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Spatiotemporal Patterns of Fish Assemblage Structure in a River Impounded by Low-Head Dams

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We studied spatiotemporal patterns of fish assemblage structure in the Neosho River, Kansas, a system impounded by low-head dams. Spatial variation in the fish assemblage was related to the location of dams that created alternating lotic and lentic stream reaches with differing fish assemblages. At upstream sites close to dams, assemblages were characterized by species associated with deeper, slower-flowing habitat. Assemblages at sites immediately downstream from dams had higher abundance of species common to shallow, swift-flowing habitat. Temporal variation in assemblage structure was stronger than spatial variation, and was associated with fish life history events such as spawning and recruitment, as well as seasonal changes in environmental conditions. Our results suggest that low-head dams can influence spatial patterns of fish assemblage structure in systems such as the Neosho River and that such assemblages also vary seasonally.

RIVERINE fish assemblage structure often varies along environmental gradients from headwaters to lower mainstem (Schlosser, 1982; Gelwick, 1990; Edds, 1993). When these gradients are interrupted, however, alternate patterns can result. Such interruptions can be natural, as is the case with waterfalls (Balon and Stewart, 1983; Maret et al., 1997) or rapids (Balon and Stewart, 1983), or anthropogenic, as occurs with river fragmentation from damming (reviewed by Baxter, 1977; Dynesius and Nilsson, 1994; and Richter et al., 1997).

Dams affect lotic systems in many ways, and their impacts are often reflected in the spatial patterns of fish assemblages. Dam construction can fragment watersheds (Dynesius and Nilsson, 1994), affecting fish assemblages directly by eliminating or reducing movement of fishes, leading to reduced upstream species richness, especially for migratory species (ReyesGavilan et al., 1996; Holmquist et al., 1998; March et al., 2003). Alteration of the natural flow regime also influences fish assemblage structure, reducing in abundance species reliant upon seasonal flow variation to complete their life cycle (Bonner and Wilde, 2000; Minckley et al., 2003). Hypolimnial-release dams can also sharply decrease downstream water temperature, resulting in decreased growth and increased time to maturity for native fishes (Clarkson and Childs, 2000) and often replacing native warmwater assemblages with non-native coldwater assemblages over time (Quinn and Kwak, 2003). Impoundment-induced changes in current velocity also cause habitat alteration, with decreased flow velocities and high siltation rates upstream of dams (Kondolf, 1997; Bennett et al., 2002) and increased flow velocities leading to substrate scouring downstream (Kondolf, 1997; Camargo and Voelz, 1998). Many of these habitat alterations create conditions favorable for non-native species (Marchetti and Moyle, 2001), which can then further alter fish assemblage composition via predation and competition (Richter et al., 1997; Godinho and Ferreira, 1998; Eby et al., 2003).

Although the number of free-flowing riverine ecosystems in the world continues to decline (Poff et al., 1997), more research is required to understand the spatial pattern of fish assemblage structure in impounded rivers. Complicating the situation is the fact that not all types of dams affect lotic ecosystems similarly. For example, deep hypolimnial release dams, with their associated cooling effect downstream, affect rivers in different ways than smaller flood-control dams that do not alter river temperature (Petts, 1984).

Low-head dams (<4 m in height) are a type of impoundment common to many North American rivers. For example, Kansas has the second-highest number of dams in the United States (5,699; Shuman, 1995), and the vast majority of these are low-head dams. The Neosho River in eastern Kansas alone is impounded by 15 such structures. Given the well-documented effects of other types of impoundments on lotic systems, low-head dams, in spite of their small size, appear likely to affect riverine fish assemblages. Indeed, Porto et al. (1999) showed that low-head dams with heights less than 1.5 m can alter fish assemblage composition, with species richness declining immediately upstream. However, Dodd et al. (2003) and Raborn and Schramm (2003) documented habitat alteration in the presence of low-head dams, but little

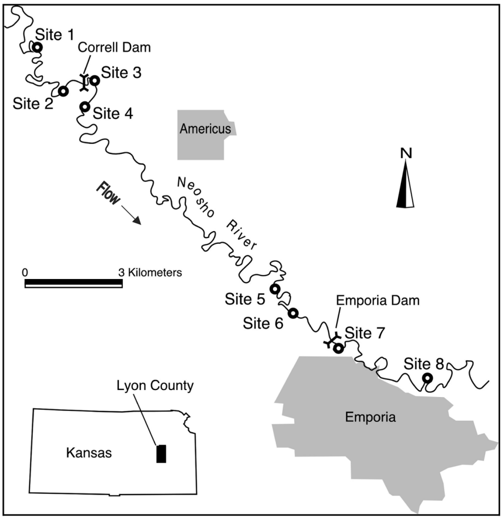

Fig. 1. Map of study area in Lyon County, KS, showing eight study sites and two low-head dams along the Neosho River from Americus to Emporia.

overall change to the fish assemblage. Although they are common throughout North America, little is know about the spatiotemporal patterns of fish assemblages within river systems impounded by low-head dams. Our objective was to quantify patterns of spatiotemporal variation in fish assemblages in the Neosho River, Kansas, and to evaluate the extent to which low-head dam impoundments affected these patterns.

