EFFECTS OF LOWHEAD DAMS ON FISH AND BENTHIC INVERTEBRATE ASSEMBLAGE STRUCTURE IN THE NEOSHO RIVER, WITH COMMENTS ON THE THREATENED NEOSHO MADTOM, *NOTURUS PLACIDUS*

A Thesis

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An Abstract for the Thesis of

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Abstract approved: David Edds

Many studies have assessed the effects of large dams on fishes and benthic invertebrates, but few have examined the effects of lowhead dams. I sampled fishes, benthic invertebrates, habitat, and physicochemistry monthly from November 2000 to October 2001 at eight gravel bar sites centered around two lowhead dams on the Neosho River, Lyon County, Kansas, including a reference site and a treatment site upstream and downstream from each dam. Multivariate analysis of variance indicated site type differences for habitat, and benthic invertebrate and fish abundance, but not physicochemistry, through there were site type*dam interactions for habitat, and benthic invertebrate and fish abundance, and site type*month interactions for benthic invertebrate and fish abundance. Analysis of variance indicated that none of the measured physicochemical variables differed among site types; however habitat did vary immediately upstream and downstream from the dams, as did benthic invertebrate and fish abundance. Compared to reference sites, upstream treatment sites were deeper with slower velocity, downstream treatment sites were shallower with faster velocity, and both treatment site types had greater substrate compaction. Benthic invertebrate abundance was lower at downstream treatment sites than other site types. Benthic invertebrate richness did not differ, but upstream treatment sites had lower evenness than other site types. A lower proportion of ephemeropterans, plecopterans, and trichopterans (%EPT) inhabited treatment sites than reference sites. I found more fish in downstream reference sites and fewer in treatment and upstream reference sites. Fish species richness did not differ between site types, but upstream site types had higher evenness than downstream site types. Abundance of Neosho madtom, *Noturus placidus,* was significantly lower immediately upstream and immediately downstream from dams compared to reference sites, whereas abundances of suckermouth minnow, *Phenacobius mirabilis*, orangethroat darter, *Etheostoma spectabile*, and slenderhead darter, *Percina phoxocephala,* were higher in downstream treatment areas than reference sites. The apparent effects of these lowhead dams on fish and benthic invertebrate assemblages were similar to the effects reported for larger dams.

Approved by Dr. David Edds – Major Advisor

Approved by Dr. Dwight Moore – Committee Member

Approved by Dr. Mark Wildhaber – Committee Member

Approved by Dr. Derek Zelmer – Committee Member

Approved by Dr. Marshall Sundberg – Department Chair

Approved for the Graduate Council

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Preface

My thesis consists of one chapter, which contains the overall summary of my project. It will be submitted to Transactions of the American Fisheries Society, thus is formatted for that journal.

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Introduction

Dams have been used to provide hydroelectric power, drinking water supplies, irrigation, navigation, flood control, and recreation activities for over 5,000 years, and now regulate most of the world's major rivers (Petts 1980). There are an estimated two million dams in the United States, including 75,000 over 2 m in height (Maclin and Sicchio 1999). Among states with the most dams, Kansas ranks second, only to Texas, with 5,699 (Shuman 1995). Dams, however, cause severe disruptions to a riverine ecosystem and have negative effects on the stream's biology (Baxter 1977; Shuman 1995; Rabeni 1996). Because habitat influences riverine fish and benthic invertebrate assemblages, high intensity anthropogenic disturbance, such as the damming of rivers, is typically associated with alterations in fish and invertebrate assemblage structure (Luttrell et al. 1999; Waite and Carpenter 2000; Onorato et al. 2000). Both large dams (> 4 m in height) (Baxter 1977; Kanehl et al. 1997; Clarkson and Childs 2000) and lowhead dams (< 4 m in height) (Watters 1996; Helfrich et al. 1999; Porto et al. 1999) act as barriers that block movement of fishes, and affect physical and chemical conditions of rivers. Dams convert lotic habitats to lentic habitats, change the flow of water, alter water quality, and change channel morphology and bed structure by increasing siltation upstream from and erosion downstream from the dam. These alterations cause changes in assemblage structure of fishes and invertebrates via shifts in species composition, abundance, species diversity, and species richness upstream and downstream from the dam (Doeg and Koehn, 1994; Porto et al. 1999).

