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Title: Spatial Pattern of Fish Assemblage Structure and Environmental Correlates in the Spring River Basin, with Emphasis on the Neosho Madtom (*Noturus placidus*)

Abstract approved: David R. Edds

Collections of the threatened Neosho madtom (*Noturus placidus*) made in 1993-94 confirm the persistence of a disjunct population in the Spring River. We captured 87 Neosho madtoms at 19 sites, extending the known distribution of the species in the Spring River 1.5 km upstream and 26 km downstream, with one downstream site representing a newly discovered subunit of the species' distribution. Mean overall Neosho madtom densities in the Spring River were 0.9 - 1.8 per 100 m^2, substantially lower than those reported from other portions of the species' range.

We also examined patterns of spatial heterogeneity in the Spring River basin fish assemblage along with environmental correlates to assess the relative importance of geographic distances and habitat differences among sites in explaining assemblage structure. Mantel tests and Mantel correlograms indicated that fish species composition and abundance were spatially autocorrelated and exhibited patch size of about 44 km at the basinwide scale. We used partial Mantel tests to remove the effects of spatial autocorrelation from habitat variables before modeling habitat factors influencing fish assemblage structure. Space-constrained cluster analysis and principal coordinates analysis revealed three primary groups of sites, reflecting relatively distinct fish faunas

within the Ozark, Lowland, and mainstream regions of the basin. Within individual streams, longitudinal pattern was more apparent than it was at the basinwide scale, and spatial autocorrelation of species and environmental differences were of varying importance, consistent with the concept that stream systems act as mosaics of interacting patches. Spatial patterns of the fish assemblage and environmental correlates were consistent with a hypothesis of vicariance biogeography as the primary organizing factor, but a linkage between mainstream and tributary assemblages, along with spatial autocorrelation in species composition, suggested biotic contagious processes are important in maintaining assemblage structure, particularly at the interface between the mainstream Spring River and its tributaries.

Spatial Pattern of Fish Assemblage Structure and Environmental Correlates in the Spring River Basin, with Emphasis on the Neosho Madtom (*Noturus placidus*)

A Thesis
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PREFACE

My thesis deals with ecology of stream fishes in the Spring River basin of Kansas, Missouri, and Oklahoma. The emphasis of Chapter One is the Neosho madtom, a catfish species listed by the U.S. Fish and Wildlife Service as threatened. Because this study involved the ecology of a federally-listed species, I felt it was important to disseminate the information through publication as soon as possible. Thus, Chapter One is organized as required for publication in *The Southwestern Naturalist*, where it has already been published in a similar form (Wilkinson, C., D. Edds, J. Dorlac, M.L. Wildhaber, C.J. Schmitt, and A. Allert. 1996. Neosho madtom distribution and abundance in the Spring River. *The Southwestern Naturalist* 41:78 - 81). The other authors have given me their permission to use the manuscript for my thesis, as this was the original intent of the study. Chapter Two is written in the format required by *The Canadian Journal of Fisheries and Aquatic Sciences*, where I intend to submit the manuscript with my major advisor, Dr. David Edds, as co-author.

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Chapter 1

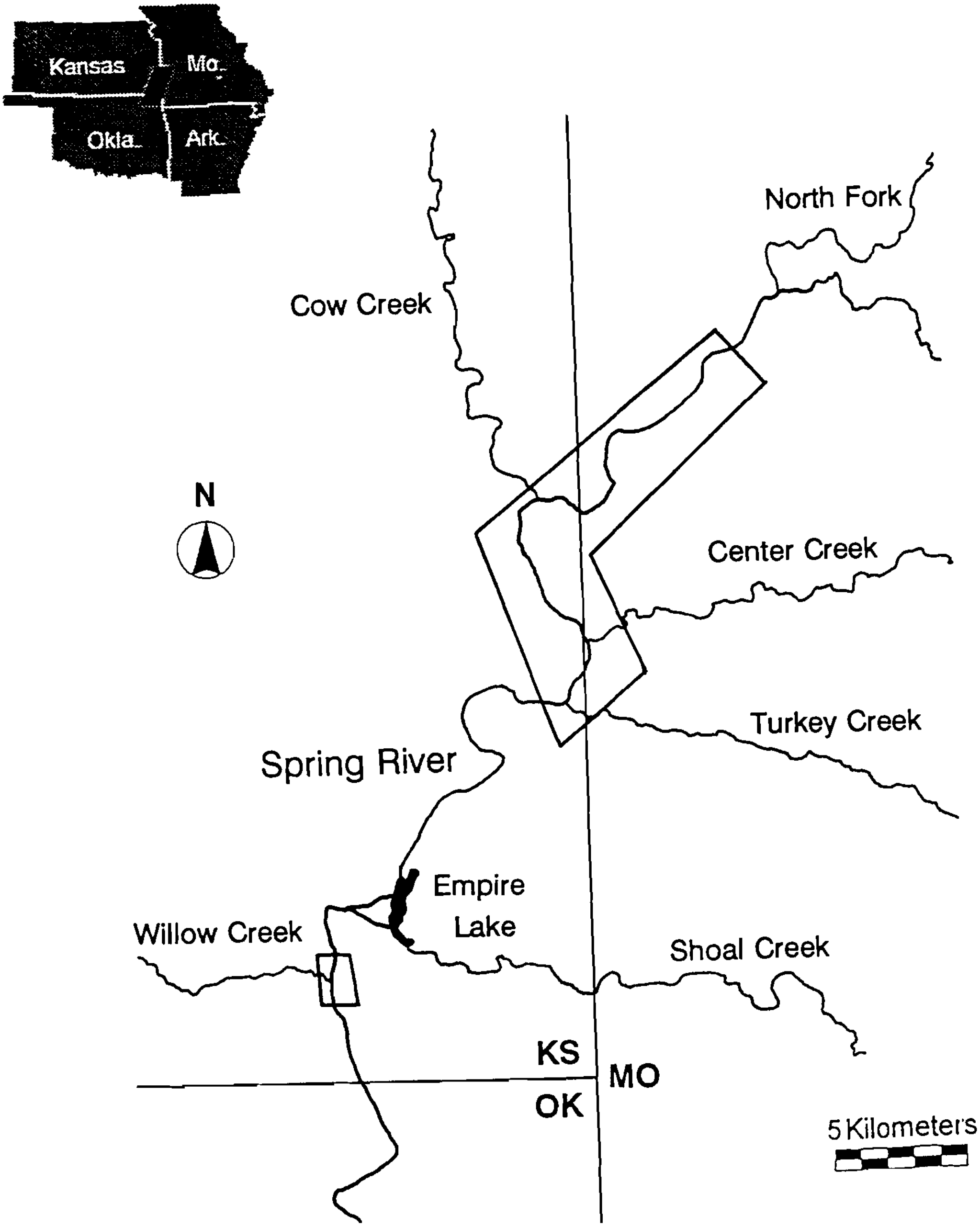
Neosho madtom distribution and abundance in the Spring River

The Neosho madtom, *Noturus placidus* Taylor, is a species of catfish listed as threatened by the U.S. Fish and Wildlife Service (55 F.R. 21148). Its distribution is restricted to the Neosho River basin upstream from Lake o' the Cherokees (Grand Lake), Oklahoma. Although its historical range extended over a larger area prior to construction of mainstream impoundments, the Neosho madtom is now found almost exclusively in the Neosho and Cottonwood rivers of Kansas (USFWS, 1991; but see Wilkinson and Fuselier, 1997). The species persists at low densities, however, in two other areas: a short stretch of the Neosho (Grand) River in Oklahoma upstream from Lake o' the Cherokees (Luttrell et al., 1992; Wenke et al., 1992) and a portion of the Spring River in extreme southwestern Missouri and southeastern Kansas (Fig. 1).

The Neosho madtom was first documented in the Spring River in 1963, but past records documented only 15 individuals from eight collections at four mainstream sites, two in Missouri and two in Kansas (Pflieger, 1971; USFWS, 1991). The historical population of Spring River Neosho madtoms is separated from conspecifics in the Neosho River by three dams, more than 50 river km, and the upper portion of Lake o' the Cherokees, impounded in 1941. Physicochemical factors, including a paucity of suitable habitat, have been suggested as potential limiting factors for the Neosho madtom in the Spring River (Moss, 1983; USFWS, 1991).

Additionally, the Spring River in Cherokee County, Kansas, and Jasper County, Missouri, drains EPA Superfund cleanup sites where abandoned lead, zinc, and coal mines have polluted surface and ground waters in the drainage (Spruill, 1984). The Neosho madtom recovery plan (USFWS, 1991) called for an intensive survey for the Neosho

Figure 1. Map of the Spring River Basin, with polygons enclosing Spring River mainstream locations where Neosho madtoms were collected during 1993-94 (Appendix 1).


Kansas
Mo.
Okla.
Ark.
N
Cow Creek
North Fork
Center Creek
Turkey Creek
Spring River
Empire
Lake
Willow Creek
Shoal Creek
KS
MO
OK
5 Kilometers

madtom in the Spring River of Missouri, Kansas, and Oklahoma. Objectives of our study were to assess Neosho madtom distribution and abundance in this river.

We sampled 106 locations along the Spring River in Missouri (53 sites), Kansas (39 sites), and Oklahoma (14 sites). Sample sites were chosen to represent the variety of habitats available from headwaters to tailwaters, and were sampled in haphazard fashion along the mainstream. Sites typically encompassed at least one riffle/run/pool series, but occasionally consisted of only one gravel bar. One crew sampled from March to September 1993 (70 sites), another from July to August 1994 (18 sites), and a third from September to October 1994 (18 sites). Sampling was performed by kick-seining with a heavily-weighted 4.7 mm-mesh seine during daylight hours. In 1993 and July through August 1994, the area of each haul (11.5 m^2; 4.6-m seine with substrate disturbed starting 2.5 m upstream) was greater than that in September and October 1994 (4.5 m^2; 1.5-m seine with substrate disturbed 3.0 m upstream). All fishes were identified and counted; Neosho madtoms were measured, photographed, and released alive at the site of capture following completion of sampling at each location.

The total number of kick-hauls performed at each site was recorded. Neosho madtom density of occurrence (species-specific density) was calculated by dividing the number of individuals captured by the area sampled in hauls that yielded the species, and overall density was calculated by dividing the number of Neosho madtoms captured by the total area sampled by kick-hauls at sites yielding the species (Wenke et al., 1992).

We collected nine Neosho madtoms at five sites in 1993, 52 at 12 sites in July and August 1994, and 26 at nine sites in September and October 1994. We captured the species at 15 of 79 different sites sampled in 1993 and July through August 1994 combined, and at nine of 18 locations in September and October 1994. All historical sites of occurrence (sites 3 and 5 in Missouri, and 11 and 13 in Kansas; Appendix 1) yielded Neosho madtoms.

Fifteen sites represented new collection localities for this species (Appendix 1): five in Missouri (sites 1, 2, 4, 6, and 7) and 10 in Kansas (sites 8-10, 12, and 14-19). Sites 1 and 2 extended the known distribution of the Neosho madtom in the Spring River 1.5 km upstream in Missouri (W.L. Pflieger, Missouri Dept. Cons., pers. comm.). Seven sites (7, 14-19) extended the known distribution 26 km downstream, covering virtually all but approximately the last 4 km of the Spring River in Kansas (Fig. 1). No Neosho madtoms were captured in the Spring River in Oklahoma.

Overall density per 100 m^2 ranged from 0.3 - 1.8 ($\bar{x} = 0.9$) in 1993, 0.3 - 4.6 ($\bar{x} = 2.1$) in July and August 1994, and 1.5 - 13.3 ($\bar{x} = 4.3$) in September 1994. Density of occurrence per 100 m^2 ranged from 8.7 - 10.9 ($\bar{x} = 9.1$) in 1993, 8.7 - 17.4 ($\bar{x} = 11.3$) in July and August 1994, and 22.2 - 66.7 ($\bar{x} = 30.0$) in September and October 1994. Maximum overall density (13.3) was documented in 15 4.5-m^2 kick hauls, and maximum density of occurrence (66.7) was based on nine individuals in three 4.5-m^2 kick hauls; both occurred at site 4 in October 1994. Thirty-nine of the 87 Neosho madtoms captured were judged to be young-of-year, based on lengths. Young-of-year ranged 26 - 43 mm total length in 1993, 27 - 50 mm in July and August 1994, and 30 - 59 mm in September and October 1994.

Our survey indicates that density of Neosho madtoms in the Spring River is low.

Their distribution in this river generally extended from downstream of the mouth of the North Fork of Spring River in Jasper County, Missouri, through the area near the mouth of Turkey Creek in Cherokee County, Kansas. Additionally, young-of-year Neosho madtoms captured for the first time upstream from the mouth of Willow Creek near Baxter Springs, Kansas, (site 19) may represent an isolated population separated from other Spring River collection localities by Empire Lake (Lowell Reservoir) and from Neosho River populations by Lake o' the Cherokees. The Neosho madtom has never been documented from the Spring River in Oklahoma (USFWS, 1991; Luttrell et al., 1992).

Collections of Neosho madtoms at 15 new locations in the Spring River was likely due, at least in part, to our intensive sampling effort over a 19-month period. Previous surveys did not specifically examine the distribution and abundance of this species in the Spring River. Lower mean densities in 1993 might have been the result of summer floods which could have hampered Neosho madtom reproduction, recruitment, or both, and might also have limited sampling effectiveness. Higher density estimates in the relatively dry summer of 1994 could have been the result of river conditions that favored recruitment, enhanced sampling effectiveness, or both. M. Eberle and W. Stark (Natural Science Research Associates, Hays, Kansas), in a 1995 report to Kansas Department of Wildlife and Parks, documented higher numbers of Neosho madtoms in the Neosho and Cottonwood rivers in 1994, compared to previous years, and suggested that higher densities in 1994 might reflect improved habitat conditions due to freshly deposited, loose gravel from 1993 floods. Though difficult to judge given the lack of sufficient previous data for comparison, it is possible that low densities of Neosho madtoms in the Spring

River in 1993 are the norm for that river (M. Eberle, pers. comm.).

Mean estimates of densities of Neosho madtoms in the Spring River for both years were lower than those reported from the Neosho and Cottonwood rivers by other investigators. Moss (1983) recorded a mean density of occurrence of 43.3/100 m^2 and a mean overall density of 32.4/100 m^2 from four night-time electroshocking samples at one Neosho River riffle west of Erie, Kansas, sampled seasonally during 1975-76. Wenke et al. (1992) documented a mean density of occurrence of 17.0/100 m^2 and a mean overall density of 6.8/100 m^2 in the Neosho and Cottonwood rivers in 1989-90. Fuselier and Edds (1994) noted a mean density of occurrence of 15.5/100 m^2 and a mean overall density of 3.3/100 m^2 in the Cottonwood River in 1992-93. One exception was the mean density of occurrence of 30.0/100 m^2 for September and October 1994. This estimate was made from a small area sampled in each kick-haul (4.5 m^2), where the minimum density of occurrence possible was 22.2/100 m^2 (i.e., one fish per haul). Nevertheless, Neosho madtom densities may typically be highest in fall, after young-of-year are added to the population.