MATERIALS AND METHODS

Study area.—The Neosho River lies within the Prairie Parkland ecosystem province (Bailey, 1983), and is part of the Arkansas River drainage. It is fifth-order in our study reach, draining mostly mixed-grass prairie and cropland, with mature riparian vegetation along some sections. We sampled eight sites along a 34-km stretch of the river from Americus to Emporia in Lyon County, Kansas (Fig. 1). Sites were selected to be representative of the Neosho River based on location relative to two low-head dams (see below) and appropriate for our sampling methodology (i.e., relatively shallow, with consistent current velocity). Overall stream gradient is low (0.44 m/km), although variation in gradient between sites varied due to impoundments. Gradient was lowest between sites 5 and 6 (negligible) and highest between sites 6 and 7 (1.31 m/km). There are no permanent tributaries along this stretch of the Neosho River. At each site, we fixed five permanent transects perpendicular to shore, spaced equally every 5 to 10 m, depending on site length.

Sampling.—We sampled each site monthly from November 2000 to October 2001. Samples were taken between the 9th and 22nd of each month during daylight hours, and sampling order of sites was randomized each month. We were unable to adequately sample Site 2 in January and February and Sites 5 and 6 from December through February due to ice cover, and Site 7 in August and December because flow velocities were too low for our sampling methodology. Sampling at each site proceeded from downstream to upstream transects, and from near shore to far shore points along each transect. We sampled up to five points along each transect, depending on river width and depth and landowner permission. At Site 8, landowner permission was only obtained for one side of the river. However, we were able to obtain representative samples of the fish assemblage at this site in spite of this limitation. All sampling points along each transect were spaced at least 0.5 m apart to minimize disturbing adjacent points. At each point we sampled fishes by kick-seining, using a 1.5-m length by 1.8-m height section of 3-mm mesh seine. Upon fixing the seine at a sampling point, we disturbed substrate beginning 3 m upstream. In this manner, fishes within a 4.5-m^2 area were carried downstream into the seine. This methodology effectively captures both water column and benthic fish species (Matthews, 1990; Wildhaber et al., 1999). We counted and identified fishes as juvenile or adult, using a 30-mm total length (TL) maximum juvenile length for minnows (*Campostoma*, *Phenacobius*, *Pimephales*, *Cyprinella*, *Notropis*, and *Lythrurus* spp.) and darters (*Etheostoma* and *Percina* spp.), and a 50-mm TL maximum juvenile length for madtoms (*Noturus* spp.) and sunfishes (*Lepomis* spp.), following Gelwick (1990). Other fishes were measured individually and classified as juvenile or adult based on published accounts. We used a 305-mm maximum juvenile cutoff length for Channel Catfish (*Ictalurus punctatus*), 380 mm for Flathead Catfish (*Pylodictis olivaris*), and 280 mm for redhorses (*Moxostoma* spp.) based on work by Deacon (1961) in the Neosho River, 220 mm for Spotted Bass (*Micropterus punctulatus*) and White Bass (*Morone chrysops*), and 240 mm for carpsuckers (Carlander, 1969, 1977, 1997). We did not distinguish between juvenile and adult *Gambusia affinis.* All fishes were held until sampling of the site was completed, then returned to the river. Juvenile redhorses and carpsuckers were difficult to identify in the field due to small size and were recorded as *Moxostoma* sp. and *Carpiodes* sp., respectively.

Habitat measurement.—We measured water depth, current velocity at 60% depth, substrate composition, and substrate compaction at all points along each cross-stream transect. Velocity was measured using a Global Flow Probe (Global Water Company, Gold River, CA). We visually estimated substrate at each point as percentage composition of clay/silt, sand, gravel, pebble, cobble, boulder, and bedrock (Mullner et al., 2000). Definition of substrate categories and sampling methodology followed Bain (1999). Compaction, a surrogate of the amount of fine sediment surrounding larger substrate types, was quantified by tactile evaluation; each point was assigned a compaction index value from 1 to 4, with 1 representing loose substrate, 2 substrate lightly packed with clay/silt, 3 substrate tightly packed with clay/silt, and 4 bedrock (Fuselier and Edds, 1996).