The U.S. Fish and Wildlife Service (USFWS) listed the Neosho madtom, *Noturus placidus*, as threatened in 1990 (55 FR 21148), primarily due to loss of habitat as a result of mainstream impoundments eliminating approximately one-third of its historic range, and noted that lowhead dams also might limit Neosho madtom populations (USFWS 1991). The Neosho madtom is a small ictalurid (generally < 75 mm in total length) presently distributed discontinuously in the Neosho (Grand) – Spring River system, and is listed by the state of Kansas as threatened, and by Missouri and Oklahoma as endangered. The Neosho madtom is found in riffles and along sloping gravel bars in moderate stream velocities, preferring deposits of loosely compacted gravel where it feeds on juvenile insects at night (Cross and Collins 1995).

Although many studies have addressed the effects of large dams on fishes (e.g. Martinez et al. 1994; Clarkson and Childs 2000; Wildhaber et al. 2000b), few have examined the effects of lowhead dams. Studies in Ontario (Porto et al. 1999), Montana (Helfrich et al. 1999), North Carolina (Beasley and Hightower 2000), and Puerto Rico (Benstead et al. 1999) suggest that lowhead dams affect riverine fish and benthic invertebrate assemblages in ways similar to, but smaller than magnitude than, those reported for larger dams. Information on the effects of lowhead dams can be used in the conservation and protection of biotic integrity of aquatic ecosystems, notably in the protection of threatened or endangered species like the Neosho madtom. The objective of my study was to investigate possible effects of two lowhead dams on fish and benthic invertebrate assemblage structure in a midwestern river, the Neosho River, Kansas.

Dam Effects

Dams act as physical barriers that block fishes' upstream and downstream movements during periods of spawning or seasonal migrations, which isolates populations and prevents recolonization, thus reducing fish abundance, species diversity, and gene flow (Winston et al. 1991; Ligon et al. 1995; Reyes-Gavilan et al. 1996; Pringle 1997; Concepcion and Nelson 1999). Unlike large dams, lowhead dams do not act as complete barriers to the upstream movement of fishes (Benstead et al. 1999; Helfrich et al. 1999; Beasley and Hightower 2000). Helfrich et al. (1999) reported that fish passage over lowhead dams was feasible during times of high flow, but was inhibited at low flow.

Both large and lowhead dams not only restrict the dispersal of riverine fishes, but also change the habitat conditions in which the fishes live, which has profound effects on the biotic integrity of a stream (Warren and Pardew 1998; Waite and Carpenter 2000). Habitat change is responsible for alterations in riverine fish and benthic invertebrate assemblage structure in areas upstream from dams, due to the conversion of lotic habitat to lentic habitat, which alters the stream's water chemistry (Martinez et al. 1994; Kanehl et al. 1997). The inundated area also acts as a nutrient trap, retaining nutrients that are then lost to the rest of the stream (Baxter 1977). Flow reduction prevents organic wastes from being swept from the bottom, causing the substrate to be inhospitable for many benthic organisms, including fishes and invertebrates (Baxter 1977). These changes in habitat result in a species composition shift from obligatory riverine fishes, those that require riverine conditions for all or part of their life history, to facultative riverine fishes, those that do not require riverine conditions (Rabeni 1996; Maret et al. 1997).

Flow modification is one of the most widespread disturbances of stream environments caused by both large and lowhead dams (Drinkwater and Frank 1994; Travnichek et al. 1995; Porto et al. 1999). Highly variable and unpredictable flow regimes caused by dams alter stream habitat, including stream velocity, turbidity, and substrate composition, which affects the distribution of fishes and invertebrates (Power et al. 1996; Stevens et al. 1997; Luttrell et al. 1999). Because many riverine fishes are triggered to spawn during high waters, a shift in the normal flow regime due to water retention could alter fish migration cues, and might inhibit spawning (Baxter 1977; Drinkwater and Frank 1994). Also, altered flow over spawning grounds could discourage reproduction of non-migratory riverine fishes.

Changes in the flow regime of streams also cause changes in habitat by increasing siltation upstream from and erosion downstream from large and lowhead dams (Power et al. 1996; Stevens et al. 1997; Bonner and Wilde 2000). Except during periods of high flow, most sediment transported by the river upstream from an impoundment is deposited within the inundated area (Wood and Armitage 1997). Sedimentation lowers productivity in aquatic ecosystems by killing periphyton and macrophytes (Waters 1995; Mullner et al. 2000). Sedimentation also causes loss of benthic habitat by occluding interstitial spaces, which reduces habitat diversity and suitability, key factors in determining and maintaining the diversity of fishes and benthic invertebrates (Doeg and Koehn 1994; Wood and Armitage 1997; Bain 1999). Sedimentation reduces suitability of spawning habitat, and hinders development of fish and benthic invertebrate eggs and larvae (Doeg and Koehn 1994; Drinkwater and Frank 1994; Wood and Armitage 1997). Siltation increases benthic invertebrate drift rates, and affects their feeding activities by impeding feeding structures and reducing feeding efficiency (Doeg and Koehn 1994). The result is a reduction in food available to fishes in that area (Weaver and Garman 1994; Wood and Armitage 1997). Sedimentation interferes with circulation of water through gravel, and hinders respiration of fishes and benthic invertebrates by clogging gills (Newcombe and MacDonald 1991; Wellman et al. 2000). Sedimentation also increases the possibility of adsorption and absorption of toxic chemicals, which might lower fish abundance by lowering benthic invertebrate abundance (food) (Wildhaber et al. 2000a) or enter the food chain through the activities of invertebrates and eventually accumulate in fishes.