Though sample size, timing, and investigators differed among the studies noted here, density of Neosho madtoms in the Spring River appears to be less than elsewhere in its range. Ongoing projects are directed at understanding why Neosho madtom numbers differ between the Spring River and the Neosho and Cottonwood rivers. Continued research into the effects of environmental factors on the density, distribution, relative abundance, recruitment, and year-to-year variation of the disjunct Neosho madtom population of the Spring River is vital to our understanding of this threatened species and its eventual recovery.

Support for this research was provided by the Kansas Department of Wildlife and Parks through USFWS Section 6 funds, an Emporia State University Faculty Research and Creativity grant, the National Biological Service, the U.S. Fish and Wildlife Service, and Region VII of the U.S. Environmental Protection Agency. A. Bissing, K. Brunson, J. Bryan, C. Charbaneau, J. Criqui, F. Durbian, R. Ferguson, D. Hardesty, P. Heine, G. Horak, P. Lovely, M. Legg, B. Mueller, D. Mulhern, M. Means, D. Munie, S. Olson, J. Pitt, B. Poulton, S. Ruessler, B. Schrage, J. Sumner, V. Tabor, T. Thorn, R. Walton, D. Whites, and D. Wright assisted with fieldwork or other aspects of the study. L. Fuselier and M. Eberle made helpful suggestions that improved the manuscript. Thanks to conservation agencies in Missouri, Kansas, Oklahoma, and to USFWS regions 2, 3, and 6 for issuing collecting permits. Special thanks to landowners along the Spring River who graciously allowed access to study sites.

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Appendix 1. Spring River Neosho madtom collection localities, with general and legal site descriptions, and dates of collections.

Jasper Co., Missouri: **Site 1)** 0.4 km downstream from county bridge 2.5 km east of Waco; NE 1/4 Sec. 18, T29N, R33W; 10 and 12 August and 10 October 1994. **Site 2)** 0.4 km upstream from MO Hwy 171 bridge; SW 1/4 Sec. 18, T29N, R33W; 11 August 1994. **Site 3)** 0.2 km downstream from MO Hwy 171 bridge; NE 1/4 Sec. 24, T29N, R34W and NW 1/4 Sec. 19, T29N, R33W; 11 August 1994. **Site 4)** 0.4 km upstream from county bridge 2.8 km south of Waco; SW 1/4 Sec. 23, T29N, R34W; 9 August and 3 October 1994. **Site 5)** 0.2 km downstream from county bridge 2.8 km south of Waco, 0.8 km east of KS-MO state line; NW 1/4 Sec. 26, T29N, R34W; 8 August and 4 October 1994. **Site 6)** 2 km downstream from county bridge 2.8 km south of Waco, 0.8 km east of KS-MO state line; NE 1/4 Sec. 35, T29N, R34W; 2 October 1994. **Site 7)** 5 km SW of Carl Junction, just downstream from Center Creek confluence; SW 1/4 Sec. 14, T28N, R34W; 15 August 1993.

Cherokee Co., Kansas: **Site 8)** 0.2 km downstream from KS-MO state line in right channel of river; SE 1/4 Sec. 1, T33S, R25E; 26 July 1994. **Site 9)** 0.7 km downstream from KS-MO state line in right channel of river; SE 1/4 Sec. 1, T33S, R25E; 27 July 1994. **Site 10)** 0.9 km downstream from KS-MO state line in right channel of river; NW 1/4 and SW 1/4 Sec. 1, T33S, R25E; 20 July 1994. **Site 11)** 0.6 km upstream from mouth of Cow Creek at bottom of island in both channels of river; SW 1/4 Sec. 1 and SE 1/4 Sec. 2, T33S, R25E; 5 September 1993 and 27-28 July 1994.

Site 12) 0.3 km upstream from KS Hwy 96 bridge; SW 1/4 Sec. 11, T33S, R25E; 4 September 1993 and 21 September 1994. **Site 13)** just upstream from KS Hwy 96 bridge; SW 1/4 Sec. 11, T33S, R25E; 4 September 1993 and 19 July and 22 September 1994. **Site 14)** 0.7 km downstream from KS Hwy 96 bridge in right channel of river; NE 1/4 Sec. 14, T33S, R25E; 3 August and 28 September 1994. **Site 15)** 1.4 km downstream from KS Hwy 96 bridge in left split of river; SE 1/4 Sec. 14, T33S, R25E; 3 August 1994. **Site 16)** 2.3 km downstream from KS Hwy 96 bridge; NW 1/4 Sec. 24, T33S, R25E; 27 September 1994. **Site 17)** 1 km upstream from Turkey Creek confluence; SE 1/4 Sec. 25, T33S, R25E; 5 September 1993. **Site 18)** immediately downstream from Turkey Creek confluence; NW 1/4 Sec. 36, T33S, R25E; 6 September 1993. **Site 19)** 0.6 km upstream from Willow Creek confluence in left channel of river; NE 1/4 Sec. 36, T34S, R24E; 6 October 1994.

Chapter 2

Spatial pattern and environmental correlates of the Spring River basin fish assemblage

Abstract

We examined patterns of spatial heterogeneity in the Spring River basin fish assemblage along with environmental correlates to assess the relative importance of geographic distances and habitat differences among sites in explaining assemblage structure. Mantel tests and Mantel correlograms indicated that fish species composition and abundance were spatially autocorrelated and exhibited a patch size of about 44 km at the basinwide scale. We used partial Mantel tests to remove the effects of spatial autocorrelation from habitat variables before modeling habitat factors influencing fish assemblage structure. Substrate particle size, mesohabitat type, nitrate, CO_2, pH, stream gradient, and stream size were significantly correlated to principal coordinate axes of spatially-corrected environmental matrices. Space-constrained cluster analysis and principal coordinates analysis revealed three primary groups of sites, reflecting relatively distinct fish faunas within the Ozark, Lowland, and mainstream regions of the basin. Within individual streams, longitudinal pattern was more apparent than it was at the basinwide scale, and spatial autocorrelation of species and environmental differences were of varying importance, consistent with the concept that stream systems act as mosaics of interacting patches. Spatial patterns of the fish assemblage and environmental correlates were consistent with a hypothesis of vicariance biogeography as the primary organizing factor, but a linkage between mainstream and tributary assemblages along with spatial autocorrelation in species composition suggested contagious biotic processes are important in maintaining assemblage structure, particularly at the interface between the mainstream Spring River and its tributaries.

Introduction

Processes underlying spatial heterogeneity in stream communities include biotic and abiotic factors which act together to influence community structure (Power et al. 1988; Palmer and Poff 1997). Stream fish communities have primarily been characterized as varying longitudinally along gradients of physical and chemical habitat variables (e.g., Schlosser 1987). Some researchers have recognized that movements by individuals are important processes in structuring lotic communities (Power et al. 1988; Freeman 1995) and, in some cases, processes occurring downstream can affect communities upstream (Osborne and Wiley 1992; Pringle 1997).

Recently ecologists have begun to emphasize the importance that spatial autocorrelation, the similarity among variables based on the proximity of collecting sites to one another, can have as a factor explaining the structure of communities (Legendre 1993; Mandrak 1995; Cooper et al. 1997). Quantifying spatial pattern in communities can be critical to identifying processes underlying community patterns (Sokal and Thomson 1987), and allows assessment of the relative importance of different hypotheses seeking to explain observed heterogeneity (Douglas and Endler 1982; Burgman 1987; Mandrak 1995). In addition, spatial autocorrelation among data can lead to spurious correlations between variables responding to a common underlying spatial pattern, and should be removed from community response data before drawing inferences about processes underlying the patterns (Legendre 1993; Mandrak 1995). Models of community structure which include the influence of spatial autocorrelation are still in their early stages of development (Legendre 1993), but statistical techniques designed to study autocorrelation among ecological data have allowed researchers to begin quantifying spatial pattern in communities. Quantification of spatial autocorrelation in stream communities provides a way to identify the scale at which patches exist and can be used to assess the importance of spatial dependence in models of community structure (Cooper et al. 1997). However, few studies have used autocorrelation techniques to examine spatial heterogeneity in stream communities (but see Douglas and Endler 1982; Cooper et al. 1997).

The Spring River basin, situated in southwestern Missouri, southeastern Kansas, and northeastern Oklahoma, provides an ideal system to study spatial pattern of fish assemblage structure. The basin contains a diverse fish assemblage and is positioned between two physiographic provinces: the Central Lowlands and the Ozark Plateaus (Fig.1; Davis and Schumacher 1992; Adamski et al. 1995), regions also known as the Central Irregular Plains and Ozark Highlands ecoregions (Omernik 1987). Differences in habitats between the two portions of the drainage presumably limit movement of fishes adapted to a specific set of physicochemical variables (Matthews 1987; Mayden 1987a; 1987b). However, movement by individuals within streams and their dispersal from source areas to sink areas might be an important factor influencing fish species composition at some locations, particularly near the mouths of tributaries (Gorman 1986; Osborne and Wiley 1992). The goals of the current study were to describe spatial pattern in the Spring River basin fish assemblage and to use this information to draw inferences about the relative importance of abiotic and biotic factors in influencing assemblage structure. Our specific objectives were to 1) quantify spatial pattern of fish assemblage structure within the Spring River basin and identify distances over which contagious biotic processes such as reproduction, mortality, and movements of individuals might affect assemblage structure, 2) assess the importance of spatial autocorrelation relative to physicochemical differences influencing fish assemblage structure on the regional scale and within individual streams, and 3) analyze patterns of species similarity to assess the relationship between mainstream and tributary fish assemblages.

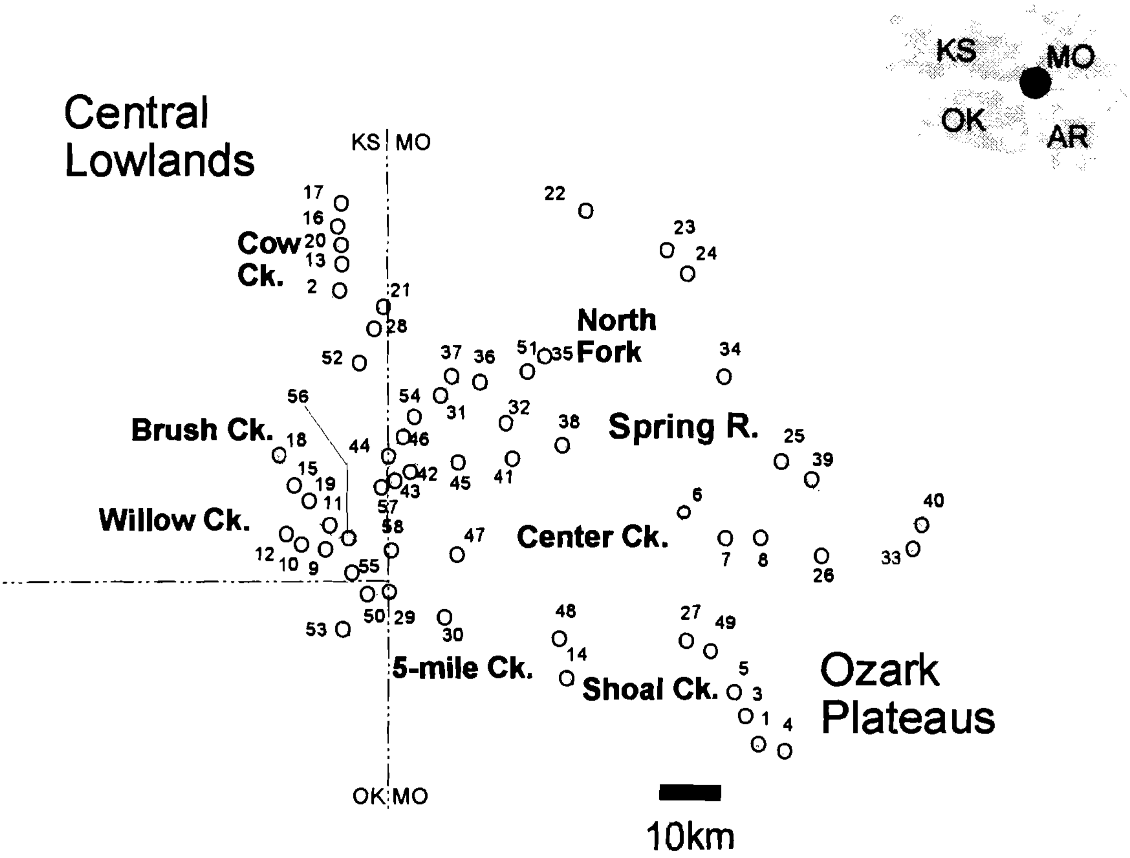
Materials and Methods

Study Site

The Spring River, part of the Arkansas River basin, forms a border between the Central Lowlands and Ozark Plateaus (Davis and Schumacher 1992; Adamski et al. 1995). Tributaries draining the Central Lowlands region in the northern and western portions of the Spring River basin (Fig. 1) are characterized by low gradients, poorly sustained base flows, and substrates consisting of mud and silt with shale and sandstone gravel (Davis and Schumacher 1992; Adamski et al. 1995). In contrast, tributaries flowing out of the Ozark Plateaus in the southeastern portion of the basin (Fig. 1) have generally higher gradients, sustained flows due to headwater springs, and substrates predominated by limestone and chert gravel (Davis and Schumacher 1992; Adamski et al. 1995). Annual precipitation averages 102 - 107 cm throughout the Spring River basin (Adamski et al. 1995), and altitude in the study site ranges from 223 m at the most downstream location sampled in the Spring River mainstream to 451 m at the headwaters of Shoal Creek.

During our study we sampled North Fork of the Spring River, Cow Creek, Brush Creek, and Willow Creek in the Central Lowlands region, and Center Creek, Shoal Creek,

Figure 1. Approximate distribution of sites where fish collections were made in the Spring River basin during 1994-95.