After fish were collected, water quality was measured immediately upstream of transects. We measured water temperature with a laboratory thermometer, and dissolved oxygen and pH with a Hach kit model AL-36B. We then took a 1-L sample of surface water for further analysis. From this sample we measured alkalinity and hardness with a Hach kit model AL-36B; nitrate, ammonia, carbon dioxide, total acidity, and orthophosphate with a Hach Surface Waters kit; chloride and sulfate with a Hach kit model DREL/1C; and turbidity with a Hach 2100P turbidimeter. Two 100-ml portions of the 1-L sample were vacuum filtered using Pall-Gelman Type A/E round 47-mm glass fiber filters, and the filtrate frozen at −10 C for future determination of chlorophyll *a* and particulate organic carbon (POC). We measured chlorophyll *a* using a model 10-AU-005 Field Flourometer (Turner Designs, Sunnyvale, CA) and POC using a Coulometrics Carbon Model 5014 Analyzer (UIC, Inc., Joliet, IL).

Data analysis.—Analyses were performed using SAS v.8 and SPSS v.7.5.1. Ordinations were conducted using PC-Ord v.4. We included only those taxa occurring in >5% of collections for ordination (Gauch, 1982).

To examine spatiotemporal patterns of fish assemblage structure, we used correspondence analysis (CA) to ordinate collections from each site during each month. We included 84 collections in the CA, composed of 17 juvenile and 16 adult taxa in addition to *G. affinis* (Table 1). We excluded samples taken in December at Site 8 and January at Site 7 because these collections consisted of only one fish. We analyzed conspecific juveniles and adults as separate taxa because spatial and trophic resource use varies ontogenetically for many stream fishes (Schlosser, 1982; Gelwick, 1990; Gido and Propst, 1999). To test for effects of low-head dam impoundments on fish assemblages, we grouped sites into one of three levels of an ''impoundment treatment,'' based on proximity to these dams. Sites less than 2 km downstream from dams (Sites 3, 4, and 7) comprised a ''downstream'' level of treatment, sites less than 5 km upstream (Sites 2, 5, and 6) an ''upstream'' level, and sites greater than 5 km from dams (Sites 1 and 8) a ''distant'' level of treatment.

To test for impoundment and temporal effects on CA 1 and 2 scores, we used the mixed linear model (SAS Proc Mixed). Scores from both axes were modeled separately as dependent variables, with month, impoundment, and the interaction between the two as fixed effects (Agresti and Finlay, 1997). Sites were modeled as repeated subjects nested within levels of impoundment treatment. The mixed linear model is a generalization of the general linear model that allows data to exhibit correlation and nonconstant variability; fixed effect parameters are associated with known explanatory variables, as in the general linear model. Where appropriate, we used a Tukey-Kramer multiple comparison test on least-square means to distinguish significant differences among treatment levels.

To examine relationships between environmental gradients and CA axes, we calculated Pearson's correlation coefficient between axis scores and environmental variables for each collection. To assess potential effects of hydrological variation on assemblage structure, we included in the correlation matrix river discharge for the day of each collection, measured at the U.S. Geological Survey gauging station on the Neosho River at Americus, KS.

Because of the large number of environmental variables measured, we used Principal Components Analysis (PCA) on a collections-by-environmental variables matrix to eliminate redundant variables. In the case of suites of variables loading similarly on the first three PCA axes, we selected the one variable most biologically meaningful to represent the group. In this analysis, water depth was selected from a group of variables including percent substrate composition of clay/silt, gravel and pebble, POC and ammonia. Dissolved oxygen was selected from a suite of water chemistry variables including sulfate, alkalinity, dissolved carbon dioxide, hardness, pH, and nitrate. Current velocity was selected from a group including substrate embeddedness and water turbidity, and percent cobble substrate composition from a group including percent boulder substrate composition.

TABLE 1. SPECIES COLLECTED FROM EIGHT SITES ON THE NEOSHO RIVER, LYON CO., KS, NOVEMBER 2000 TO OCTOBER 2001, SHOWING PERCENT COMPOSITION BY SPECIES, INCLUSION OF ADULT (A) AND JUVENILE (J) TAXA IN CA ORDINATION, AND CORRELATIONS (PEARSON'S *R*) OF TAXON ABUNDANCE WITH CA 1 AND 2. Criterion for inclusion was occurrence in at least 5% of collections. (*Juvenile and adults were not distinguished for *Gambusia affinis*).

