	3.7	21.9	0.15
3	8	11	70	11	0	0	4.9	34.0	0.14
4	0	18	33	24	6	18	10.8	39.4	0.15
5	0	3	53	29	15	0	4.0	29.1	0.13
6	0	10	23	45	23	0	3.7	30.0	0.02
7	0	16	16	42	26	0	6.7	40.0	0.09
8	0	3	21	21	9	47	6.0	30.0	0.07
9	0	0	21	38	41	0	7.9	36.1	0.19
10	0	62	31	4	0	4	2.8	22.1	0.05
11	3	26	43	23	3	3	4.9	28.6	0.13
12	0	34	6	23	37	0	11.3	34.7	0.13

Substrate compostion is reported for November 1996 samples under ambient flow conditions. Means for other variables are calculated across the entire study period.

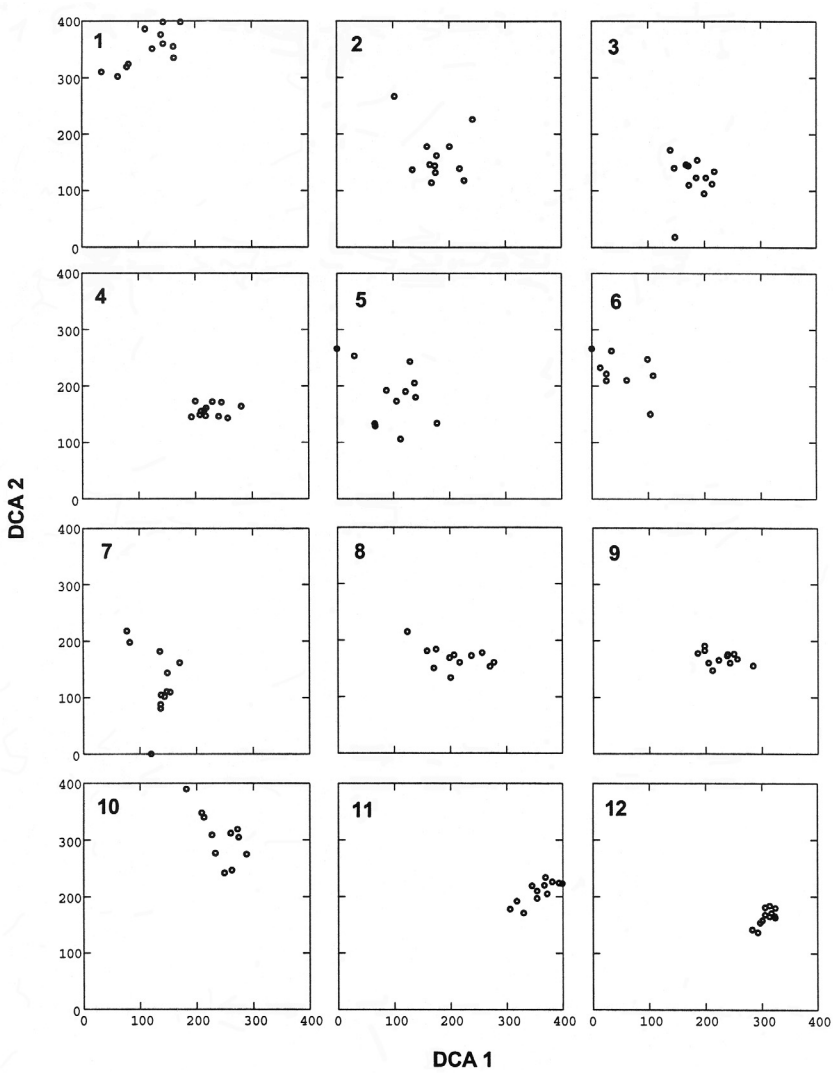

Figure 2—Detrended correspondence analysis (DCA) of all site and samples across the three year period. Sample scores are plotted in multivariate space defined by DCA axes 1 and 2.

Detrended correspondence analysis of all samples at each site indicated considerable variability in the structure of site-specific assemblages across time (fig. 2). The overall large spread of points in the two-dimensional space was indicative of high species turnover (beta diversity) among the sites. This was especially evident when comparing sites from the Little Glazypeau system (sites 10, 11, and 12) with sites from the Alum Fork system (sites one through nine). For samples from individual sites, the variability was considerably less at larger sites as compared to smaller sites. Sites 4, 9, and 12 were the largest sites (see mean width, table 2) and samples from these sites clustered together very closely in ordination space (fig. 2). In contrast, samples from the smallest sites (e.g. sites 1, 2, 5, 6, and 10) were much more spread out in ordination space. This pattern indicated that assemblages at smaller sites were much more variable across time in species composition and abundance than assemblages from larger sites. Despite variability in assemblage structure for each site across time, each locality was confined to a relatively small proportion of the overall two-dimensional ordination plot (fig. 2).