KS
MO
OK
AR
Central Lowlands
KS MO
17
16
Cow Ck.
20
13
2
22
23
24
21
28
North Fork
52
37
36
51
35
34
56
54
31
32
38
Spring R.
25
39
Brush Ck.
18
44
46
42
45
41
15
19
43
11
57
6
40
Willow Ck.
58
47
Center Ck.
12
10
9
55
7
8
26
33
50
29
30
48
27
49
53
14
5
5-mile Ck.
Shoal Ck.
3
1
4
Ozark Plateaus
OK MO
10km

and Five-mile Creek in the Ozark region (Fig. 1). In addition we sampled the Spring River mainstream which, upstream from its confluence with North Fork of the Spring River, has characteristics of other Ozark streams (Davis and Schumacher 1992). At the beginning of the study we recognized Ozark tributaries, Lowland tributaries, and the mainstream Spring River, downstream from its confluence with North Fork of the Spring River, as three distinct regions based on the well-documented physicochemical differences between the Ozark and Lowland regions (Omernik 1987; Davis and Schumacher 1992; Adamski et al. 1995), and our prediction that the mainstream Spring River would have a distinct fish fauna because of its size and position within the drainage network.

Sampling

During spring and summer of 1994 and 1995, we collected fishes at 58 sites within the Spring River basin (Fig. 1). Sites were selected primarily to fulfill our goal of sampling representative streams from headwaters to tailwaters, including all stream orders. We chose stream order (Strahler 1957) as an *a priori* criterion in site selection because it allowed us to assess longitudinal patterns within individual streams. In some streams we sampled more than one site in a reach of a particular order. Further criteria in site selection were accessibility and landowner permission.

Fishes were collected by seining, performed during daylight hours with a 4.6-m by 1.8-m seine with 4.7-mm mesh. To assess relative abundance of fishes, standardized sampling was conducted by three persons kick-seining and sweep-seining until all available mesohabitats had been thoroughly sampled; in each sample we made approximately 25 to

35 seine hauls in a stream reach 100 to 300 m long, in 1.5 to 3 hours, depending on the number of distinct habitats at each collection site. All fishes were identified and counted. Protected species were released alive at their sites of capture following completion of sampling at each location; voucher specimens of non-listed fishes were preserved for each collection, and are housed in the Division of Biological Sciences at Emporia State University.

To assess habitat differences among sites as factors explaining differences in fish species composition, we characterized each collecting site with 28 variables and used them to construct four environmental matrices. One of us (CW) visually estimated percent coverage of 15 physical habitat variables at each site to make the physical habitat matrix. Substrate types, categorized according to a modified Wentworth scale, were mud, sand, gravel, small cobble, large cobble, boulder, and bedrock. Other habitat variables were mesohabitat type (i.e., riffle, run, pool, backwater), emergent vegetation, submergent vegetation, canopy cover, and woody structure. For the water quality matrix we measured dissolved oxygen, carbon dioxide, total alkalinity, hardness, nitrate, phosphate, and pH with Hach water chemistry kits, as well as water temperature. In addition we constructed an elevation matrix consisting of altitude and gradient, obtained from topographic maps, and a stream size matrix consisting of drainage area, obtained from on-screen digitizing of USGS 250K Digital Elevation Models using IDRISI for Windows (version 1.01, Clark Labs, Worcester, MA), cross-sectional area, and maximum stream width.

Statistical Analyses

Multivariate analyses used in measuring the influence of spatial autocorrelation were conducted using the R-package for Macintosh computers (version 3.0, University of Montreal, Montreal, Canada). Mantel tests (Mantel 1967; Sokal and Rohlf 1995) were used to test for spatial autocorrelation in fish species data and to assess the importance of environmental variables in influencing fish species composition. The Mantel test compares two symmetric matrices of association by calculating a standardized Mantel statistic *r*, equivalent to a Pearson product-moment correlation coefficient, between off-diagonal elements of the matrices (Legendre and Vaudor 1991; Fortin and Gurevitch 1993; Sokal and Rohlf 1995). Significance of correlations is assessed by randomly rearranging the rows and columns of one of the matrices being compared, and constructing a null distribution against which the initial Mantel *r* is compared. Mantel statistics significantly larger than scores in the null distribution indicate a positive association between the two matrices, whereas significantly smaller Mantel statistics indicate a negative association. All Mantel and partial Mantel tests were conducted at $\alpha = 0.05$, with Bonferroni corrections in cases where multiple tests were conducted on the same matrices. Significance was assessed using 5000 permutations for each test.

To analyze spatial pattern at the scale of the entire basin, we constructed a series of 58 by 58, off-diagonal, symmetric matrices representing the geographic distances, environmental variables, and fish species dissimilarities. In addition, subsets of these matrices were used to assess factors influencing species composition within individual streams of the basin; longitudinal spatial pattern within individual stream channels was investigated by constructing dissimilarity matrices using all sites connected in a unidirectional pathway between the headwaters of a stream and the most downstream site in the Spring River mainstream. We did not separately analyze longitudinal pattern within Brush, Willow, and Five-mile creeks because of the small number of collections made in these streams.

Before analyzing fish species data we removed from the data set species occurring in less than five percent of collections (Gauch 1982). We then constructed a fish species dissimilarity matrix (hereafter the species matrix), comparing presence-absence of 59 species among all sites, using Jaccard's coefficient subtracted from unity (Marczewski-Steinhaus distance: Pielou 1984). In addition, we investigated patterns of species abundances by constructing a separate matrix of Euclidean distances between sites based on log (ln(x+1)) transformed abundance data (hereafter the abundance matrix).

To construct the geographic distance matrix we used the Geographic Distances program in the R-package to calculate the shortest straight-line distance between sites based on their geographic coordinates. We concluded that this method of calculating geographic distances was more appropriate than calculating distances along the stream channel as preliminary investigation revealed that the correlation between stream-channel distances and species dissimilarities was lower due to sites in adjacent streams that contained similar species yet were very distant via the stream channel. We believe this methodological concern is noteworthy because it reflects the important linkage between streams and their terrestrial setting (e.g., Omernik 1987).

After testing the species presence-absence and abundance data for spatial autocorrelation, we used Mantel correlograms (Legendre and Fortin 1989; Legendre 1993; Cooper et al. 1997) to describe the spatial pattern of the fish assemblage. In a Mantel correlogram the geographic distance matrix is divided into a series of binary matrices, each representing a distinct distance class interval, which are then compared against a matrix representing associations among the variable of interest. Significance of correlations in a Mantel correlogram is assessed using a Bonferroni-corrected error rate (Legendre and Fortin 1989).

As a *post hoc* test of the importance of ecoregion in describing differences in species composition among sites, we constructed a binary matrix consisting of zeroes to characterize sites occurring in the same *a priori* predicted ecoregion, and ones to characterize sites occurring in different ecoregions, then compared the resulting matrix against the species matrix using a Mantel test. This technique is designed to assess whether there is a greater difference within predetermined groups or among predetermined groups, as a type of nonparametric analysis of variance (Fortin and Gurevitch 1993, Sokal and Rohlf 1995). Then, to determine the extent to which spatial autocorrelation among species data was explained by differences among ecoregions, we conducted a partial Mantel test comparing the species matrix against the geographic distance matrix while holding the effects of the ecoregion matrix constant.

To investigate the species data for groups existing at the basinwide scale, we conducted space-constrained cluster analysis (Legendre 1987; Legendre and Vaudor 1991; Legendre 1993) and principal coordinates analysis (PCoA) on the basinwide species matrix. Legendre (1987) explains that space-constrained cluster analysis is appropriate for identifying groups within spatially autocorrelated data because it incorporates the spatial structure into the analysis. The technique uses a proportional-link clustering algorithm as in other clustering techniques, but restricts clustering to sites adjacent to one another (Legendre and Vaudor 1991). PCoA allowed us to validate species groups identified by cluster analysis. Before cluster analysis, we chose 20% as the connectedness level for the clustering algorithm (Legendre 1987; Legendre and Vaudor 1991), and determined linkage of sites using a Delaunay triangulation. In triangulation, three points (i.e., collecting sites) are considered linked if the circle passing through the three points fails to encompass any other points under study (Legendre and Vaudor 1991). We modified the triangulation by adding two links between sites adjacent along stream channels, thus allowing potential movement of fishes between sites, but not identified as linked by triangulation. Sokal and Oden (1978) present a case in which they make a similar modification to a linkage network.

To assess correlations among the species, geographic distance, and environmental data sets we constructed environmental matrices by calculating Euclidean distances between all pairwise combinations of sites, and compared matrices using Mantel tests. Before constructing environmental matrices we arcsine transformed percentage data in the physical habitat matrix (Sokal and Rohlf 1995) and, except for pH, ln(x+1) transformed values in the elevation, stream size, and water quality matrices, to standardize and normalize variables. To identify gradients which might have influenced assemblage structure we conducted PCoA on environmental matrices. For environmental matrices identified as spatially autocorrelated, we used partial Mantel tests to remove the influence of common spatial structure in the environmental and species data sets (Smouse et al. 1986; Mandrak 1995) before subjecting the spatially corrected matrices to PCoA (Mandrak 1995). We then calculated bivariate correlations between environmental variables and principal coordinate axes to determine axis loadings.

In addition to identifying gradients in the environmental data, we used PCoA to determine whether sites that formed groups in cluster analysis grouped together in ordinations of their environmental characteristics. In these analyses, and in PCoA of the species matrix, we used uncorrected environmental matrices because our goal was to describe the spatial pattern of variables without assuming environmental control of assemblage structure (Legendre 1993).

Results

The Mantel test comparing the species and geographic distance matrices indicated spatial autocorrelation among fish species presence-absence data (r=0.58, p=0.0002; Table 1). The corresponding Mantel correlogram (Fig. 2) indicated positive autocorrelation among the smallest distance classes and negative autocorrelation among the largest classes, reflecting a pattern which can either be interpreted as describing species distributed along a gradient, or with a sharp step between two relatively homogenous taxonomic zones (Legendre and Fortin 1989). Significant positive correlations for each of the four smallest distance classes indicated a zone of influence of approximately 44 km within which fish collections tended to have a more similar species composition than expected by chance. The species abundance data were also spatially

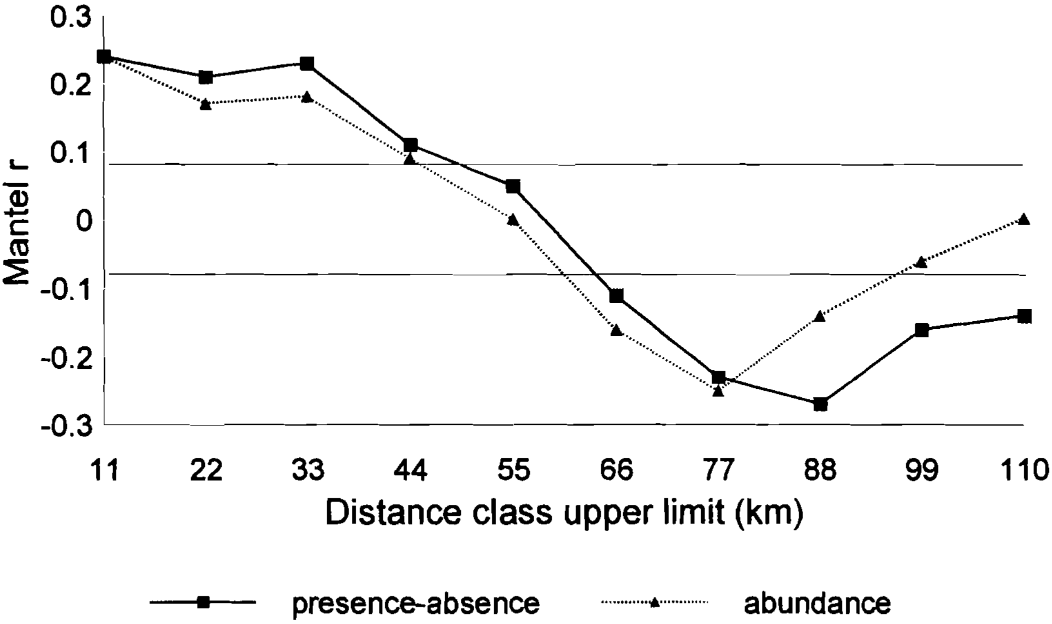
Table 1. Mantel correlations for comparisons between geographic distance, species presence-absence, and environmental matrices. Number of collections used for each site group in parentheses. Above the diagonal: results of Mantel tests. Below the diagonal: results of partial Mantel tests for autocorrelated data sets. Significance assessed using Bonferroni-corrected error rate, $\alpha'=0.05/25$ (25 possible comparisons for each site group) = 0.002. Probability based on 5000 permutations, *$p<0.002$, **$p=0.0002$.

Site group	Matrix	1. Species	2. Physical Habitat	3. Water Quality	4. Elevation	5. Size
All (n=58)	Distance	0.58**	0.14**	0.33**	0.22**	-0.08
	1.	—	0.39**	0.41**	0.26**	0.14**
	2.	0.36**	—	0.50**	0.10	0.10
	3.	0.29**	0.47**	—	0.04	0.15**
	4.	0.16**	0.07**	-0.04	—	0.38**
	5.					—
Spring R. (n=15)	Distance	0.83**	-0.006	0.14	0.57**	0.83**
	1.	—	0.08	0.28	0.35*	0.61**
	2.		—	-0.036	-0.14	-0.16
	3.			—	-0.12	0.10
	4.	-0.26			—	0.69**
	5.	-0.23				—
North Frk. (n=17)	Distance	0.65**	-0.004	-0.04	0.38**	0.68**
	1.	—	0.43**	0.36**	0.36**	0.62**
	2.		—	0.38**	0.34*	0.24
	3.			—	-0.03	-0.004
	4.	0.16			—	0.85**
	5.	0.31*				—

Table 1 cont.

Shoal Ck. (n=12)	Distance	0.69**	0.16	0.22	0.83**	0.93**
	1.	—	0.71**	0.66**	0.69**	0.74**
	2.		—	0.78**	0.24	0.28
	3.			—	0.35	0.44*
	4.	0.30			—	0.80**
	5.	0.34				—
Center Ck. (n=12)	Distance	0.58**	0.009	0.34	0.88**	0.83**
	1.	—	0.21	0.34	0.60**	0.69**
	2.		—	-0.32	0.01	0.03
	3.			—	0.61**	0.56*
	4.	0.23			—	0.76**
	5.	0.46*				—
Cow Ck. (n=12)	Distance	0.57**	-0.31	0.62**	0.78**	0.85**
	1.	—	-0.09	0.76**	0.71**	0.70**
	2.		—	-0.31	-0.33	-0.05
	3.	0.62**		—	0.85**	0.56**
	4.	0.51**			—	0.70**
	5.	0.50**				—

Figure 2. Mantel correlogram comparing spatial pattern of species presence-absence and abundance data. Significance of correlations assessed using a Bonferoni-corrected error rate, $\alpha' = 0.05/10$ (10 distance classes) $= 0.005$. Significant positive correlations above the upper line, significant negative correlations below the lower line.