Species	% Assemblage composition	Taxa included in CA	CA 1 *r*	CA 2 *r*
Cyprinella lutrensis	45.04	A	−0.15	−0.51
		J	0.41	−0.10
Notropis buchanani	11.13	A	−0.64	0.19
		J	−0.07	−0.02
Pimephales notatus	10.88	A	−0.28	0.05
		J	−0.01	0.36
Lepomis humilis	7.67	A	−0.22	−0.17
		J	0.01	0.13
Percina phoxocephala	7.56	A	−0.26	−0.45
		J	−0.30	0.06
Pimephales vigilax	4.94	A	0.04	0.02
		J	0.25	0.10
Etheostoma spectabile	3.04	A	0.40	−0.15
		J	−0.17	−0.12
Pimephales tenellus	2.78	A	−0.34	0.03
		J	−0.06	0.04
Phenacobius mirabilis	1.29	A	−0.11	−0.53
Campostoma anomalum	1.20	A	−0.15	−0.24
		J	−0.37	0.06
Notropis stramineus	0.85	A	−0.09	<0.01
Ictalurus punctatus	0.75	J	0.05	0.03
Percina caprodes	0.56	A	−0.24	−0.34
		J	−0.30	0.02
Noturus placidus	0.44	A	−0.03	0.03
		J	0.01	0.13
Gambusia affinis	0.42	*	0.23	0.09
Percina copelandi	0.42	A	−0.28	−0.02
Lepomis cyanellus	0.36	A	−0.14	−0.15
		J	0.09	0.17
Lepomis macrochirus	0.22	J	0.25	0.24
Noturus flavus	0.16	A	0.08	−0.16
		J	−0.06	−0.10
Cyprinella camura	0.06			
Aplodinotus grunniens	0.06	J	−0.19	−0.05
Moxostoma sp.	0.04	J	−0.14	−0.12
Lepomis megalotis	0.03			
Fundulus notatus	0.02			
Pylodictis olivaris	0.02			
Lythrurus umbratilis	0.02			
Micropterus punctulatus	0.01			
Morone chrysops	0.01			
Dorosoma cepedianum	0.01			
Etheostoma flabellare	0.01			
Carpiodes sp.	0.01			

This resulted in the following 10 variables retained for correlation analysis with CA axes: percent substrate composition of sand, cobble, and bedrock, water depth and current velocity, water temperature, dissolved oxygen, chloride, chlorophyll *a* and river discharge.

RESULTS

We collected 15,215 fishes of 31 species, accounting for 44 taxa inclusive of juveniles and adults (Table 1). Ten families from five orders were represented; Cyprinidae had the greatest

TABLE 2. MEAN AND STANDARD DEVIATION OF ENVIRONMENTAL VARIABLES FOR EIGHTY-FOUR COLLECTIONS MADE OVER TWELVE MONTHS FROM EIGHT SITES. Eight collections were omitted from upstream sites (two from December and three from both January and February), three from downstream sites (one in December, one in January, and one in August), and one from distant sites (December).

	Upstream		Downstream		Distant	
	Mean	S. D.	Mean	S. D.	Mean	S. D.
Substrate composition (%)						
Bedrock	0.0	0.0	27.7	39.5	0.0	0.0
Boulder	1.6	3.4	0.2	0.5	0.0	0.0
Cobble	4.7	7.0	2.1	2.9	0.3	1.0
Pebble	33.4	8.7	26.1	17.1	36.4	7.1
Gravel	38.1	8.1	30.7	18.8	41.8	6.2
Sand	3.4	1.4	3.9	3.9	6.0	2.9
Clay/Silt	18.9	16.5	8.3	8.7	15.7	7.9
Other microhabitat variables						
Substrate compaction	2.2	0.3	2.4	1.0	1.8	0.3
Water depth (cm)	58.2	8.7	26.7	13.5	38.1	17.3
Flow velocity (m/s)	0.1	0.1	0.4	0.2	0.4	0.2
Water properties						
Dissolved oxygen (mg/L)	8.3	2.2	10.0	2.4	8.5	2.9
pH	8.0	0.1	8.0	0.2	8.0	0.2
Alkalinity (mg/L)	171.2	54.8	183.2	60.0	171.2	49.6
Hardness (mg/L)	232.8	42.8	239.7	51.4	237.9	47.9
Turbidity (NTU)	33.4	27.6	38.9	44.9	43.4	40.7
Dissolved carbon dioxide (mg/L)	10.2	3.5	10.4	4.0	10.7	4.2
Ammonia (mg/L)	0.0	0.0	0.0	0.0	0.0	0.0
Nitrate (mg/L)	0.0	0.0	0.0	0.0	0.0	0.0
Chloride (mg/L)	9.1	4.6	9.2	5.5	8.7	3.5
Sulfate (mg/L)	28.1	9.7	27.5	7.1	28.4	8.2
Particulate organic carbon (μg/L)	1555.8	931.7	1556.8	925.9	1793.7	1027.8
Chlorophyll *a* (μg/L)	704.0	604.7	510.7	620.8	506.5	487.1

number of species (10), followed by Percidae (5), Centrarchidae (5), and Ictaluridae (4).