Because sediments settle out in impounded areas, water leaving the impounded area is said to be "sediment hungry;" that is, the water will pick up a new load of sediments, eroding the shores and streambed downstream from the dam (Power et al. 1996; Wood and Armitage 1997). As a result, the streambed coarsens to such an extent that fish are not capable of moving substrate to create nests, virtually eliminating suitable spawning habitats (Kondolf 1997). Destabilization of substrate also changes the foraging strategies of fishes by decreasing the available habitat for benthic invertebrates (Rabeni 1996). In eroded zones directly downstream from a dam, invertebrates that inhabit exposed streambed substrates are subjected to scouring, which makes them more susceptible to predation through dislodgment (Newcombe and MacDonald 1991). Other invertebrates die or move out of the area due to a reduction in particulate organic carbon, which they utilize as food, causing a reduction in prey items for fishes (Baxter 1977).

There are 16 lowhead dams on the Neosho River in Kansas. Helfrich et al. (1999) suggested that a series of lowhead dams might present a serious cumulative fish passage challenge, which gradually could alter fish assemblage structure in a river. My research focused on the effects of lowhead dams on riverine fishes, benthic invertebrates, habitat, and physicochemistry. Because of the potential cumulative effects of dam-related stress on riverine ecosystems, it is important to measure both physical habitat and physicochemical variables to understand riverine fish and benthic invertebrate assemblage structures (Luttrell et al. 1999; Waite and Carpenter 2000). I examined abundance, evenness (equitability), species richness, and composition of fishes and benthic invertebrates, and measured 10 habitat and 15 physicochemical variables at eight sites centered around two lowhead dams. Associated with each dam were four site types: an upstream reference site, an inundated site (i.e., upstream treatment), a site immediately downstream from the dam (i.e., downstream treatment), and a downstream reference site. Because no pre-impoundment data on fish and benthic invertebrate assemblage structure were available, sites directly upstream from and downstream from each dam were considered treatment sites while the other sites, which were free-flowing and assumed to be minimally affected by the dams, were considered reference sites. I compared results among treatment and reference sites to test for effects of the lowhead dams on fish and benthic invertebrate assemblages. I predicted that, because of differences in habitat and physicochemistry, fish and benthic invertebrate assemblages would differ at treatment sites compared to reference sites. I predicted that upstream treatment sites would be deeper, and have less stream velocity, greater siltation and substrate compaction, and higher productivity than reference sites. Compared to references sites, I expected these sites to have fewer lotic-type fishes (e.g. madtoms and darters) and benthic invertebrates (e.g. mayflies, stoneflies, and caddisflies), but more lentic-type fishes (e.g. sunfishes) and benthic invertebrates (e.g. dragonflies), with lower abundance, evenness, and richness. I predicted that downstream treatment sites would be shallower, and have greater stream velocity, scoured substrate, and less productivity than reference sites. Compared to reference sites, I expected these sites to have lower abundance, evenness, and richness. I predicted that, due to differences in habitat, Neosho madtom abundance would be lower in treatment sites than reference sites.