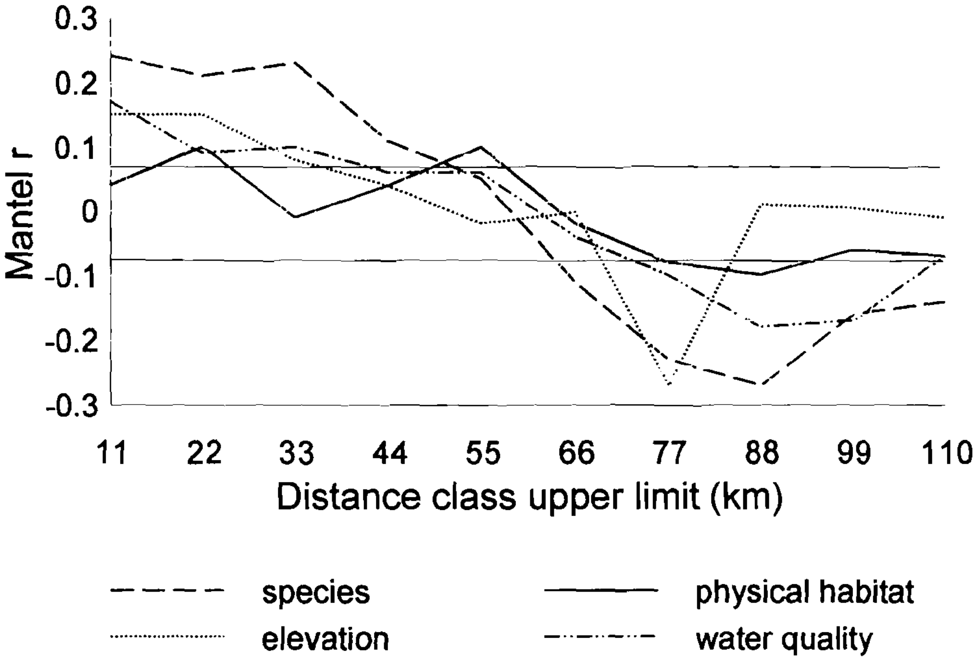

0.3
0.2
0.1
0
-0.1
-0.2
-0.3
Mantel r
11
22
33
44
55
66
77
88
99
110
Distance class upper limit (km)
presence-absence
abundance

autocorrelated (*r*=0.42, *p*=0.0002) and exhibited roughly the same pattern (Fig. 2), with positive autocorrelation among smaller, and negative autocorrelation among larger distance classes. However, the 99 and 110 km distance classes were not significantly autocorrelated (Fig. 2), possibly reflecting both the relatively small number of samples in these distance classes (47 and 26 site-pairs, respectively) and the weaker overall association between species abundances and geographic distances, compared with that of species presence-absence.

Comparisons between the geographic distance matrix and each environmental matrix indicated spatial autocorrelation among variables in the physical, water quality, and elevation matrices, but not the stream size matrix (Table 1). Correlograms of autocorrelated environmental data exhibited different spatial patterns at the basinwide scale, which we interpret here following Legendre and Fortin (1989). Peaks in the correlogram of the physical habitat matrix, reflecting positive autocorrelation of the 22 and 55 km distance classes, contrasted with significant negative autocorrelation of the 77 and 88 km distance classes (Fig. 3), suggest that these data were distributed in a patchy spatial pattern. Water quality data appeared to be distributed as a gradient or a sharp step, similar to the distribution of the species data, but with a 33 km zone of influence. Elevation exhibited a patchy distribution with a patch size of 33 km and a sharp trough of negative autocorrelation over the 77 km distance class.

There was a relatively weak but significant correlation (*r*=0.15, *p*=0.0002) between the binary ecoregion matrix and the geographic distance matrix, suggesting that although differences among ecoregions explained some of the observed spatial autocorrelation

Figure 3. Mantel correlogram comparing spatial pattern of species presence-absence data and spatially autocorrelated environmental variables. Significance of correlations assessed using a Bonferoni-corrected error rate, $\alpha' = 0.05/10$ (10 distance classes) = 0.005. Significant positive correlations above the upper line, significant negative correlations below the lower line.


0.3
0.2
0.1
0
-0.1
-0.2
-0.3
Mantel r
11
22
33
44
55
66
77
88
99
110
Distance class upper limit (km)
species
physical habitat
elevation
water quality

among species, there was additional spatial dependence that could not be explained by these differences. Results of the partial Mantel test between the species and geographic distance matrices, holding the effects of ecoregion constant, indicated further spatial structure in the species data besides that influenced by ecoregions (r=0.57, p=0.0002).

Because spatial structure of the species data was better represented in the species matrix than in the abundance matrix, the remaining analyses were conducted using presence-absence data. Results of Mantel tests indicated significant correlations between the species matrix and each of the environmental matrices (Table 1). After partialling out the influence of common spatial structure from the data sets, the physical, water quality, and elevation matrices remained significantly correlated to species dissimilarities (Table 1), suggesting that variables in these matrices, as well as variables in the stream size matrix, may have been important in structuring the fish assemblage. However, significant correlations between some environmental matrices led us to believe that covariation among variables in these matrices might have resulted in spurious correlations between the species and environmental matrices (Table 1). To address this potential problem we conducted partial Mantel tests to compare environmental matrices with the species matrix while holding the effect of the covariable matrix constant. Because correlations between environmental and species matrices remained significant after removing the influence of covariates, we subjected all four matrices to PCoA (i.e., spatially-corrected physical, water quality, and elevation matrices, and the uncorrected size matrix).

The amount of variation explained by the first two PCoA axes for each data set was small. The first two axes of the spatially-corrected physical habitat PCoA accounted for only 6.2% of the total variation in the data set. PCoA 1 (3.6%) contrasted sites where mud substrate and pool mesohabitat were prevalent, with sites characterized by gravel, small cobble, riffles, and runs (Table 2). Similarly, PCoA 2 of physical habitat (2.6%) contrasted sites dominated by gravel and small cobble with sites characterized by mud and bedrock (Table 2). The first two PCoA axes of the spatially-corrected water quality matrix explained 6.8% of the total variation in the data set; PCoA 1 explained 4.4% and was correlated most highly with gradients of nitrate, CO_2, and pH (Table 2). The first and second axes of the spatially-corrected elevation matrix explained 3.4% and 2.1% of the total variation among sites, respectively. Gradient had higher correlations with the first and second axes than did altitude, and both variables were significantly correlated with PCoA 1 (Table 2). The first two principal coordinate axes of the uncorrected stream size matrix explained 10.2% of the variation in the data set. Drainage area, cross-sectional area, and maximum width were correlated with the first axis (6.6%), and cross-sectional area was significantly correlated with PCoA 2 (Table 2).

Comparing subsets of the geographic distance and species matrices indicated significant spatial autocorrelation of species within all streams tested (Table 1). Physicochemical differences were of variable importance in explaining species differences at sites within individual streams, as indicated by significant correlations between species dissimilarities and physical habitat and water quality differences in some instances, but not others (Table 1). Elevation and stream size matrices were significantly correlated with species dissimilarities in all streams tested; however, when the effects of spatial autocorrelation were removed from these data sets using partial Mantel tests, correlations

Table 2. Bivariate correlations between variables in environmental matrices and the first two PCoA axes of spatially-corrected physical habitat, water quality, and elevation matrices, and uncorrected stream size matrix. Significance of correlations assessed using Bonferroni-corrected error rate, α' = 0.05/28 = 0.0018, **p* < 0.0018, ***p* < 0.001.

	PCoA 1	PCoA 2
Physical habitat (variation explained)	3.6%	2.6%
riffle	0.44*	0.26
run	0.60**	0.07
pool	-0.87**	-0.25
backwater	0.27	0.31
mud	-0.67**	-0.44*
sand	-0.08	-0.23
gravel	0.42*	0.66**
small cobble	0.45**	0.56**
large cobble	0.41	0.32
boulder	0.11	-0.08
bedrock	0.22	-0.42*
canopy	-0.18	-0.18
submergent vegetation	-0.01	-0.31
emergent vegetation	-0.01	0.19
woody structure	-0.14	-0.18

Table 2 cont.

Water quality (variation explained)	4.4%	2.4%
dissolved oxygen	-0.37	0.03
carbon dioxide	-0.76*	0.05
total alkalinity	-0.38	0.13
hardness	0.11	-0.08
nitrate	-0.78*	-0.01
phosphate	-0.23	0.04
temperature	-0.37	0.22
pH	-0.73*	0.32
Elevation (variation explained)	3.4%	2.1%
altitude	0.65**	0.07
gradient	0.94**	0.23
Stream size (variation explained)	6.6%	3.6%
drainage area	-0.94**	-0.29
cross-sectional area	-0.84**	0.70**
maximum width	-0.82**	-0.19

between stream size and species differences remained significant only in North Fork of the Spring River, Center Creek and Cow Creek, while the correlation between elevation and species differences remained significant only in Cow Creek (Table 1). Higher correlations in individual streams, compared with correlation between the complete data sets, demonstrate that analyzing spatial autocorrelation at the basinwide scale does not completely account for longitudinal patterns present within streams.

Cluster analysis of the overall species matrix identified three groups (Table 3) which fit closely to the groups based on ecoregions predicted *a priori*. Exceptions were two Ozark sites (4 and 8), eliminated from the analysis because they were outliers which would have prevented the fusion of their neighboring groups (Legendre 1987), and seven sites (bold in Table 3) located at the downstream positions in tributaries, adjacent to mainstream locations. Mainstream fish collections, forming a cluster along with these seven downstream tributary sites, were characterized by *Pimephales notatus*, *Notropis rubellus*, *Labidesthes sicculus*, *Lepomis macrochirus*, and *Percina copelandi* (Appendix 1) as the most frequently occurring species. Collections in Ozark tributaries tended to cluster together (Ozark group, Table 3), except for sites in the most downstream positions in Shoal Creek, Center Creek, and the Spring River headwater upstream from its confluence with North Fork of the Spring River, which were more similar to mainstream collections. The most frequently occurring species in the Ozark group were *Campostoma anomalum*, *Luxilus cardinalis*, *N. rubellus*, *Cottus carolinae*, and *Etheostoma spectabile* (Appendix 1). Similarly, Lowland tributary collections clustered together (Lowland group, Table 3), except for three sites in North Fork of the Spring River, and the most

Table 3. Groups of sites identified by space-constrained cluster analysis using modified triangulation to assess linkage among sites (connectedness = 0.20, clustering level = 0.33). Site numbers refer to collection localities designated in Figure 1. Numbers in bold distinguish tributary and Spring River headwater sites that clustered with collections from mainstream sites.

Mainstream group

11 31 **32** **36** **37** **42** 43 44 46 **51** 53
54 55 56 57 **58**

Ozark group

1 3 5 6 7 14 25 26 27 29 30
33 38 39 40 41 45 47 48 49 50

Lowland group

2 9 10 12 13 15 16 17 18 19 20
21 22 23 24 28 34 35 52

downstream site in Brush Creek, all of which clustered with mainstream collections. The most frequently occurring species in the Lowland group were *Lythrurus umbratilis*, *Gambusia affinis*, *Lepomis cyanellus*, *L. macrochirus*, and *Micropterus salmoides* (Appendix 1).

PCoA of the uncorrected species matrix (Fig. 4) for the most part corroborated species groups identified in space-constrained cluster analysis. PCoA 1 (20.0%) described a contrast between Ozark and Lowland collections, with mainstream sites between and overlapping the other groups. PCoA 2 (13.7%) further distinguished most sites belonging to the Mainstream species cluster from those in the Ozark and Lowland groups. Sites positioned at the interface between Mainstream and Lowland groups included 11 and 55, which grouped with Mainstream sites in cluster analysis, as well as site 52, which grouped with Lowland sites (Table 3). In addition, site 11 in Brush Creek and site 51 in North Fork of the Spring River (Fig. 1) did not group together with other mainstream sites in PCoA of uncorrected physical habitat and water quality matrices (Fig. 5), suggesting that these sites had different habitat characteristics than other Mainstream sites despite having species compositions which included “mainstream species.”

Figure 4. Plot of the first and second principal coordinate axes of fish species dissimilarity. Symbols represent groups of sites which clustered together in space-constrained cluster analysis identified in Table 3; crosses = Mainstream, triangles = Lowland, circles = Ozark.