Habitat varied among upstream, downstream, and distant sites (Table 2). Upstream sites were deeper and slower-flowing than downstream and distant sites. Downstream sites were shallowest, had the highest percentage substrate composition of bedrock, and had the lowest percentage composition of clay/silt.

Relative abundance of fishes varied with impoundment treatment and season (Table 3). *Cyprinella lutrensis* was the most abundant taxa at downstream and distant sites, and *P. notatus* or *N. buchanani* most abundant at upstream sites, depending on season. *Percina phoxocephala* was more abundant at downstream and distant sites than at upstream sites, and *Lepomis humilis* more abundant at upstream sites than at downstream or distant sites.

Axis 1 of the CA showed a temporal pattern of fish assemblage structure, covering a gradient of 5.6 standard deviations with an eigenvalue of 0.399, and explaining 16.8% of the variance. Month significantly affected Axis 1 scores (Table 4), with winter collections scoring highest and early summer collections lowest (Figs. 2, 3). There were no significant impoundment or interaction effects (Table 4). Axis 1 was positively correlated with dissolved oxygen and negatively correlated with water temperature, chlorophyll *a*, water depth and current velocity, percent substrate composition of sand, and river discharge (Table 5). Axis 1 thus represented a pattern of fish assemblage structure along a gradient from cold, shallow, and slow-flowing winter conditions to warm, deeper, and swifter-flowing summer conditions.

Taxa characteristic of winter collections were positively correlated with Axis 1, and taxa characterizing summer collections were negatively correlated (Tables 1, 3). Strong positive correlates included *G. affinis*, which was only collected in November and December, adult *E. spectabile*, and juvenile *C. lutrensis*, *P. vigilax*, and *L. macrochirus* (Table 1). Strong negative correlates of CA 1 included juvenile *P. caprodes*, *C. anom-*

TABLE 3. RELATIVE ABUNDANCE OF TAXA COLLECTED FROM UPSTREAM, DOWNSTREAM, AND DISTANT SITES DURING WINTER AND SPRING (A) AND SUMMER AND FALL (B). Abundance of some species differed by less than 0.1%; others were equal in abundance. (A = adult, J = juvenile).

Upstream			Downstream			Distant		
Rank	Taxon	%	Rank	Taxon	%	Rank	Taxon	%
A. Winter–Spring								
1	*P. notatus* A	21.5	1	*C. lutrensis* A	43.9	1	*C. lutrensis* A	65.8
2	*N. buchanani* A	20.6	2	*P. phoxocephala* A	11.7	2	*P. notatus* A	5.2
3	*L. humilis* J	14.7	3	*N. buchanani* A	10.7	3	*P. phoxocephala* A	4.8
4	*P. tenellus* A	7.4	4	*P. notatus* A	7.4	4	*C. lutrensis* J	4.7
5	*C. lutrensis* A	6.8	5	*C. lutrensis* J	6.0	5	*P. tenellus* A	3.8
6	*P. vigilax* A	5.7	6	*L. humilis* J	4.9	6	*L. humilis* J	3.4
7	*P. notatus* J	5.6	7	*P. vigilax* A	4.0	7	*P. vigilax* A	3.0
8	*P. phoxocephala* A	4.9	8	*E. spectabile* A	3.5	8	*N. buchanani* A	2.5
9	*C. lutrensis* J	3.7	9	*P. mirabilis* A	1.9	9	*E. spectabile* A	2.0
10	*E. spectabile* A	3.3	10	*N. stramineus* A	1.2	10	*P. copelandi* A	0.9
B. Summer–Fall								
1	*N. buchanani* A	18.6	1	*C. lutrensis* A	38.2	1	*C. lutrensis* A	20.5
2	*C. lutrensis* A	17.9	2	*C. lutrensis* J	23.3	2	*N. buchanani* A	16.3
3	*L. humilis* J	14.6	3	*P. phoxocephala* A	7.3	3	*C. lutrensis* J	15.4
4	*C. lutrensis* J	13.6	4	*P. notatus* A	5.4	4	*P. notatus* A	8.9
5	*P. notatus* A	8.9	5	*E. spectabile* A	4.3	5	*P. phoxocephala* A	7.4
6	*P. notatus* J	4.5	6	*N. buchanani* A	4.1	6	*P. vigilax* A	4.5
7	*P. tenellus* A	3.8	7	*P. vigilax* A	3.0	7	*P. notatus* J	3.6
7	*P. phoxocephala* A	3.8	8	*L. humilis* J	2.0	8	*L. humilis* J	3.1
9	*P. vigilax* A	3.3	9	*P. mirabilis* A	2.0	9	*E. spectabile* A	3.0
10	*E. spectabile* A	1.2	10	*P. vigilax* J	1.9	10	*P. mirabilis* A	2.9