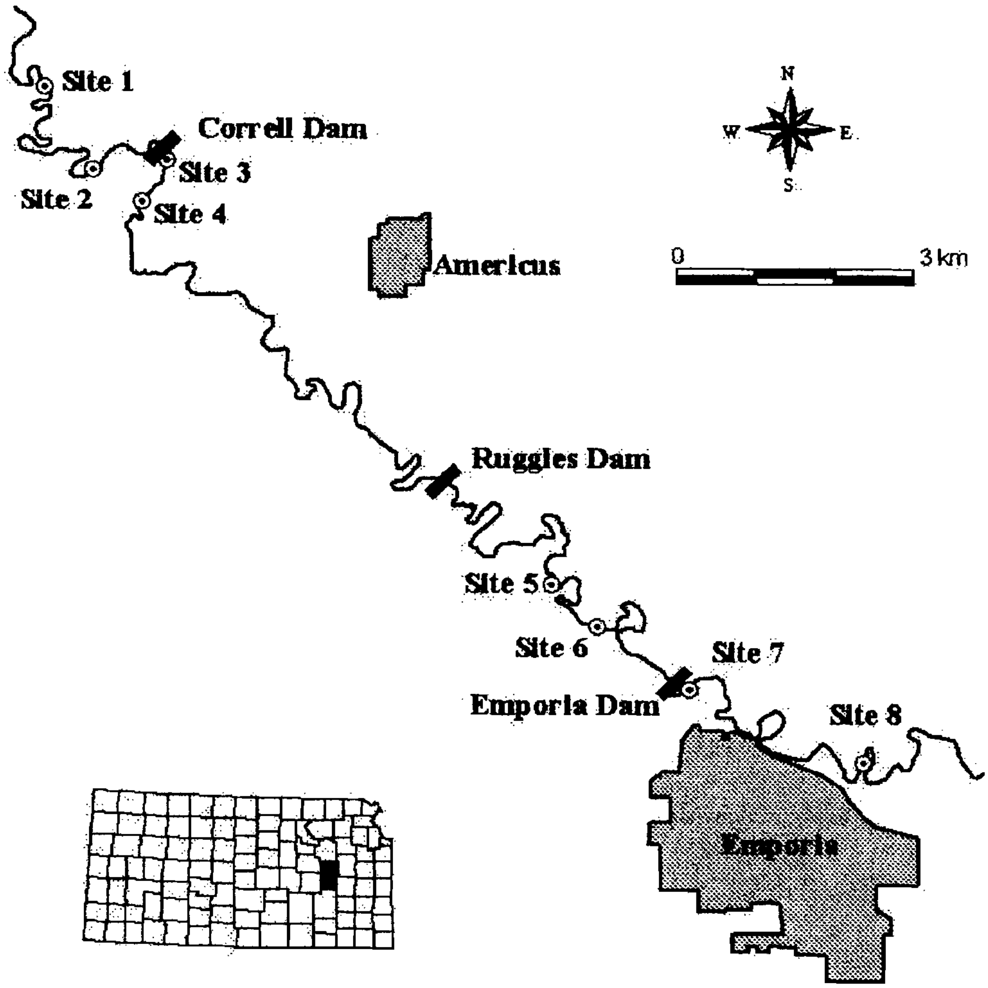
Though there were confounding interactions between site types and dams, and between site types and months, my findings suggest that these lowhead dams have caused changes in habitat, including depth, velocity, and substrate composition, but not physicochemistry, immediately upstream and downstream. As a result of differences in habitat, there were differences in fish and benthic invertebrate abundance and evenness, but not richness. Neosho madtom abundance was lower in treatment sites than reference sites. Except for water chemistry, these differences around lowhead dams were similar to those seen in association with larger dams.

Methods

Study Area

My study sites consisted of eight gravel bars along a 34 km stretch of the Neosho River in Lyon County, Kansas (Figure 1), within the Prairie Parkland Province Ecoregion (Chapman et al. 2001). This portion of the Neosho River is a fifth-order stream impounded by three lowhead dams (Correll Dam, Ruggles Dam, and Emporia Dam). I did not sample near the Ruggles Dam because landowner permission could not be obtained. The Neosho River basin is primarily an agricultural area where the principal crops are mixed grasses, corn, wheat, and soybeans, with few mature riparian zones adjacent to the crop fields. The segment of river that I sampled has a mean gradient of 0.54 m/km, and my study sites had a mean width ranging from 14 to 35 m. Council Grove Reservoir is located 39 km upstream from Site 1.

Figure 1. Study area along the Neosho River in Lyon County, Kansas. (Site 1: N 38° 32' 06", W 96° 19' 40"; Site 2: N 38° 31' 19", W 96° 19' 05"; Site 3: N 38° 31' 25", W 96° 18' 16"; Site 4: N 38° 30' 58", W 96° 18' 36"; Site 5: N 38° 27' 15", W 96° 13' 55"; Site 6: N 38° 27' 02", W 96° 13' 44"; Site 7: N 38° 26' 11", W 96° 12' 28"; Site 8: N 38° 25' 35", W 96° 10' 19").