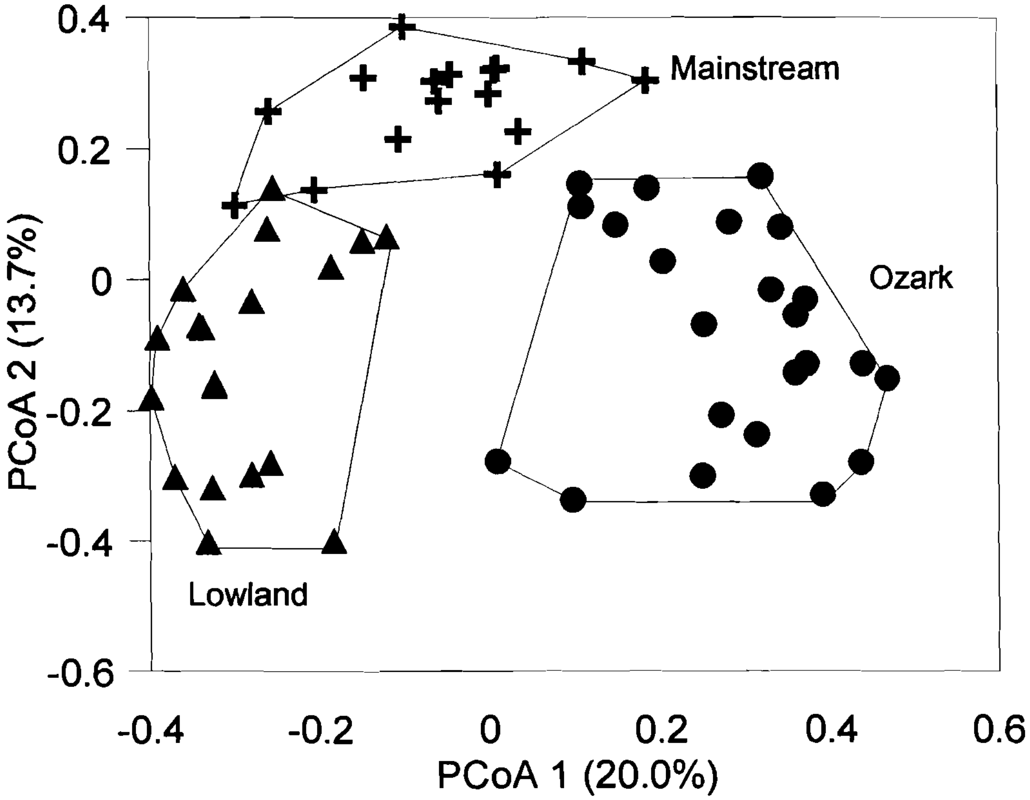
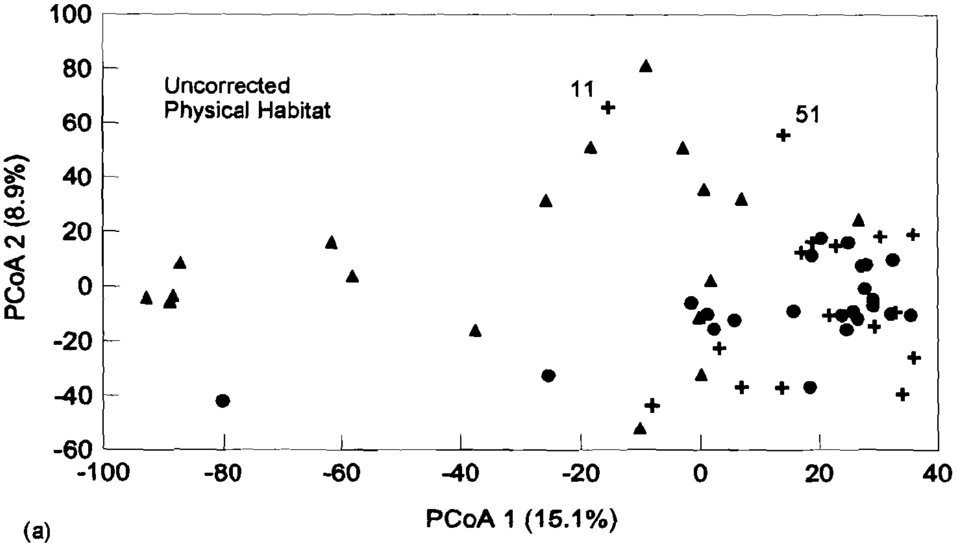
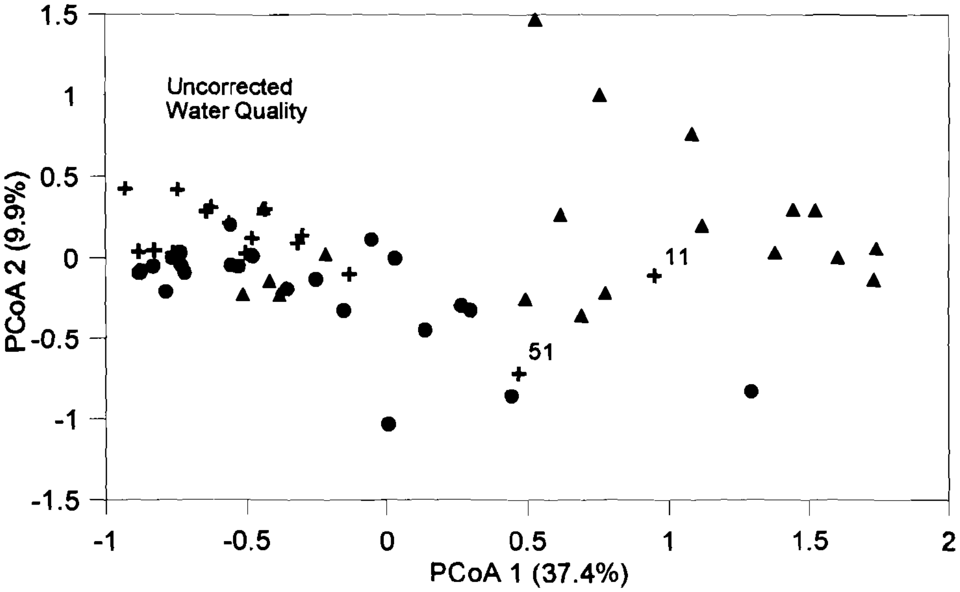

0.4
0.2
0
-0.2
-0.4
-0.6
PCoA 2 (13.7%)
-0.4
-0.2
0
0.2
0.4
0.6
PCoA 1 (20.0%)
Mainstream
Ozark
Lowland

Figure 5. Plot of the first and second principal coordinate axes of uncorrected (a) physical habitat and (b) water quality matrices. Symbols represent groups of sites which clustered together in space-constrained cluster analysis (Table 3); crosses = Mainstream, triangles = Lowland, circles = Ozark.


Uncorrected
Physical Habitat
11
51
PCoA 2 (8.9%)
PCoA 1 (15.1%)
100
80
60
40
20
0
-20
-40
-60
-100
-80
-60
-40
-20
0
20
40

(a)


Uncorrected
Water Quality
11
51
PCoA 2 (9.9%)
PCoA 1 (37.4%)
1.5
1
0.5
0
-0.5
-1
-1.5
-1
-0.5
0
0.5
1
1.5
2

(b)

Discussion

Studies of community structure indicate that abiotic and biotic influencing factors are not mutually exclusive (Borcard et al. 1992), and assemblage structure in stream systems responds to a combination of factors (Schoener 1987; Power et al. 1988). Whereas correlational studies cannot conclusively identify causative mechanisms responsible for ecological patterns, describing and quantifying spatial pattern in communities can lead to a better understanding of the relative importance of processes which act to create the observed patterns.

The spatial pattern of the Spring River basin fish assemblage comes as no surprise considering the distinctive fish faunas of the Ozark Highlands and Central Lowlands (Mayden 1987a; 1987b). Distributional patterns of fishes in the Spring River basin, together with the geological history of the region, are consistent with vicariance biogeography as the primary process underlying present structure of the basinwide fish assemblage (Mayden 1987a; 1987b). In this scenario, the Arkansas River separated the Ozark Plateaus from the Ouachita Mountains and made habitats in the intervening region more like the adjacent Central Lowlands (Mayden 1987b). Thus, the close fit between species clusters and physiographic provinces supports the applicability of ecoregions as a means of describing biotic assemblages (Hughes et al. 1987; Edds 1993; Lyons 1996). In addition, the distributional pattern of the fish assemblage, identified by Mantel correlograms, reflects the distinction between the Lowland and Ozark portions of the drainage, and the distance between most sites of each region falls within the 44 km zone of influence, or patch size. However, the three groups of sites identified by PCoA and space-constrained cluster analysis reflect not only disparate fish faunas of the two biogeographic provinces in the basin, but a distinct fish fauna in the Spring River mainstream as well.

Though environmental and species differences in our study were significantly correlated, the small proportion of species variation explained by environmental differences (Table 1) suggests that other factors were important in organizing the community as well. Further, physical habitat variables we measured exhibited a patchy distribution not closely matching the pattern exhibited by the assemblage (Fig. 3). This suggests that mesohabitat type and substrate size, factors significantly correlated to physical habitat PCoA axes (Table 2), might have a more localized than regional influence in the Spring River basin. Considering the congruence between species clusters and ecoregions, other factors that differ between regions, such as soil type and stream productivity (Omernik 1987; Lyons 1996), or stream flow variability (Poff and Allan 1995; Taylor et al. 1996) might have further accounted for observed species differences at the basinwide scale. However, the high degree of spatial autocorrelation which remained among species after partialling out the effect of ecoregions suggests that other factors, besides those encompassed in ecoregions, were responsible for the observed community structure.

Autocorrelation analysis offers circumstantial evidence that contagious biotic processes may also explain variation in the species assemblage not explained by environmental differences among sites. In the overall analysis and in most individual streams of the basin, spatial autocorrelation explained more of the variation in species composition than did habitat differences (Table 1). For instance, spatial analysis of longitudinal pattern in the Spring River (Table 1) indicated that distance between sites accounted for 69% (coefficient of determination = $r^2 = 0.83^2 = 0.69$) of the variation in species, whereas none of the environmental matrices were significantly correlated to species differences after the influence of spatial autocorrelation was removed (Table 1).

Partial Mantel tests helped reveal several spurious correlations between species and environmental matrices that were the result of common spatial structure among variables in those data sets. Particularly within individual stream channels, positive correlations between species differences and both the elevation and stream size matrices gave the false impression that variables in these matrices accounted for a high degree of variation in species composition, when spatial autocorrelation among sites explained more of the variation. The usefulness of elevation as an explanatory variable for aquatic community structure has been questioned by some researchers who consider it a surrogate for other environmental factors such as stream hydraulics (Statzner and Higler 1986). Similarly, stream size may be a surrogate for habitat complexity (Gorman and Karr 1978; Schlosser 1987) or stability (Schlosser 1987). Though our attempt to model factors important in structuring the Spring River basin fish assemblage was not intended to be exhaustive, these results suggest that much of the influence attributed to environmental differences can be alternatively explained by the spatial pattern underlying the data.

The influence that processes occurring downstream can have on the biota of upstream reaches in some drainage networks has recently been emphasized by ecologists who have recognized that the familar upstream-downstream linkage described in the River Continuum Concept (Vannote et al. 1980; Minshall et al. 1985) is an oversimplification of the processes affecting assemblage structure (Osborne and Wiley 1992; Pringle 1997). For fishes in the Spring River basin, groups of sites identified by cluster analysis reflect the influence of the mainstream fish assemblage on species composition in tributaries, in that sites in downstream positions of some tributaries were occupied by species more characteristic of the mainstream fish assemblage than of adjacent tributary collections. For example, *Cyprinella spiloptera* was collected from the most downstream sites in North Fork of the Spring River (sites 36 and 37), Brush Creek (site 11), Center Creek (site 42), and Shoal Creek (site 58), but not at any other tributary site. Other species primarily occurring in mainstream collections and downstream tributary sites were *Notropis volucellus*, *Cyprinella camura*, *Pimephales tenellus*, *P. vigilax*, *Ictalurus punctatus*, *Percina phoxocephala*, and *P. copelandi*. The presence of "mainstream species" in tributaries was not restricted to tributary collections that grouped with mainstream collections in cluster analysis, as exemplified by the most downstream site in Cow Creek (52), which clustered with other Lowland tributary sites, but contained species such as *P. tenellus*, *P. vigilax*, *I. punctatus* and *P. phoxocephala*. Although the fish assemblage at this site had a higher proportion of species present at adjacent tributary sites than at adjacent mainstream sites, the presence of "mainstream species" provides evidence of a linkage between the mainstream and Cow Creek not apparent in the cluster analysis.

Another characteristic of the basinwide fish assemblage that cluster analysis did not adequately assess is the longitudinal pattern of fishes and environmental correlates in individual streams of the basin. The importance of longitudinal patterns was somewhat reflected in PCoA of the basinwide species matrix, however, with larger tributary reaches located nearer to, and in some cases overlapping, the mainstream group (Fig. 4). Using autocorrelation techniques to analyze patterns in individual streams, in some cases, revealed substantial longitudinal gradients. These gradients were not apparent in the basinwide analysis which compared sites in adjacent streams and thus tended to favor regional patterns. This distinction may be partially a matter of scale, in that longitudinal distribution in streams appears to be more important on a local scale than on a regional scale, possibly as a reflection of processes, such as predation and competition, which act at a local scale, versus historical biogeography and differences in stream productivity, which act at a regional scale. The varying importance of geographic distance and habitat differences as variables explaining species composition at sites within different streams may reflect differences among streams in the processes acting to structure fish assemblages (Table 1). In addition, the differing degrees of spatial autocorrelation exhibited by fish assemblages in individual streams compared to the entire basin supports the idea that stream systems function as "mosaics of patches" (Pringle et al. 1988).

Though our analysis cannot distinguish between fish movements and other contagious processes such as reproduction and mortality, movements of individuals are known to be important controlling processes in stream systems (Power et al. 1988). At least two species characteristic of mainstream Spring River collections have been reported to seasonally migrate into tributaries to reproduce, *C. spiloptera* (Gorman 1986) and *I. punctatus* (Dames et al. 1989). Migration of fishes presumably requires certain habitat patches to be present along the migratory pathway (Pringle et al. 1988), so it is not surprising that PCoA (Fig.5) reflected the similarity among habitat characteristics at sites belonging to the Mainstream species group. However, the fact that sites 11 and 51 in the downstream portions of two tributaries were distinguished from mainstream sites based on ordination of physical habitat and water quality differences suggests that the linkage between mainstream and tributary species assemblages is capable of transcending boundaries of habitat patches. This possibility is further reflected in the greater patch size of the species assemblage compared with patch sizes of habitat variables (Fig. 3).

It is possible that the observed linkage between the mainstream and its tributaries is only exhibited during part of the year when individuals are reproductively active and "mainstream species" migrate into the tributaries. However, we do not believe this is the case because, in Kansas, some of the species characteristic of the Mainstream group, including *P. copelandi* and *P. phoxocephala,* spawn earlier in the year (Cross 1967) than when we made our collections. In addition, all the species in the Mainstream group have been collected in the downstream reaches of tributaries during other times of the year as well (Branson et al. 1969). Rather, we believe it is plausible to view the mainstream-tributary interface as a patch boundary which changes its location in response to dynamic biotic interactions and bi-directional contagious processes. One manner in which changes at the mainstream-tributary interface appear to be brought about is through disturbances, such as those resulting from dams, in the lower portions of drainage networks (Pringle 1997). Using autocorrelation techniques to assess temporal changes in spatial pattern at local and regional scales, together with manipulative experiments, might lead to additional understanding of how these processes affect the perceived linkage between tributary and mainstream assemblages.

Autocorrelation techniques used here are just a few of the multivariate and univariate analyses designed to deal with spatially explicit data (e.g., Legendre and Fortin 1989, Legendre 1993, Ver Hoef and Cressie 1993, Fortin and Gurevitch 1993, Cooper et al. 1997). Hopefully, stream ecologists will become more aware of the influence that spatial autocorrelation can have in testing significance of correlations used in models of community structure, and will consider its influence before interpreting the results of statistical tests on spatially autocorrelated data. Additionally, spatial autocorrelation can be interpreted as a reflection of the relative importance of biotic processes in structuring lotic communities, a factor that might otherwise be overlooked in community analyses. In the future, if more stream ecologists incorporate spatial pattern as a factor in studies of community ecology, models of patch dynamics will become more sophisticated, leading to a better understanding of the causes and effects of spatial heterogeneity in streams.