Interpretation of the variability in assemblage structure is facilitated by simultaneously examining the ordination plot (fig. 3) and correlations of species abundance with the two DCA axes (table 3). For example, *Semotilus atromaculatus* (SEMATR) has the highest species score on DCA axis 2 (top of figure 3). Samples from Site 1 (fig. 2) all clustered in this region of the ordination space indicating the importance of this species at this site. As expected, *S. atromaculatus* showed a strong positive correlation with DCA axis 2 (r = 0.576; table 3). *Lepomis cyanellus* (LEPCYA) also was an important species at site 1 and showed a strong positive correlation with DCA axis 2 (r = 0.399). *Etheostoma radiosum* (ETHRAD) had the highest score on DCA axis 1 (far right in figure 3) and was found only in the two largest sites in the

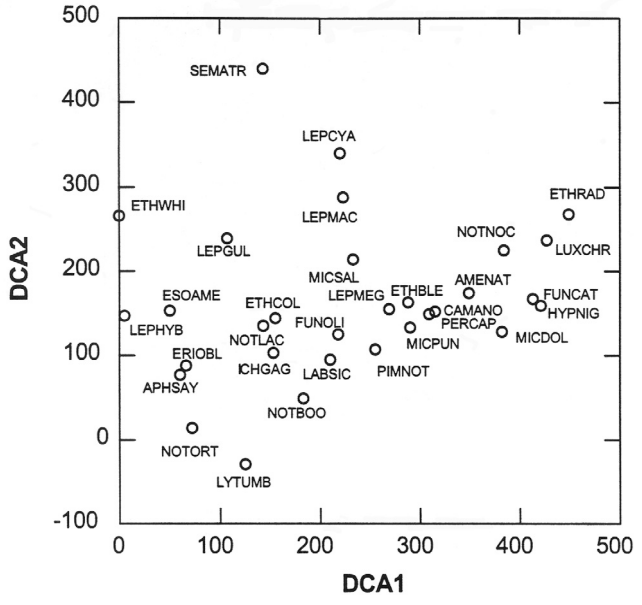

Figure 3—Detrended correspondence analysis (DCA) of all site and samples across the three year period. Species scores are plotted in multivariate space defined by DCA axes 1 and 2.

Table 3—Pearson correlations of species abundance and first two DCA ordination axes

Species	Axis 1 correlations	Axis 2 correlations
Ameiurus natalis	0.378	-0.152
Aphredoderus sayanus	-0.253	-0.270
Campostoma anomalum	0.582	-0.349
Chaenobryttus gulosus	-0.058	-0.042
Erimyzon oblongus	-0.290	-0.307
Esox americanus	-0.363	-0.126
Etheostoma blennioides	0.166	-0.117
Etheostoma collettei	-0.027	-0.326
Etheostoma radiosum	0.620	0.103
Etheostoma whipplei	-0.531	0.128
Fundulus catenatus	0.508	-0.058
Fundulus olivaceous	0.137	-0.423
Hypentelium nigricans	0.454	-0.042
Ichthyomyzon gagei	-0.008	-0.137
Labidesthes sicculus	0.039	-0.138
Lepomis cyanellus	0.120	0.399
Lepomis hybrid	-0.186	-0.030
Lepomis macrochirus	0.040	-0.015
Lepomis megalotis	0.359	-0.364
Lythrurus umbratilis	-0.085	-0.473
Luxilus chrysocephalus	0.564	0.016
Micropterus dolomieu	0.347	-0.115
Micropterus punctulatus	0.240	-0.165
Micropterus salmoides	0.081	-0.086
Notropis boops	0.012	-0.220
Notropis ortenburgeri	-0.155	-0.365
Noturus nocturnus	0.154	-0.029
Noturus lachneri	-0.076	-0.367
Percina caprodes	0.204	-0.127
Pimephales notatus	0.138	-0.212
Semotilus atromaculatus	-0.143	0.576

DCA = Detrended correspondence analysis.

Little Glazypeau system (sites 11 and 12, figure 2). This species showed a very strong correlation with DCA axis 1 (r = 0.620). By superimposing sites in figure 2 onto figure 3 and examining the correlations in table 3, a visual picture emerges of the species that are important assemblage components at the 12 localities.