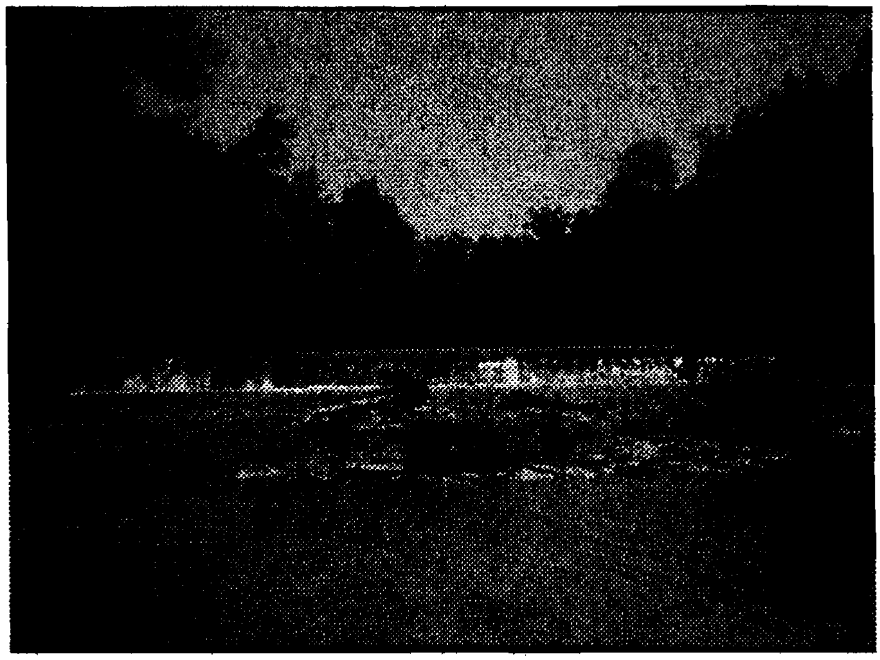

Site 1
Correll Dam
Site 3
Site 2
Site 4
Americus
N
W
E
S
0
3 km
Ruggles Dam
Site 5
Site 6
Site 7
Emporia Dam
Site 8
Emporia

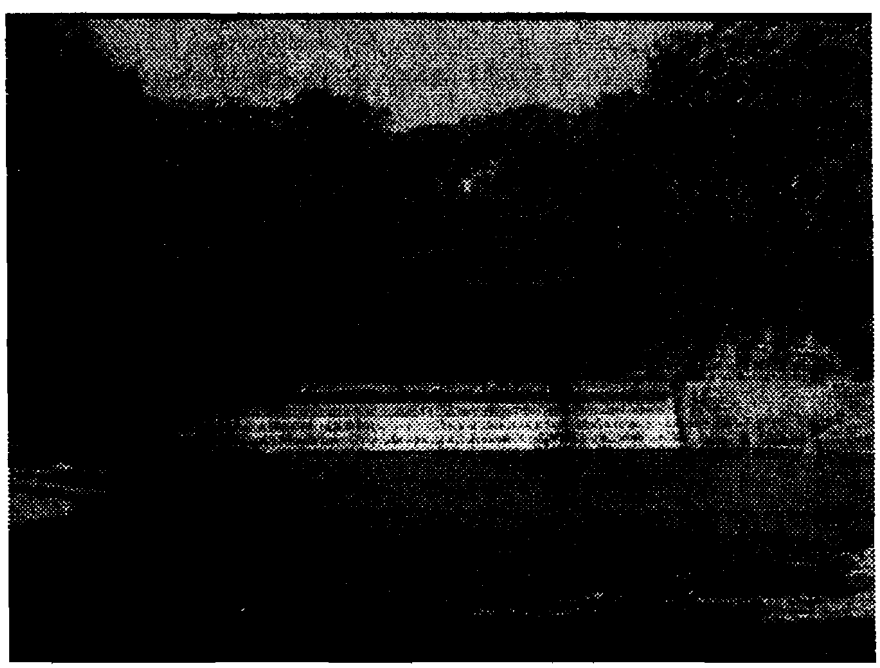
Between the 9th and 22nd of each month from November 2000 to October 2001, an assistant and I sampled the eight sites in random order during daylight hours (Table 1). The eight sites consisted of two sites upstream from and two sites downstream from each of two lowhead dams owned by the City of Emporia. The upstream dam, the Correll Dam [S½ SE¼ Sec. 33 T17S R10E] (Figure 2), is 2.3 m high, 45 m long, and was built in 1929 to provide a backup water supply for Emporia but is in disrepair and is no longer used by the City of Emporia. The downstream dam, the Emporia Dam [SE ¼ SE ¼ Sec. 32 T18S R11E] (Figure 2), is 3.7 m high, 22 m long, and was built in the 1950s and currently impounds Emporia's water supply. Site 1 was the upstream reference site for the Correll Dam and was located 7.0 km upstream from the dam (Figure 1). Site 2 was the upstream treatment, or inundated, site for the Correll Dam and was located 1.9 km upstream from the dam. Site 3 was the downstream treatment site for the Correll Dam and was located 0.1 km downstream from the dam. Site 4 was the downstream reference site for the Correll Dam and was located 1.1 km downstream. Site 5 was the upstream reference site for the Emporia Dam and was located 4.1 km upstream from the dam. Site 6 was the upstream treatment, or inundated, site for the Emporia Dam and was located 2.7 km upstream from the dam. Site 7 was the downstream treatment site for the Emporia Dam and was located 0.1 km downstream from the dam. Site 8 was the downstream reference site for the Emporia Dam and was located 7.0 km downstream. The reference sites were free-flowing, with no obvious effects from the dams. Sites were selected based on proximity to the dams, the presence of a gravel bar composed mainly of gravel < 64 mm, and landowner permission. To reduce the effects of field samples on each other, I sampled in the following order at each site: fishes, water depth and stream