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Appendix 1. Fish species used in community analyses, with number of sites where each species was collected within groups identified by space-constrained cluster analysis; M = Mainstream, O = Ozark, L = Lowland.[1]

Family	Species	Common name	M	O	L
Clupeidae					
	Dorosoma cepedianum	gizzard shad	3		1
Cyprinidae					
	Campostoma anomalum	central stoneroller	12	20	7
	Cyprinella camura	bluntface shiner	12	3	1
	C. lutrensis	red shiner	12		10
	C. spiloptera	spotfin shiner	8		
	Cyprinus carpio	common carp	1	2	2
	Luxilus cardinalis	cardinal shiner	11	18	
	Lythrurus umbratilis	redfin shiner	6	1	13
	Nocomis asper	redspot chub		10	
	Notropis boops	bigeye shiner	2	2	3
	N. buchanani	ghost shiner	4		1
	N. nubilis	Ozark minnow	2	11	
	N. rubellus	rosyface shiner	14	15	
	N. volucellus	mimic shiner	7		1
	Notemigonous crysoleucas	golden shiner			7
	Pimephales notatus	bluntnose minnow	15	7	11
	P. promelas	fathead minnow		2	2
	P. tenellus	slim minnow	10		1
	P. vigilax	bullhead minnow	7		4
	Phenacobius mirabilis	suckermouth minnow	6		3
	Phoxinus erythrogaster	southern redbelly dace		11	
	Semotilus atromaculatus	creek chub	2	13	

Catostomidae					
	Catostomus commersoni	white sucker	1	4	
	Hypentelium nigricans	northern hogsucker	6	6	
	Moxostoma duquesnei	black redhorse	2	5	
	M. erythrurum	golden redhorse	4	3	1
	Minytrema melanops	spotted sucker	2		2
Ictaluridae					
	Ameiurus melas	black bullhead			6
	A. natalis	yellow bullhead	1	1	5
	Ictalurus punctatus	channel catfish	11	1	3
	Noturus exilis	slender madtom	10	14	2
	N. flavus	stonecat	4		
Fundulidae					
	Fundulus notatus	blackstripe topminnow	3	3	6
Poeciliidae					
	Gambusia affinis	western mosquitofish	13	12	14
Atherinidae					
	Labidesthes sicculus	brook silverside	14	2	12
Cottidae					
	Cottus carolinae	banded sculpin	5	18	
Centrarchidae					
	Lepomis cyanellus	green sunfish	3	9	15
	L. gulosus	warmouth	1		6
	L. humilis	orangespotted sunfish	8		8
	L. macrochirus	bluegill	14	10	16
	L. megalotis	longear sunfish	13	13	11
	L. microlophus	redear sunfish	1	1	3
	Micropterus dolomieu	smallmouth bass	2	4	
	M. punctatus	spotted bass	6	2	1
	M. salmoides	largemouth bass	12	9	18
	Pomoxis annularis	white crappie	5	2	4

Percidae				
Etheostoma blennioides	greenside darter	5	7	1
E. cragini	Arkansas darter	3	7	
E. flabellare	fantail darter	3	13	2
E. gracile	slough darter			4
E. nigrum	Johnny darter	5		
E. spectabile	orangethroat darter	10	20	6
E. stigmaeum	speckled darter	4	3	
E. whipplei	redfin darter			5
E. zonale	banded darter	12	9	
E. sp.	sunburst darter		10	
Percina caprodes	logperch	11	5	5
P. copelandi	channel darter	14	1	1
P. phoxocephala	slenderhead darter	13		1

[1] Species not included in analyses because they occurred in less than 5% of collections were *Lepisosteus osseus, L. oculatus, Erimystax x-punctatus, Luxilus chrysocephalus, Notropis atherinoides, N. stramineus, Ictiobus bubalus, Pylodictis olivaris, Noturus miurus, N. placidus, Fundulus olivaceus, Morone chrysops, Ambloplites rupestris, Pomoxis nigromaculatus, Etheostoma chlorosomum, E. microperca, Percina shumardi, Stizostedion vitreum,* and *Aplodinotus grunniens.*

Appendix 2. Sites sampled in the Spring River basin during 1994-95, with abundance of fishes collected at each site. Site numbers correspond to locations indicated in Figure 1. Abbreviations refer to the following fish species: LOSS = *Lepisosteus osseus,* LOCU = *Lepisosteus oculatus,* DCEP = *Dorosoma cepedianum,* CARP = *Cyprinus carpio,* NCRY = *Notemigonus crysoleucas,* SATR = *Semotilus atromaculatus,* PERY = *Phoxinus erythrogaster,* NASP = *Nocomis asper,* EX-P = *Erimystax x-punctatus,* PMIR = *Phenacobius mirabilis,* LUMB = *Lythrurus umbratilis,* LCAR = *Luxilus cardinalis,* LCHR = *Luxilus chrysocephalus,* NRUB = *Notropis rubellus,* NATH = *Notropis atherinoides,* NBOO = *Notropis boops,* NSTR = *Notropis stramineus,* NVOL = *Notropis volucellus,* NBUC = *Notropis buchanani,* CSPI = *Cyprinella spiloptera,* CCAM = *Cyprinella camura,* CLUT = *Cyprinella lutrensis,* PTEN = *Pimephales tenellus,* PNOT = *Pimephales notatus,* PPRO = *Pimephales promelas,* PVIG = *Pimephales vigilax,* CANO = *Campostoma anomalum,* AMEL = *Ameiurus melas,* ANAT = *Ameiurus natalis,* IPUN = *Ictalurus punctatus,*POLI = *Pylodictis olivaris,* NEXI = *Noturus exilis,* NFLA = *Noturus flavus,* NMIU = *Noturus miurus,* NPLA = *Noturus placidus,* IBUB = *Ictiobus bubalus,*CCOM = *Catostomus commersoni,* HNIG = *Hypentelium nigricans,* MDUQ = *Moxostoma duquesnei,* MERY = *Moxostoma erythrurum,* MMEL = *Minytrema melanops,* FNOT = *Fundulus notatus,* FOLI = *Fundulus olivaceus,* GAFF = *Gambusia affinis,* LSIC = *Labidesthes sicculus,* CCAR = *Cottus carolinae,* MCHR = *Morone chrysops,* AGRU = *Aplodinotus grunniens,* MDOL = *Micropterus dolomieu,* MPUN = *Micropterus punctulatus,* MSAL = *Micropterus salmoides,* LGUL = *Lepomis gulosus,* LCYA = *Lepomis cyanellus,* LMIC = *Lepomis microlophus,* LHUM = *Lepomis humilis,* LMEG = *Lepomis megalotis,* LMAC = *Lepomis macrochirus,* LHYB = *Lepomis* hybrid, ARUP = *Ambloplites rupestris,* PANN = *Pomoxis annularis,* PNIG = *Percina nigromaculatus,*PPHO = *Percina phoxocephala,* PCAP = *Percina caprodes,* PCOP = *Percina copelandi,* PSHU = *Percina shumardi,* ENIG = *Etheostoma nigrum,* ESTI = *Etheostoma stigmaeum,* EZON = *Etheostoma zonale,* EBLE = *Etheostoma blennioides,* EWHI = *Etheostoma whipplei,* ECRA = *Etheostoma cragini,* ESPE = *Etheostoma spectabile,* EFLA = *Etheostoma flabellare,* EGRA = *Etheostoma gracile,* ECHL = *Etheostoma chlorosomum,* E sp = *Etheostoma* sp. (undescribed species split from *Etheostoma punctulatum*).

site	LOSS	LOCU	DCEP	CARP	NCRY	SATR	PERY	NASP	EX-P	PMIR	LUMB
1	0	0	0	0	0	8	97	0	0	0	0
2	0	0	1	0	0	0	0	0	0	0	2
3	0	0	0	0	0	32	671	0	0	0	0
4	0	0	0	0	0	8	0	0	0	0	0
5	0	0	0	0	0	31	74	1	0	0	0
6	0	0	0	0	0	2	11	7	0	0	0
7	0	0	0	0	0	3	19	0	0	0	0
8	0	0	0	0	0	0	129	0	0	0	0
9	0	0	0	0	8	0	0	0	0	0	56
10	0	0	0	0	1	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0	47
12	0	0	0	0	32	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0	1	11
14	0	0	0	0	0	1	18	0	0	0	0
15	0	0	0	0	9	0	0	0	0	0	1
16	0	0	0	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	0	0	0
18	0	0	0	0	17	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	0	0	29
20	0	0	0	0	4	0	0	0	0	0	0
21	0	0	0	1	0	0	0	0	0	14	7
22	0	0	0	1	0	0	0	0	0	0	50
23	0	0	0	0	0	0	0	0	0	1	174
24	0	1	0	0	0	0	0	0	0	0	72
25	0	0	0	0	0	2	0	3	0	0	0
26	0	0	0	0	0	0	10	0	0	0	0
27	0	0	0	1	0	2	55	7	0	0	0
28	0	0	0	0	24	0	0	0	0	0	11
29	0	0	0	2	0	0	0	1	0	0	0
30	0	0	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0	0	3	0
32	0	0	0	0	0	0	0	0	0	0	5
33	0	0	0	0	0	2	22	8	0	0	0
34	0	0	0	0	0	0	0	0	0	0	56
35	0	0	0	0	0	0	0	0	0	0	12
36	0	0	0	0	0	0	0	0	0	0	8
37	0	0	0	0	0	0	0	0	0	0	7

site	LOSS	LOCU	DCEP	CARP	NCYR	SATR	PERY	NASP	EX-P	PMIR	LUMB
38	0	0	0	0	0	6	0	0	0	0	2
39	0	0	0	0	0	8	0	6	0	0	0
40	0	0	0	0	0	8	3	0	0	0	0
41	0	0	0	0	0	0	0	1	0	0	0
42	0	0	0	0	0	0	0	0	0	0	0
43	0	0	0	0	0	0	0	0	0	1	0
44	0	0	0	0	0	0	0	0	0	23	0
45	0	0	0	0	0	0	0	0	0	0	0
46	0	0	0	0	0	0	0	0	0	0	0
47	0	0	0	0	0	0	0	0	0	0	0
48	0	0	0	0	0	0	1	1	0	0	0
49	0	0	0	0	0	1	5	7	0	0	0
50	0	0	0	0	0	0	0	0	0	0	0
51	0	0	0	0	0	0	0	0	0	1	4
52	0	0	0	0	0	0	0	0	0	0	9
53	1	0	123	1	0	0	0	0	0	0	1
54	0	0	0	0	0	0	0	0	12	8	0
55	0	0	42	0	0	0	0	0	0	0	0
56	0	0	1	0	0	1	0	0	2	0	0
57	0	0	0	0	0	20	0	0	0	5	0
58	0	0	0	0	0	0	0	0	3	0	0

site	LCAR	LCHR	NRUB	NATH	NBOO	NSTR	NVOL	NBUC	NNUB	CSPI	CCAM
1	5	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0	0
3	28	0	0	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	0	0	0
5	117	0	3	0	0	0	0	0	0	0	0
6	31	0	14	0	0	0	0	0	24	0	0
7	127	0	0	0	0	0	0	0	6	0	0
8	19	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0	0
11	0	0	7	0	0	0	3	5	0	1	0
12	0	0	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0	0	0
14	42	0	0	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	1	1	0	0	0
23	0	0	0	0	33	0	0	0	0	0	0
24	0	0	0	0	219	0	0	0	0	0	0
25	70	0	68	0	0	0	0	0	9	0	0
26	0	0	0	0	0	0	0	0	0	0	0
27	371	0	49	0	0	0	0	0	35	0	0
28	0	0	0	0	0	0	0	0	0	0	0
29	59	0	52	0	0	0	0	0	4	0	0
30	0	0	0	0	0	0	0	0	0	0	0
31	8	0	36	0	0	0	3	0	0	0	50
32	40	0	25	0	3	0	0	0	0	7	19
33	278	0	59	0	0	0	0	0	25	0	0
34	0	0	0	0	38	0	0	0	0	0	0
35	0	0	0	0	0	0	0	0	0	0	0
36	1	0	2	0	0	0	4	16	0	12	0
37	0	0	8	0	0	0	2	29	0	10	0

site	LCAR	LCHR	NRUB	NATH	NBOO	NSTR	NVOL	NBUC	NNUB	CSPI	CCAM
38	30	0	72	0	23	0	0	0	0	0	9
39	109	0	43	0	0	0	0	0	0	0	0
40	299	0	37	0	0	0	0	0	12	0	0
41	52	0	20	0	2	0	0	0	3	0	0
42	0	0	0	0	0	0	0	0	0	0	11
43	1	0	12	0	0	0	0	0	0	0	3
44	97	0	32	0	0	0	2	0	0	6	36
45	21	0	2	0	0	0	0	0	0	0	1
46	0	0	33	0	0	0	1	0	0	1	16
47	83	7	1	0	0	0	0	0	6	0	0
48	178	0	89	0	0	0	0	0	5	0	2
49	199	0	40	0	0	0	0	0	59	0	0
50	28	0	167	0	0	0	0	0	0	0	0
51	0	0	1	0	0	0	6	2	0	0	5
52	0	0	0	0	0	0	0	0	0	0	2
53	11	0	2	3	3	0	0	0	1	0	0
54	34	0	32	0	0	1	0	0	0	9	72
55	84	0	0	0	0	0	0	0	0	0	11
56	33	1	18	0	0	0	0	0	0	0	2
57	145	0	10	0	0	0	0	0	0	0	16
58	551	0	122	0	0	0	0	0	78	3	8

site	CLUT	PTEN	PNOT	PPRO	PVIG	CANO	AMEL	ANAT	IPUN	POLI	NEXI
1	0	0	0	0	0	2	0	0	0	0	0
2	7	0	6	0	0	2	2	0	0	0	0
3	0	0	0	0	0	25	0	0	0	0	1
4	0	0	0	0	0	1	0	0	0	0	0
5	0	0	0	0	0	17	0	0	0	0	9
6	0	0	1	0	0	14	0	0	0	0	6
7	0	0	0	0	0	1	0	0	0	0	2
8	0	0	0	0	1	44	0	0	0	0	0
9	0	0	20	0	0	1	0	1	0	0	0
10	0	0	1	0	0	0	0	0	0	0	0
11	7	1	30	0	42	3	0	0	1	0	0
12	0	0	0	0	0	0	0	0	0	0	0
13	12	0	22	0	0	0	1	0	1	0	0
14	0	0	0	0	0	0	0	0	0	0	0
15	0	0	5	1	0	1	1	8	0	0	0
16	0	0	0	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	11	0	0	0	0
19	0	0	4	0	8	0	0	0	0	0	0
20	4	0	0	0	0	0	0	1	0	0	0
21	146	0	43	0	0	2	5	0	0	0	0
22	26	0	0	0	18	0	0	0	1	0	0
23	72	0	27	0	0	63	0	0	0	0	17
24	112	0	117	0	0	6	0	0	0	0	0
25	0	0	0	0	0	36	0	0	0	0	0
26	0	0	0	3	0	142	0	0	0	0	0
27	0	0	0	0	0	530	0	0	0	0	0
28	0	0	1	0	0	0	7	1	0	0	0
29	0	0	0	0	0	7	0	0	2	0	1
30	0	0	0	0	0	93	0	1	0	0	4
31	10	5	5	0	2	2	0	0	0	0	14
32	8	1	11	0	0	13	0	0	0	0	9
33	0	0	2	0	0	7	0	0	0	0	13
34	48	0	44	0	0	170	0	0	0	0	1
35	10	0	0	0	4	0	0	0	0	0	0
36	14	3	9	0	0	13	0	2	1	0	6
37	16	9	1	0	4	0	0	0	0	0	3