CCA allowed us to examine the importance of stream size and hydrologic variability in structuring fish assemblages. Correlations between the environmental variables and CCA axes one and two (table 4) indicate the relative contribution of each variable to the CCA axes. For the stream size analysis, the Monte Carlo randomization test indicated that the relationship between the stream size variables and assemblage structure was highly significant for the first two axes (p = 0.001, both axes). Thus, assemblage structure was strongly associated with stream size.

CCA also indicated that variation in stream flow was associated with assemblage structure. A Monte Carlo randomization procedure indicated that the relationship between flow variability and assemblage structure was significant for the first CCA axis (p = 0.054) and marginally significant for the

Table 4—Environmental correlates of first two CCA axes from two separate analyses[a b]

	Size		Variability	
Variable	CCA Axis 1	CCA Axis 2	CCA Axis 1	CCA Axis 2
Mean width	0.440	0.756	-0.339	0.157
Maximum width	0.238	0.925	0.382	0.041
Mean depth	0.054	0.614	0.466	-0.432
Maximum depth	0.502	0.441	0.594	-0.564
Mean current	0.193	0.326	0.041	0.558
Maximum current	0.076	0.462	0.833	0.408

CCA = Canonical correspondence analysis.
[a] For the size analysis all environmental variables represent means, calculated for each site across all sample dates.
[b] For the variability analysis all environmental variables represent coefficients of variation, calculated for each site across all sample dates.

second CCA axis ($p = 0.104$). The strongest correlate was variability in maximum current velocity (table 4), and this vector separated the largest sites (4, 8, 9, 11, and 12) from the other sites (larger sites showed less variability in maximum current velocity). Other strong correlates on the first CCA axes were related to CVs of depth, width, and current (table 4). Thus, variability in the flow regime (CVs of stream size and current speed) was also an important predictor of local fish assemblage structure.

An interesting pattern emerged between drainage systems when sites were plotted in two-dimensional space defined by CCA axes 1 and 2 from the stream flow analysis. Assemblages from the three sites in the Little Glazypeau system (sites 10, 11, and 12) separated from the rest of the sites based on variables associated with the flow regime (fig. 4).

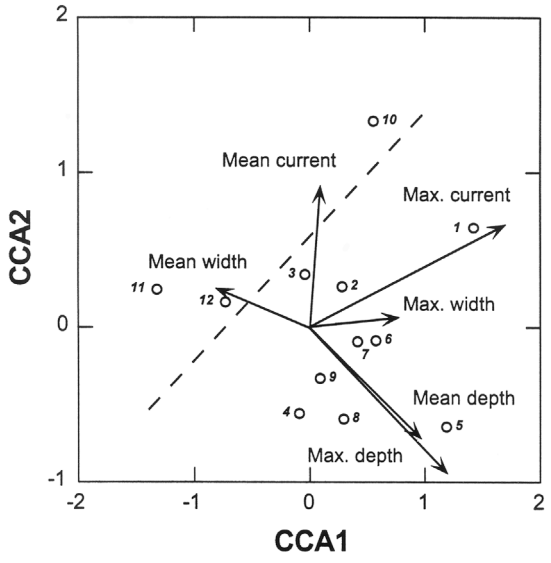

Figure 4—Canonical correspondence analysis (CCA) of 12 sites. Environmental variables are coefficients of variation, calculated across the 3-year period. Species abundances are summed across time for each site.

Multi-response permutation procedures indicated that this separation was significant ($p = 0.032$). Thus, the Little Glazypeau system differed from the Alum Fork system in its variability with respect to the flow regime, and these differences were also associated with differences in fish assemblage structure.

CONCLUSIONS

Our results suggested that assemblages in these Ouachita Mountain streams were strongly associated with factors related to stream size and flow variability. Furthermore, Taylor and Warren (Taylor, C.M.; Warren, M.L. Dynamics in species composition for stream fish assemblages: environmental variability and nested species subsets. Manuscript in preparation) found that stream size and flow variability were correlated negatively for these streams. Thus, hydrologic variability was spatially structured in this system. Smaller stream localities were more variable with respect to flow than larger stream localities, and this variation was associated with the structure of the resident fish assemblages. Further, the Alum Fork and Little Glazypeau systems showed significant differences in assemblage structure that were associated with variability in the flow regime. The Little Glazypeau system generally has less variable flows than the Alum Fork system due to geological differences in groundwater discharge. The two systems also differed for historical reasons. Little Glazypeau and Alum Fork systems are geographically separated, and this separation has produced differences in the regional species pools.

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