Table 1. Sampling dates for each site from November 2000 to October 2001.

Month	Date	Sites
November 2000	10th	1, 2
	11th	3,7
	12th	8
	13th	4
	15th	5
	17th	6
December 2000	9th	4, 3
	10th	7, 2
	17th	8, 1 *5, 6 were frozen and not sampled
January 2001	13th	1, 4, 8
	14th	3, 7 *2, 5, 6 were frozen and not sampled
February 2001	10th	7, 1
	18th	3, 8
	19th	4 *2, 5, 6 were frozen and not sampled
March 2001	10th	2, 6
	11th	7, 3, 1, 8
	12th	4
	14th	5
April 2001	14th	3, 7, 1, 4
	21st	8
	22nd	6, 5, 2
May 2001	11th	8
	12th	4, 7
	13th	3
	15th	6, 1, 5, 2
June 2001	18th	3, 1
	19th	6, 2, 8, 4, 5
	20th	7
July 2001	9th	6, 4
	10th	8, 5, 3, 1
	11th	7
	12th	2
August 2001	13th	1, 5, 4, 7
	14th	8, 3, 2, 6
September 2001	10th	2, 7, 4
	11th	3
	12th	6, 5, 8
	13th	1
October 2001	10th	6, 3, 7
	11th	4
	12th	2, 5, 8, 1

Figure 2. Photographs of the two lowhead dams in my study, the Correll Dam (top) and the Emporia Dam (bottom). Photographs taken June 2001.





velocity, substrate compaction and composition, benthic invertebrates, and physicochemical variables.

Habitat and Physicochemistry Measurements

At each sampling point along transects, I assessed depth, velocity, substrate compaction, and substrate composition. Scores for all sampling points at a site were averaged to give a mean site score for each month (Bain 1999; Wildhaber et al. 2000a). I measured water depth with a meter stick and velocity at 60% depth from the surface with a Global Flow Probe FP101 current meter (Global Water: Gold River, CA). I estimated substrate compaction by touch, where loose substrate was coded as 1, medium as 2, firm as 3, and bedrock as 4 (Fuselier and Edds 1995). I sampled substrate with a shovel (Grost et al. 1991; Bain 1999), and estimated composition visually (Mullner et al. 2000). I used a modified Wentworth scale (Cummins 1962) to estimate percentages of clay and silt (< 0.059 mm), sand (0.06 to 1 mm), gravel (2 to 15 mm), pebble (16 to 63 mm), cobble (64 to 256 mm), boulder (> 256 mm), and bedrock (unfragmented bed material). Reference samples were taken to the laboratory to verify field estimates at the beginning and end of the study. I calculated substrate geometric mean and fredle index (geometric mean adjusted for distribution of particle sizes) for each site (McMahon et al 1996).

At the head of each gravel bar, upstream from the area sampled for fishes and invertebrates, I measured temperature with a thermometer and dissolved oxygen and pH with a Hach kit model AL-36B (Hach Chemical Company, Loveland, CO). I then collected a water sample to be analyzed in the laboratory for free acidity, alkalinity, carbon dioxide, and hardness using a Hach kit model AL-36B; nitrate, ammonia, and orthophosphate using a Hach Surface Waters kit; chloride and sulfate using a Hach kit model DREL/1C; and turbidity using a Hach 2100P turbidimeter. Using a vacuum pump and Poll type A/C glass fiber filters, I filtered 100 ml of water each and stored filters at −10° C for subsequent chlorophyll *a* and particulate organic carbon (POC) analysis at the Columbia Environmental Research Center (CERC) in Columbia, MO. At the CERC, I used a Model 10-AU-005 Field Fluorometer (Turner Designs, Sunnyvale, CA) to measure chlorophyll *a* and a Coulometrics Carbon Model 5014 Analyzer (UIC, Incorporated, Joliet, IL) to measure POC in the filtered samples.