site	CLUT	PTEN	PNOT	PPRO	PVIG	CANO	AMEL	ANAT	IPUN	POLI	NEXI
38	0	0	21	0	0	70	0	0	0	0	4
39	0	0	0	0	0	42	0	0	0	0	0
40	0	0	3	0	0	37	0	0	0	0	26
41	0	0	1	0	0	34	0	0	0	0	7
42	0	4	3	0	0	11	0	0	1	0	2
43	1	0	1	0	0	25	0	0	0	0	3
44	16	20	21	0	0	3	0	0	1	0	3
45	0	0	0	0	0	152	0	0	0	0	0
46	2	2	9	0	0	0	0	0	1	0	3
47	0	0	16	0	0	5	0	0	0	0	2
48	0	0	0	0	0	5	0	0	0	0	12
49	0	0	5	1	0	31	0	0	0	0	1
50	0	0	0	0	0	13	0	0	0	1	1
51	14	14	10	0	4	0	0	0	3	0	0
52	16	2	0	1	5	0	0	1	4	0	0
53	1	0	7	0	2	9	0	0	7	0	0
54	16	17	42	0	10	26	0	0	13	0	17
55	0	0	2	0	0	0	0	0	0	0	0
56	1	0	53	0	59	1	0	0	36	0	0
57	0	0	0	0	0	52	0	0	3	0	5
58	0	0	24	0	0	27	0	0	1	0	0

site	NFLA	NMIU	NPLA	IBUB	CCOM	HNIG	MDUQ	MERY	MMEL	FNOT	FOLI
1	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	5	0
3	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	0	0	0
5	0	0	0	0	0	3	0	0	0	0	0
6	0	0	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	1	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	35	0
10	0	0	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	1	1	0
12	0	0	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	0	1	0
20	0	0	0	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	0	10	0
25	0	0	0	0	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	1	0	0	0	2
28	0	0	0	0	0	0	0	0	1	2	0
29	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0	0	0
31	1	0	0	0	0	1	0	0	0	0	0
32	0	0	0	0	0	1	0	0	0	3	0
33	0	0	0	0	4	0	0	0	0	0	0
34	0	0	0	0	0	0	0	0	2	5	0
35	0	0	0	0	0	0	0	0	0	0	0
36	0	0	0	0	0	0	0	1	0	0	0
37	0	1	0	0	0	0	0	0	0	0	0

site	NFLA	NMIU	NPLA	IBUB	CCOM	HNIG	MDUQ	MERY	MMEL	FNOT	FOLI
38	0	0	0	0	1	1	1	0	0	4	0
39	0	0	0	0	2	0	0	0	0	0	0
40	0	0	0	0	2	0	0	0	0	0	0
41	0	0	0	0	0	0	0	1	0	2	0
42	0	0	0	1	0	0	0	0	0	0	0
43	0	0	0	0	0	1	0	0	0	0	0
44	2	0	0	0	0	1	0	0	0	0	0
45	0	0	0	0	0	0	1	0	0	0	0
46	1	0	4	0	0	0	0	0	0	0	0
47	0	0	0	0	0	0	2	8	0	0	29
48	0	0	0	0	0	1	1	0	0	0	5
49	0	0	0	0	0	1	0	3	0	0	0
50	0	0	0	0	0	1	0	0	0	2	0
51	0	1	0	0	1	0	0	0	0	0	0
52	0	0	0	0	0	0	0	1	0	0	0
53	0	0	0	0	0	4	0	4	2	0	0
54	1	1	5	0	0	0	1	0	0	0	0
55	0	0	0	0	0	0	0	0	0	0	0
56	0	0	0	0	0	0	0	1	0	0	0
57	0	0	0	0	0	0	0	0	0	2	0
58	0	0	0	0	0	3	16	1	0	0	0

site	GAFF	LSIC	CCAR	MCHR	AGRU	MDOL	MPUN	MSAL	LGUL	LCYA	LMIC
1	0	0	0	0	0	0	0	0	0	0	0
2	114	2	0	0	0	0	0	2	1	3	1
3	0	0	0	0	0	0	0	0	0	4	0
4	0	0	0	0	0	0	0	0	0	15	0
5	1	0	1	0	0	0	0	0	0	0	0
6	11	0	1	0	0	0	0	0	0	0	0
7	0	0	15	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0	0	0
9	6	53	0	0	0	0	0	1	0	2	0
10	8	0	0	0	0	0	0	10	0	1	0
11	16	8	0	0	0	0	0	13	3	1	0
12	12	0	0	0	0	0	0	0	0	6	0
13	2	0	0	0	0	0	0	3	0	1	0
14	0	0	12	0	0	0	0	0	0	2	0
15	117	1	0	0	0	0	0	7	1	26	0
16	250	0	0	0	0	0	0	4	1	0	0
17	3	0	0	0	0	0	0	1	0	0	0
18	10	0	0	0	0	0	0	3	1	11	0
19	0	15	0	0	0	0	0	22	1	0	0
20	631	0	0	0	0	0	0	7	1	11	0
21	95	1	0	0	0	0	0	4	0	12	0
22	0	40	0	0	0	0	0	5	0	2	1
23	0	17	0	0	0	0	0	2	0	1	0
24	0	25	0	0	0	0	0	8	0	1	0
25	2	0	65	0	0	0	0	0	0	0	0
26	0	0	1	0	0	0	0	0	0	4	0
27	0	0	2	0	0	0	0	20	0	0	0
28	19	2	0	0	0	0	0	14	0	1	1
29	0	0	7	0	1	4	1	0	0	0	0
30	19	0	0	0	0	0	0	5	0	1	0
31	1	0	1	0	0	0	0	0	0	0	0
32	6	1	2	0	0	0	0	2	0	0	0
33	4	0	3	0	0	0	0	0	0	0	0
34	0	9	0	0	0	0	0	2	0	0	0
35	5	3	0	0	0	0	0	4	0	1	0
36	4	5	1	0	0	0	0	3	0	0	0
37	3	1	0	0	0	0	0	4	0	1	0

site	GAFF	LSIC	CCAR	MCHR	AGRU	MDOL	MPUN	MSAL	LGUL	LCYA	LMIC
38	12	0	3	0	0	0	0	4	0	3	0
39	0	0	55	0	0	0	0	0	0	1	0
40	5	0	3	0	0	0	0	4	0	0	0
41	1	0	10	0	0	1	0	2	0	2	0
42	3	1	5	0	0	0	3	0	0	0	0
43	1	10	4	0	0	0	1	3	0	0	0
44	0	2	0	0	0	0	0	0	0	0	0
45	3	0	4	0	0	0	0	1	0	0	0
46	0	22	0	0	0	0	0	3	0	0	0
47	5	2	20	0	0	0	0	8	0	0	9
48	0	0	5	0	0	2	0	6	0	0	0
49	3	0	8	0	0	0	0	2	0	6	0
50	6	2	7	0	0	2	22	0	0	0	0
51	4	6	0	0	0	0	0	2	0	0	0
52	13	4	0	0	0	0	1	2	0	1	0
53	46	45	0	117	0	1	21	16	0	0	0
54	46	2	0	0	0	0	0	11	0	0	0
55	1	71	0	7	2	0	3	1	0	0	0
56	9	319	0	0	0	1	11	19	0	0	0
57	48	97	0	0	0	0	0	10	0	1	2
58	0	0	0	0	0	0	2	0	0	0	0

site	LHUM	LMEG	LMAC	LHYB	ARUP	PANN	PNIG	PPHO	PCAP	PCOP	PSHU
1	0	0	0	0	0	0	0	0	0	0	0
2	0	27	26	0	0	3	0	0	0	0	0
3	0	3	1	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	0	0	0
6	0	0	5	0	0	0	0	0	0	0	0
7	0	0	0	0	0	1	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0	0	0
9	0	15	41	1	0	0	0	0	0	0	0
10	0	0	7	0	0	0	0	0	0	0	0
11	11	6	21	0	0	1	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0
13	2	21	9	1	0	0	0	0	3	0	0
14	0	0	0	0	1	0	0	0	0	0	0
15	0	1	7	3	0	0	0	0	1	0	0
16	0	0	43	1	0	0	0	0	0	0	0
17	0	0	3	0	0	0	0	0	0	0	0
18	0	0	1	4	0	0	0	0	0	0	0
19	0	0	18	0	0	2	0	0	0	0	0
20	2	0	27	14	0	0	0	0	0	0	0
21	7	9	12	2	0	0	0	0	0	0	0
22	11	7	69	3	0	2	0	0	5	21	0
23	6	1	0	0	0	0	0	0	4	0	0
24	0	21	0	0	0	0	0	0	1	0	0
25	0	0	0	0	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0	0	0	0	0
27	0	1	1	0	0	0	0	0	0	0	0
28	4	0	72	1	0	0	0	0	0	0	0
29	0	2	2	0	0	0	0	0	2	0	0
30	0	0	1	0	0	0	0	0	0	0	0
31	1	1	1	0	0	0	0	6	1	7	0
32	2	4	14	0	0	1	0	3	0	3	0
33	0	3	0	0	0	0	0	0	1	0	0
34	1	5	1	0	0	0	0	0	0	0	0
35	1	1	4	0	0	1	0	0	0	0	0
36	1	2	2	0	0	1	0	1	0	29	0
37	3	5	1	0	0	0	0	1	1	5	0

site	**LHUM**	**LMEG**	**LMAC**	**LHYB**	**ARUP**	**PANN**	**PNIG**	**PPHO**	**PCAP**	**PCOP**	**PSHU**
38	0	13	3	0	0	0	0	0	0	1	0
39	0	2	0	0	0	0	0	0	0	0	0
40	0	47	0	0	0	0	0	0	0	0	0
41	0	24	2	0	0	1	0	0	1	0	0
42	0	4	2	0	0	0	0	0	5	3	0
43	12	5	19	1	0	0	1	3	3	36	0
44	0	0	0	0	0	0	0	19	0	23	0
45	0	14	0	0	0	0	0	0	2	0	0
46	0	7	2	0	0	1	0	1	4	2	0
47	0	4	13	0	0	0	0	0	0	0	0
48	0	1	0	0	1	0	0	0	1	0	0
49	0	3	1	0	0	0	0	0	0	0	0
50	0	9	11	0	0	0	0	0	0	0	0
51	0	0	5	0	0	1	0	2	1	4	0
52	0	4	2	0	0	0	0	1	0	0	0
53	0	7	10	0	0	0	0	2	13	0	0
54	0	10	5	0	0	0	0	5	7	5	0
55	2	3	3	0	0	0	0	2	0	1	0
56	14	6	1	0	0	0	0	2	21	3	0
57	0	6	8	0	0	0	0	0	1	10	0
58	0	0	0	0	0	0	0	2	21	4	0

site	ENIG	ESTI	EZON	EBLE	EWHI	ECRA	ESPE	EFLA	EGRA	ECHL	E sp
1	0	0	0	0	0	2	16	2	0	0	2
2	0	0	0	0	0	0	0	0	0	0	0
3	0	0	0	0	0	14	16	14	0	0	10
4	0	0	0	0	0	0	0	0	0	0	0
5	0	0	0	0	0	14	27	24	0	0	4
6	0	0	2	2	0	0	16	10	0	0	2
7	0	0	0	0	0	0	4	22	0	0	0
8	0	32	0	0	0	6	0	0	0	0	1
9	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	2	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	2	0	0
13	0	0	0	0	2	0	0	0	0	0	0
14	0	0	0	0	0	1	12	25	0	0	1
15	0	0	0	0	7	0	0	0	1	0	0
16	0	0	0	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	5	0	0
19	0	0	0	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	0	0	0
21	0	0	0	0	7	0	43	0	0	0	0
22	0	0	0	1	0	0	4	0	0	0	0
23	0	0	0	0	0	0	13	19	0	0	0
24	0	0	0	0	0	0	2	0	0	0	0
25	0	0	0	0	0	0	3	0	0	0	0
26	0	0	0	0	0	1	2	0	0	0	0
27	0	1	8	0	0	3	14	2	0	0	2
28	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	5	3	0	0	0
30	0	0	0	0	0	0	34	32	0	0	5
31	0	0	4	0	0	0	0	0	0	0	0
32	4	0	1	2	0	0	4	0	0	0	0
33	0	0	2	2	0	0	5	0	0	0	0
34	0	0	0	0	0	0	12	4	0	0	0
35	0	0	0	0	0	0	0	0	5	0	0
36	0	0	2	0	0	1	3	0	0	0	0
37	0	0	4	0	0	0	0	0	0	0	0

site	ENIG	ESTI	EZON	EBLE	EWHI	ECRA	ESPE	EFLA	EGRA	ECHL	E sp
38	0	0	4	3	0	0	20	0	0	0	9
39	0	0	0	0	0	0	3	1	0	0	0
40	0	0	1	0	0	0	27	9	0	0	2
41	0	0	1	1	0	1	12	2	0	0	0
42	0	0	1	0	0	1	4	0	0	0	0
43	0	1	0	0	0	0	3	0	0	0	0
44	0	2	2	0	0	0	1	1	0	0	0
45	0	3	4	1	0	0	3	0	0	0	0
46	0	0	2	3	0	0	1	0	0	0	0
47	0	0	1	1	0	0	1	0	0	0	0
48	0	9	8	2	0	0	20	0	0	0	0
49	0	0	0	0	0	3	37	2	0	0	0
50	0	0	0	0	0	0	1	1	0	0	1
51	1	0	1	1	0	0	26	2	0	0	0
52	0	0	0	0	2	0	2	0	0	1	0
53	1	0	0	0	0	0	0	0	0	0	0
54	0	0	35	0	0	1	3	1	0	0	0
55	0	0	0	0	0	0	0	0	0	0	0
56	1	1	4	1	0	0	0	0	0	0	0
57	4	0	1	0	0	0	2	0	0	0	0
58	0	3	9	1	0	0	2	0	0	0	0