alum, and *P. phoxocephala*; these age-0 fishes were present only from June through early Fall. Low-scoring adult taxa included *N. buchanani* and *P. tenellus*; these two taxa were collected most frequently from April through August, with *N. buchanani* almost completely absent in other months.

Axis 2 of the CA showed a spatial pattern of fish assemblage structure related to low-head dams, with a slight temporal component, covering a gradient of 3.5 standard deviations with an eigenvalue of 0.315, and explaining 13.3% of the variance. Impoundment, month, and impoundment-by-month interaction significantly affected Axis 2 scores (Table 4). Upstream sites scored higher than downstream sites (Fig. 2). Relative position of distant site scores varied temporally, grouping with downstream sites in winter and spring, and upstream sites in summer and fall (Fig. 2). Axis 2 was negatively correlated with current velocity and dissolved oxygen and positively correlated with water depth and chloride (Table 5). Axis 2 thus represented a pattern of fish assemblage structure along a gradient from lotic habitat downstream from dams to lentic habitat upstream from dams.

Correlations of fish taxa with Axis 2 differed between riffle species, predominant at downstream sites, and pool species, prevalent at upstream sites (Tables 1, 3). With the exception of

TABLE 4. RESULTS OF TWO-WAY REPEATED-MEASURES ANALYSIS OF CA 1 AND CA 2 SCORES FOR COLLECTIONS FROM THE NEOSHO RIVER, KS, 2000–2001, WITH MONTH AND IMPOUNDMENT AS TREATMENTS.

Axis	Effect	Numerator d.f.	Denominator d.f.	*F*	*P*
CA 1	Impoundment	2	5	0.66	0.558
	Month	11	45	31.34	<0.0001
	Interaction	20	45	1.21	0.291
CA 2	Impoundment	2	5	24.51	0.003
	Month	11	45	3.78	0.001
	Interaction	20	45	2.59	0.004

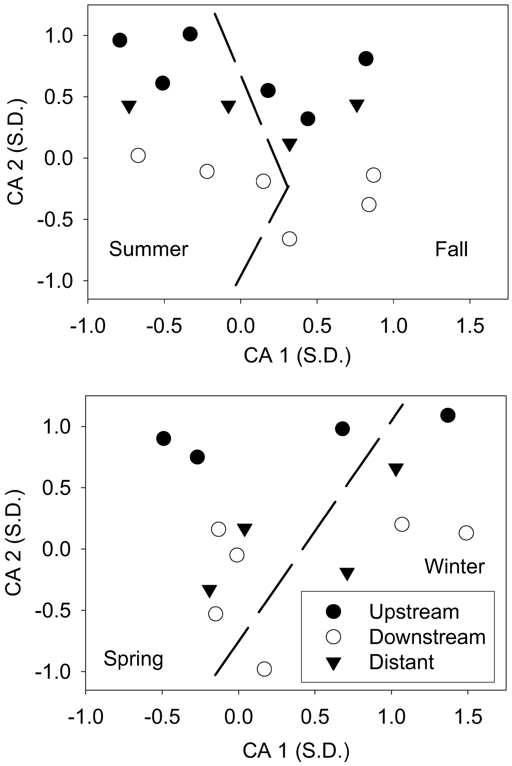

Fig. 2. Plot of CA 1 vs. CA 2 scores by season for collections from the Neosho River, KS, 2000–01, grouped by impoundment treatment. Seasons were defined monthly as Winter (December–February), Spring (March–May), Summer (June–August), and Fall (September–November).

C. lutrensis, most strong negative correlates of Axis 2 were benthic riffle fishes, such as *P. phoxocephala*, *P. mirabilis*, *C. anomalum*, and *P. caprodes*. Strong positive correlates included midwater species most abundant in slow waters of upstream sites, such as *P. notatus* juveniles, *Lepomis* spp., and *N. buchanani* adults (Table 1).