Benthic Invertebrate Sampling

I sampled benthic invertebrates each month at three random points per site in undisturbed substrate at the head of the gravel bar, in accordance with the strong upstream-biased distribution pattern of benthic invertebrates within gravel bars (Brown and Basinger-Brown 1984). I used a D-net to dredge a 0.09 m^2 (1 ft^2) area of substrate, and placed the sample into a bucket partially filled with water. I stirred the substrate for 2 min, strained the water through an aquarium dip net, and preserved the contents in 45% isopropyl alcohol. In the laboratory, I sorted samples to family, except nematodes, which were identified to order. Identification to family is widely used in studies of aquatic insects because of the large number of taxa and inherent identification difficulties (Merritt and Cummins 1996).

Fish Sampling

I used the fish sampling methods of Wildhaber et al. (2000a), with slight modifications. At each site, five transects perpendicular to the river channel were spaced evenly, at least 5 m apart, along the length of the gravel bar. Up to five points were sampled along each transect, with a minimum of 0.5 m between points for a total of six to 25 points per site. The number of points sampled was limited by depth (depths > 1.25 m were not sampled) and landowner permission. To minimize disturbance, I sampled transects from downstream to upstream and stations from near shore to far shore. I collected fishes from a 4.5 m^2 area by disturbing the substrate 3 m upstream from a stationary 1.5 m, 3 mm-mesh seine, proceeding downstream to the seine. I identified, counted, and released fishes upon completion of sampling at each site.

During winter months (December through February), not all sites were sampled or contained five transects due to ice cover. Sites 5 and 6 were not sampled in December, January, or February, and Site 2 was not sampled in January or February. In December, only three transects were sampled at Site 7 and four at Site 8. In January, only three transects were sampled at Site 8. Site 7 had no water flowing over the dam in August, therefore sampling occurred in the plunge pool immediately downstream from the dam.

Statistical Analysis

I summarized data at the site level (eight sites) and analyzed them at the treatment level (upstream reference, upstream treatment, downstream treatment, and downstream reference) to assess the effects of lowhead dams on fish and benthic invertebrate assemblages and habitat and physicochemical variables. All statistical tests were conducted using the Statistical Analysis System, Version 8.1 (SAS Institute, Incorporated, Cary, NC). The distribution of sample means for fish species, benthic invertebrate taxa, and habitat and physicochemical variables was evaluated for normality using the Shapiro-Wilk test (Zar 1999), and for homogeneity of variance using Levene's test (Milliken and Johnson 1984). Non-normal variables were $\log_{10}$ transformed and proportional variables were transformed with the arcsine square root transformation (Zar 1999). Transformation normalized the data, and I accepted the premise that F-statistics used to compare means of normally distributed variables are effective whether or not variances are equal, especially when sample sizes are equal or almost so (Milliken and Johnson 1984). Tests were considered significant at $P \leq 0.05$. Tukey's studentized range test was used for pairwise comparisons among treatments. Because of multiple tests, sequential Bonferroni correction of α was applied where appropriate to help control overall experimental Type I error rate (Rice 1989).

For each sample, I calculated fish and benthic invertebrate abundance (catch per unit effort) as number per m^2. Fish species and benthic invertebrate taxa occurring in less than 5% of all samples (< 5 of the 88 samples) were eliminated from multivariate analyses and individual analyses of variance following Gauch (1982), who recommended eliminating rare species because their occurrence is usually more due to chance than ecological condition. Also, rare species are perceived as outliers, which obscure analysis of the data set (Gauch 1982).

Separate three-way (site type, dam, month) multivariate analyses of variance (MANOVA) were performed to test for effects of lowhead dams on all non-invariable habitat (depth, velocity, substrate compaction, geometric mean, and fredle index) and physicochemical variables (temperature, dissolved oxygen, pH, carbon dioxide, ammonia, orthophosphate, chloride, sulfate, chlorophyll a, particulate organic carbon, and turbidity) and fish and benthic invertebrate abundance. Significant MANOVAs using Wilk's Lambda test (Zar 1999) were followed with a step-down analysis of covariance (ANCOVA) (Tabachnick and Fidell 1983) to examine the contribution of individual variables to the MANOVA. Tabachnick and Fidell (1983) suggested that "step-down analysis helps avoid inflated Type I error from non-independent *F* tests. In this procedure, dependent variables (e.g. the abundance of taxa) are tested in a series of ANCOVAs where the most significant dependent variable is tested first in a univariate analysis of variance (ANOVA) after appropriate adjustment of alpha. Each successive dependent variable is tested with the higher significant dependent variables as covariates to determine if the new dependent variable significantly adds to the combination of dependent variables already tested" (Tabachnick and Fidell 1983).