Appendix 3. Sites sampled in the Spring River basin during 1994 (sites 53-58) and 1995 (sites 1-52), with date of collection, geographic coordinates, and values of environmental variables. Site numbers correspond to locations indicated in Figure 1. Abbreviations refer to the following variables, with units of measurement in parentheses: date = day of the month, lat = north latitudinal geographic coordinate (decimal degrees), long = west longitudinal geographic coordinate (decimal degrees), riffle = riffle mesohabitat (%), run = run mesohabitat (%), pool = pool mesohabitat (%), back = backwater mesohabitat (%), mud = mud substratum (%), sand = sand substratum (%), gravel = gravel substratum (%), smcob = small cobble substratum (%), lgcob = large cobble substratum (%), bould = boulder substratum (%), bed = bedrock substratum (%), can = canopy cover (%), sub = submergent vegetation (%), emerg = emergent vegetation (%), struct = woody structure (%), DO = dissolved oxygen (mg/L), CO2 = carbon dioxide (mg/L), alk = total alkalinity (mg/L), hard = hardness (ppm), nitr = nitrate (mg/L), phos = phosphate (mg/L), temp = water temperature (C°), pH = pH, DA = drainage area (km^2), cs area = cross-sectional area (m^2), width = maximum stream width (m), alt = altitude (km), grad = gradient (m/km). Missing values are denoted by 999.

site	date	lat	long	riffle	run	pool	back	mud	sand
1	17-18 May	36.76	94.02	60	38	2	0	0	1
2	18 May	37.41	94.72	0	45	0	55	60	34
3	23 May	36.77	94.02	20	40	20	20	0	5
4	23 May	36.73	93.97	1	0	99	0	70	5
5	24 May	36.79	94.03	40	35	5	20	5	2
6	25 May	37.07	94.11	10	60	0	30	15	2
7	25 May	37.04	94.06	15	65	5	15	2	1
8	26 May	37.03	93.99	60	15	10	15	20	5
9	30 May	37.03	94.78	20	5	65	10	21	40
10	30 May	37.06	94.80	7	13	60	20	60	30
11	31 May	37.08	94.74	0	90	0	10	75	22
12	1 June	37.05	94.82	0	2	98	0	94	5
13	5 June	37.44	94.72	10	88	0	2	61	2
14	6 June	36.86	94.35	80	10	0	10	1	1
15	1 August	37.18	94.82	20	70	0	10	34	20
16	13 June	37.55	94.71	5	70	20	5	80	2
17	13 June	37.56	94.72	5	0	95	0	70	20
18	14 June	37.21	94.83	5	0	93	2	84	5
19	14 June	37.13	94.80	0	0	95	5	69	5
20	15 June	37.53	94.72	10	20	68	2	85	5
21	16 June	37.31	94.65	30	30	20	20	20	10
22	19 June	37.53	94.25	5	80	0	15	10	5
23	20 June	37.41	94.10	37	43	10	10	18	2
24	20 June	37.36	94.04	40	5	50	5	1	4
25	21 June	37.12	93.90	50	40	3	7	2	1
26	21 June	36.96	93.86	12	6	80	2	3	10
27	22 June	36.90	94.13	20	70	2	5	2	5
28	27 June	37.34	94.63	2	3	85	10	93	3
29	28 June	36.99	94.68	50	40	0	10	3	6
30	29 June	36.97	94.56	50	45	0	5	1	3
31	7 July	37.28	94.53	87	10	0	3	1	2
32	8 July	37.27	94.52	55	35	0	10	2	10
33	9 July	37.06	93.84	999	999	999	999	2	1
34	10 July	37.34	94.02	60	20	15	5	1	0
35	10 July	37.40	94.30	0	100	0	0	48	48
36	11 July	37.28	94.51	10	50	0	40	5	30
37	11 July	37.28	94.52	5	60	5	30	4	20

site	**date**	**lat**	**long**	**riffle**	**run**	**pool**	**back**	**mud**	**sand**
38	12 July	37.19	94.31	15	70	0	15	1	2
39	13 July	37.07	93.84	50	40	0	10	1	3
40	13 July	37.05	93.80	35	40	0	20	1	5
41	17 July	37.11	94.22	999	999	999	999	3	1
42	18 July	37.16	94.62	1	79	0	20	3	10
43	18 July	37.17	94.60	40	45	0	15	5	5
44	19 July	37.18	94.65	68	25	0	7	1	5
45	20 July	37.18	94.46	45	45	0	10	7	5
46	25 July	37.22	94.59	10	85	0	5	3	5
47	26 July	37.02	94.48	5	55	0	40	20	5
48	27 July	36.90	94.36	55	30	0	15	10	5
49	27 July	36.89	94.09	5	55	0	40	10	5
50	3 August	36.98	94.70	65	20	7	8	15	5
51	7 August	37.35	94.32	0	100	0	0	44	5
52	8 August	37.28	94.67	10	70	0	20	32	5
53	21 July	36.93	94.74	50	8	32	10	2	10
54	27-28 July	37.19	94.63	39	40	6	15	3	5
55	29 July	37.02	94.72	2	83	2	13	1	1
56	2 August	37.06	94.71	30	20	20	30	2	10
57	4 August	37.13	94.63	45	5	50	0	5	10
58	5 August	37.05	94.64	60	20	20	0	1	4

site	**gravel**	**smcob**	**lgcob**	**bould**	**bed**	**can**	**sub**	**emerg**	**struct**	**DO**	**CO2**
1	20	29	49	1	0	85	0	1	1	8	15
2	3	1	1	1	0	60	0	0	15	6	25
3	50	24	20	1	0	30	0	20	10	7	20
4	10	10	5	0	0	1	0	0	2	11	25
5	31	31	30	1	0	2	0	5	1	9	25
6	30	31	15	5	45	2	2	0	5	9	25
7	30	50	11	5	1	85	0	0	5	9	25
8	23	40	10	2	0	60	0	0	5	8	20
9	20	10	5	2	2	55	2	0	5	7	15
10	9	0	0	1	0	95	30	0	5	5	25
11	2	0	0	1	0	30	0	0	10	7	10
12	1	0	0	0	0	5	20	29	0	5	20
13	2	30	5	0	0	85	0	0	15	6	30
14	4	9	4	1	80	20	5	5	5	9	20
15	20	10	10	5	1	85	60	5	20	5	25
16	7	5	5	1	0	10	20	25	2	7	15
17	3	2	0	0	5	95	0	0	15	7	15
18	10	1	0	0	0	90	0	0	15	3	20
19	1	0	0	20	5	60	0	0	20	5	20
20	2	2	1	5	0	5	0	10	15	3	20
21	25	15	15	10	5	3	7	0	3	7	15
22	65	15	4	1	0	20	0	10	15	10	15
23	45	10	5	2	18	80	0	15	5	8	15
24	15	20	9	1	50	5	0	0	1	10	15
25	50	36	10	1	0	30	1	3	10	7	25
26	25	40	20	2	0	35	0	5	2	8	25
27	43	39	10	1	0	25	0	5	999	8	20
28	2	0	0	2	0	50	999	999	50	3	15
29	40	35	10	1	0	35	0	1	10	7	20
30	35	39	20	2	0	90	0	0	2	6	15
31	27	55	10	3	2	15	0	3	2	5	20
32	44	35	4	5	0	5	80	30	5	6	20
33	35	50	12	0	0	55	0	5	3	6	20
34	5	10	11	3	70	70	0	1	1	7	15
35	2	1	1	0	0	80	0	0	55	5	20
36	40	21	3	1	0	20	0	5	10	6	20
37	62	12	2	0	0	20	0	3	5	5	20

site	gravel	smcob	lgcob	bould	bed	can	sub	emerg	struct	DO	CO2
38	30	50	10	7	0	45	1	3	3	7	20
39	23	70	2	1	0	75	3	0	5	8	20
40	50	39	4	1	0	7	0	7	3	9	20
41	36	45	10	5	0	15	0	15	3	8	20
42	36	15	5	1	30	1	0	5	2	999	15
43	56	25	3	1	5	3	0	0	2	7	25
44	73	20	1	0	0	5	0	0	1	8	15
45	35	40	10	3	0	3	0	4	2	7	15
46	48	30	12	2	0	15	0	15	1	7	20
47	44	30	1	0	0	5	0	5	20	8	15
48	70	10	5	0	0	15	0	5	15	7	15
49	45	35	5	0	0	10	2	3	25	8	15
50	57	20	3	0	0	75	0	0	15	6	10
51	20	15	15	1	0	20	0	3	5	5	15
52	5	3	12	3	40	20	0	7	30	5	15
53	37	50	1	0	0	1	0	0	7	7	15
54	30	40	20	1	0	20	0	0	5	8	20
55	2	3	3	3	87	1	0	0	2	7	20
56	14	14	10	20	30	5	0	0	20	8	15
57	40	40	5	0	0	5	0	0	7	7	20
58	29	50	15	1	0	15	0	0	1	12	10

site	alk	hard	nitr	phos	temp	pH	DA	cs area
1	13.68	102.6	3	0.06	15.0	7.5	90	0.52
2	34.20	239.4	0	0.12	19.0	7	500	6.48
3	47.88	119.7	3	0.06	14.5	7	114	0.89
4	20.52	68.4	1	0.08	20.0	6.5	43	999
5	47.88	119.7	3	0.04	16.0	7.5	137	1.34
6	47.88	171.0	3	0.08	14.0	8	194	8.65
7	61.56	153.9	4	0.06	15.0	8	83	3.98
8	54.72	153.9	3	0.00	15.0	7.5	52	0.42
9	34.20	102.6	1	0.12	19.0	7	39	0.83
10	20.52	119.7	0	0.10	17.0	6.5	22	0.73
11	20.52	0.0	1	0.10	17.0	7	159	9.60
12	13.68	85.5	0	0.04	18.5	7	13	999
13	47.88	478.8	0	0.10	24.0	7.5	135	4.60
14	47.88	119.7	2	0.00	14.5	7	101	3.04
15	41.04	171.0	1	0.10	23.0	7	49	1.74
16	27.36	85.5	0	0.10	25.0	7.5	99	0.25
17	27.36	85.5	0	0.00	22.0	7	50	999
18	27.36	102.6	0	0.20	18.0	7	26	999
19	20.52	136.8	2	0.10	24.0	7	80	999
20	54.72	171.0	0	0.22	22.0	7.5	123	0.53
21	13.68	119.7	0	0.00	22.0	7	14	0.21
22	41.04	136.8	2	0.00	26.0	8	213	16.30
23	47.88	119.7	3	0.06	24.0	8	114	0.68
24	41.04	119.7	3	0.10	26.0	8	42	0.54
25	47.88	171.0	4	0.10	17.0	7.5	628	8.28
26	27.36	102.6	6	0.18	21.0	7	28	999
27	54.72	153.9	5	0.06	18.0	8	416	15.63
28	20.52	119.7	0	0.06	21.0	7	21	999
29	47.88	136.8	2	0.00	21.0	7.5	104	1.32
30	34.20	102.6	2	0.06	18.0	7.5	7	0.54
31	47.88	136.8	3	0.12	23.0	7.5	3058	37.96
32	61.56	171.0	3	0.10	21.0	8	1451	999
33	61.56	171.0	3	0.10	19.0	8	183	4.19
34	41.04	136.8	4	0.06	24.0	8	32	0.35
35	34.20	119.7	2	0.16	25.0	7	583	11.14
36	61.56	171.0	3	0.12	24.0	7.5	1323	23.70
37	61.56	171.0	3	0.12	26.5	7.5	1329	999

site	alk	hard	nitr	phos	temp	pH	DA	cs area
38	68.40	171.0	4	0.06	22.0	7.5	1350	999
39	68.40	188.1	4	0.06	19.0	7.5	611	6.30
40	61.56	171.0	4	0.06	21.0	8	183	5.45
41	61.56	171.0	5	0.06	22.0	8	286	7.32
42	54.72	205.2	5	0.06	26.0	8	4757	999
43	61.56	188.1	5	0.14	25.5	8	771	9.01
44	61.56	171.0	4	0.06	25.0	8	3970	19.01
45	54.72	188.1	5	0.06	23.0	8	687	5.91
46	61.56	205.2	3	0.10	24.0	8	3191	20.66
47	61.56	153.9	4	0.06	23.0	8	1365	23.76
48	61.56	171.0	4	0.08	21.0	8	919	999
49	61.56	171.0	5	0.10	23.0	8	390	7.05
50	54.72	153.9	2	0.06	23.5	7.5	109	3.43
51	27.36	85.5	3	0.12	26.0	7	1157	17.25
52	41.04	376.2	4	0.14	27.0	7.5	707	3.43
53	47.88	205.2	2.5	0.12	26.0	8	7081	999
54	61.56	205.2	3	0.08	24.0	8	3202	999
55	47.88	171.0	3	0.08	25.0	8	6892	999
56	54.72	188.1	2.5	0.08	28.0	8.5	7885	999
57	75.24	273.6	4	0.46	24.0	8	4910	999
58	54.72	153.9	2.5	0.06	23.5	8	1464	999

site	width	alt	grad
1	7.2	418	6.06
2	14.6	268	1.52
3	13.8	418	3.03
4	4.0	451	9.09
5	19.5	412	6.06
6	22.9	326	1.52
7	29.4	341	1.52
8	15.8	378	3.03
9	15.2	245	1.52
10	6.6	253	1.52
11	16.2	241	0.00
12	3.3	270	3.03
13	10.4	274	1.52
14	9.3	322	1.52
15	7.7	259	1.52
16	6.0	293	3.03
17	2.0	293	3.03
18	6.0	268	1.52
19	33.5	253	1.52
20	4.2	287	1.52
21	1.8	262	1.52
22	51.0	280	0.00
23	19.6	302	1.52
24	1.8	322	4.55
25	16.5	328	1.52
26	7.6	421	4.55
27	19.2	331	1.52
28	12.0	268	1.52
29	8.0	236	3.03
30	8.5	312	9.09
31	50.0	256	0.00
32	999	259	1.52
33	10.0	341	3.03
34	7.0	323	4.55
35	13.0	271	0.00
36	40.0	256	0.00
37	30.5	256	0.00

site	width	alt	grad
38	21.5	280	0.00
39	9.5	332	1.52
40	18.0	352	1.52
41	15.8	299	1.52
42	46.3	247	0.00
43	17.0	247	0.00
44	54.9	247	0.00
45	22.0	265	0.00
46	50.5	250	0.00
47	46.0	274	0.00
48	50.0	296	0.00
49	18.0	338	3.03
50	15.0	232	1.52
51	23.7	268	0.00
52	11.0	256	0.00
53	75.0	223	0.00
54	35.0	247	0.00
55	63.0	235	0.00
56	345.0	238	0.00
57	32.0	244	0.00
58	22.0	247	0.00

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Christopher D. Wilkinson
Signature of Author

December 16, 1997
Date

Spatial Pattern of Fish Assemblage Structure and Environmental Correlates in the Spring River Basin, with Emphasis on the Neosho Madtom *(Noturus placidus)*
Title of Thesis

Signature of Graduate Office Staff Member

December 19, 1997
Date Received