Differences in seasonal abundance patterns among species led to the significant temporal and interaction effects on Axis 2 scores (Table 3). Several positively-correlated taxa (*N. buchanani* adults, *P. notatus* juveniles, and *Lepomis humilis* juveniles) were more abundant, and negatively-correlated taxa (*C. lutrensis* adults, *P. phoxocephala* adults, and *P. mirabilis* adults) less abundant, at upstream sites than at downstream sites in all seasons (Table 3). Abundance at distant sites, however, varied seasonally (Fig. 2). As a consequence of these temporal changes in fish species composition, Axis 2 scores for distant sites were relatively higher in summer and fall than in winter and spring, leading to the significant interaction. Several taxa, including *N. buchanani* adults, *P. vigilax* juveniles, and *G. affinis*, loaded strongly on both Axis 1 and Axis 2, and thus were important in defining both temporal and impoundment gradients. The fact that these taxa were strongly associated with lentic habitat upstream from dams and also varied temporally in abundance likely contributed to the significant month effect on Axis 2 scores.

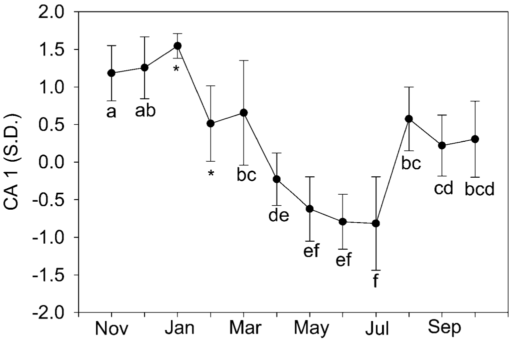

Fig. 3. Plots of monthly mean and standard deviation collection CA 1 scores. Months not differing significantly, as determined by Tukey-Kramer tests on CA 1 scores, share lowercase letters. Means for which sample sizes were too small to calculate least square means used in Tukey-Kramer tests are denoted by an asterisk.

DISCUSSION

This study indicated that low-head dams can influence structure of small-bodied fish assem-

TABLE 5. PEARSON'S CORRELATION COEFFICIENT OF SELECTED ENVIRONMENTAL VARIABLES WITH CA 1 AND CA 2 COLLECTION SCORES. Correlations significant at α = 0.05 are denoted by an asterisk, and those significant at α = 0.01 by two asterisks.

	CA 1	CA 2
Percent substrate composition		
Sand	−0.333**	0.006
Cobble	−0.030	−0.041
Bedrock	0.197	−0.209
Other microhabitat variables		
Water depth	−0.331**	0.344**
Water flow velocity	−0.213*	−0.558**
Water chemistry variables		
Dissolved oxygen	0.540**	−0.252*
Chloride	0.021	0.249*
Other variables		
Chlorophyll *a*	−0.223*	0.182
Water temperature	−0.638**	0.086
River kilometer	−0.182	−0.214
River discharge	−0.471**	−0.172

blages in shallow waters of rivers via habitat alteration. Sites upstream from dams were deepest with slow-flow velocities and high siltation levels, with fish assemblages characterized by a high abundance of lentic habitat fishes. Sites downstream from low-head dams were shallowest, with scoured substrata including bedrock, and low levels of silt accumulation. Fish assemblages at these sites showed a higher abundance of riffle species commonly found in shallow, high-current velocity habitats. Fish assemblages intermediate to these two extremes occurred at sites distant from low-head dams. This pattern of upstream and downstream habitat alteration is similar to that shown for larger dams (e.g., Kondolf, 1997; Camargo and Voelz, 1998; Bennett et al., 2002), but ours is one of the first studies to document these patterns of habitat alteration and associated fish assemblage differences in a river impounded by low-head dams.

Our results differed slightly from those of previous investigators studying fish assemblages in systems with low-head dams. Raborn and Schramm (2003) and Dodd et al. (2003) showed differences in habitat, but not fish assemblages, between dammed and free-flowing streams and stream segments. The discrepancy between our results and theirs is likely due to spatial scale; we compared small sites within a river, as opposed to stream reaches or entire streams. Our sites were shorter than those of the above investigators and spaced adjacent to multiple impoundments, allowing detection of these smaller-scale alterations of the fish assemblage. In rivers impounded by large dams, fish assemblages can be influenced by impoundments for many kilometers downstream (Kinsolving and Bain, 1993). Effects of low-head dams, however, appear to be more localized, restricted to habitat alteration immediately upstream and downstream. In addition, low-head dams such as those in our study do not severely alter river temperature and discharge as hydroelectric dams do (Kinsolving and Bain, 1993; Clarkson and Childs, 2000). This may explain the high abundance of benthic fishes we observed downstream from dams, as compared to the low abundance of these fishes shown by Travnichek and Maceina (1994) downstream of a hydroelectric dam. Likewise, we did not find the pattern of decreased upstream species richness shown by Porto et al. (1999); rather, fish assemblage structure followed repeated gradients of lentic habitat upstream from dams to lotic habitat downstream. This result is not surprising, given that the species we collected in the Neosho River are not migratory, thus eliminating the need to cross these barriers for species to persist. In addition, the Neosho River is a much larger system than the Great Lakes tributaries studied by Porto et al. (1999), perhaps limiting downstream transport of fishes and providing sufficient habitat to maintain fish populations upstream. Despite these differences with previous studies, our results do show that low-head dams can produce noticeable changes in the spatial pattern of lotic fish assemblages.

Study sites also exhibited a great deal of temporal variation in assemblage structure, as shown by CA Axis 1 scores. Because CA calculates axes of decreasing ecological significance (Gauch, 1982), it may be inferred that assemblage patterns associated with Axis 1 were stronger than those associated with Axis 2. Complete faunal turnover typically occurs across an axis length of 4 standard deviations (Gauch, 1982); thus, Axis 1's length of 5.6 standard deviations represented a strong temporal pattern. The temporal nature of Axis 1 is confirmed by strong correlations of axis scores with environmental variables that vary seasonally, such as water temperature (Table 5). A high degree of overlap among multiple comparison groupings indicates that seasonal fish assemblages were not mutually exclusive, but rather components of a gradual assemblage shift over the study year. These results are consistent with Gelwick's (1990) conclusion that lotic fish assemblages in shallow water show a great deal of temporal variation. Separation of species into juvenile and adult taxa could inherently bias our study towards temporal variation because of natural processes such as recruitment. However, a parallel analysis on species only also showed assemblage variation to be greater temporally than spatially (D. P. Gillette, 2002, unpubl. data). This supports the conclusion that, at least at the spatial scale of the present study, temporal patterns of shallow-water fish assemblages in the Neosho River, as measured by position in multivariate space, are stronger than spatial patterns.

Temporal assemblage variation came from two sources: fish life history processes and assemblage responses to changing abiotic conditions. As an example of the former, *N. buchanani* was absent from our study sites until early summer, when it occurred in great numbers. This was likely a spawning migration from nearby pools; Pflieger (1997) stated that this pool species spawns over riffles from late April through August, dates corroborated in Kansas by Cross and Collins (1995). Reproduction of *E. spectabile*, *P. phoxocephala*, *P. caprodes*, *P. mirabilis*, and *C. anomalum* also changed assemblage composition through an influx of juveniles persisting from June through September. In addition to these patterns, many species also declined greatly in abundance or were absent during winter. This pattern appears to be unrelated to life history events, because all of these species spawn from late spring through summer in Kansas (Cross and Collins, 1995) and were present at our study sites during both early spring and late fall. Rather, this pattern is likely due to a sharp drop in water temperature from November to December that, coupled with shallower river depths in winter, caused these species to vacate gravel bars and retreat to nearby pools. With the exception of *N. flavus*, all of these species have been shown to inhabit pools at various times. *Noturus flavus* spawns in pools with moderate current in Kansas (Cross and Collins, 1995), so it may also be able to use pool habitat when water temperatures on shallow gravel bars become too cold. After water temperatures rose sharply from March to April, these species returned to gravel bars. The fact that adults of many species survived the winter to spawn, but were not collected on gravel bars during winter, suggests that deeper water may play a major role in providing winter refugia for species that frequent gravel bars in warmer months. This conclusion supports recent conceptual models of stream fish ecology emphasizing the spatial arrangement of habitat patches used by fishes under varying abiotic conditions and during different life history stages (Schlosser, 1991, 1995; Fausch et al., 2002).

Given the high degree of habitat variability, variable sampling efficiency among our study sites cannot be ruled out. Although there are no published accounts of sampling efficiency for the kick-set methodology we employed, Peterson et al. (2004) showed that estimation of salmonid abundance by multipass electrofishing varied with stream area and substrate composition. As mentioned in Materials and Methods, we eliminated two collections because flow velocity was insufficient to allow effective sampling. However, water depth, flow velocity, and substrate composition varied among sites and months during our study, possibly resulting in variable sampling efficiency.

Few studies have examined spatial patterns of fish assemblage structure on scales large enough to assess assemblage response to multiple impoundments. Reyjol et al. (2001) showed that flow alteration by hydroelectric impoundments along a salmoniform-cypriniform transitional gradient caused an oscillation in dominant taxa corresponding to alterations in current velocity. With few free-flowing river systems remaining in the world, other situations similar to that in the Neosho River likely exist where multiple impoundments affect the spatial pattern of riverine fish assemblages via localized habitat alteration. Effective conservation of these lotic systems and their biota requires knowledge of the spatiotemporal structure of fish assemblages in response to such alterations.

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