For each sample, I calculated species richness and evenness (Shannon diversity divided by log of number of species) (Pielou 1966) for fishes and benthic invertebrates, plus percentage of individuals belonging to the orders Ephemeroptera, Plecoptera, and Trichoptera (%EPT) (Merritt and Cummins 1996) for benthic invertebrates. High %EPT is indicative of good water and environmental quality (Weigel et al. 2000). Species richness values depend upon area sampled; therefore, I estimated species richness using species rarefaction for fishes (unequal area per site) but not for benthic invertebrates (equal area per site). Species rarefaction determines the expected number of species at each sample when a given number of taxa are collected (Glowacki and Penczak 2000; Wildhaber et al. 2000a). Species rarefaction adjusts the estimate of species richness to a constant level of effort to make it comparable among samples, following the algorithm:

$$E(S) = \sum_{i=1}^{S}\left(1 - \left(\frac{\binom{N-N_i}{n}}{\binom{N}{n}}\right)\right)$$

where $E(S)$ is the expected number in a random sample of n individuals, S is the number of species, n is the standardized sample size, N is the total number of individuals collected, and N_i is the total number of individuals collected in the i^{th} species (Glowacki and Penczak 2000). For benthic invertebrates, I calculated species richness as the number of taxa divided by the square root of the number of individuals (Menhinick 1964).

I performed three-way ANOVAs on habitat and physicochemical variables, and fish and benthic invertebrate richness and evenness, benthic invertebrate %EPT, and individual fish and benthic invertebrate taxa abundances to test for effects of lowhead dams on given parameters. I also calculated Pearson's correlation coefficient to examine relationships between significant habitat and physicochemical variables, and fish and benthic invertebrate abundance, richness, and evenness, plus benthic invertebrate %EPT.

I calculated percent similarity index (PSI) (PSI = $1 - \{\Sigma[p_i - q_i]/2\}$ where p^i is the proportion of species i in sample p and q^i is the proportion of species i in sample q} to compare differences in species composition between sites and site types for fishes and benthic invertebrates (Taylor et al. 1996; Lienesch et al. 2000). ANOVAs were performed to test for differences in mean PSI values per site and site type. PSI ranges from 0 for sites that share no species to 100 for sites that are identical in species composition.

Results

Habitat and Physicochemistry Variables

Habitat characteristics varied upstream and downstream from the dams (Table 2; see Tiemann et al. 2002 for values of variables for each collection). MANOVA for habitat variables indicated significant differences by site type ($\lambda = 0.004$; n = 88; $P < 0.0001$), dam ($\lambda = 0.13$; n = 88; $P < 0.0001$), and month ($\lambda = 0.01$; n = 88; $P < 0.0001$). There was a significant site type*dam ($\lambda = 0.02$; n = 88; $P < 0.0001$) interaction, but not a dam*month ($\lambda = 0.16$; n = 88; $P = 0.57$) or site type*month ($\lambda = 0.009$; n = 88; $P = 0.15$) interaction. Step-down ANCOVA indicated that substrate geometric mean ($F = 425.23$; df = 60, 27; $P < 0.0001$) and substrate compaction ($F = 16.29$; df = 3, 30; $P < 0.0001$) contributed most to variation among site types.

Individual ANOVAs showed that all habitat variables differed significantly among site types (Table 3). Upstream treatment sites were deeper with slower velocity than reference sites, whereas downstream treatment sites were shallower with higher velocity than reference sites (Figure 3). Mean velocity at downstream treatment sites varied from 0 m/s in December and August to 1.01 m/s in April. The U.S. Army Corps of Engineers regulates discharge from Council Grove Reservoir, affecting the Neosho River downstream. Measured discharge readings of the river (USGS 2001) mirrored the release from Council Grove (USACE 2001). Substrate compaction was greater at upstream treatment sites and downstream treatment sites than at reference sites (Figure 3). As a result of differences between upstream treatment sites and between downstream treatment sites, there were significant site type*dam interactions, but not dam*month or site type*month interactions for depth, velocity, and substrate compaction (Table 4). Site

Table 2. Means (standard deviation) for habitat and physicochemical variables by site type in the Neosho River from November 2000 to October 2001. *N* is the number of samples per site type.

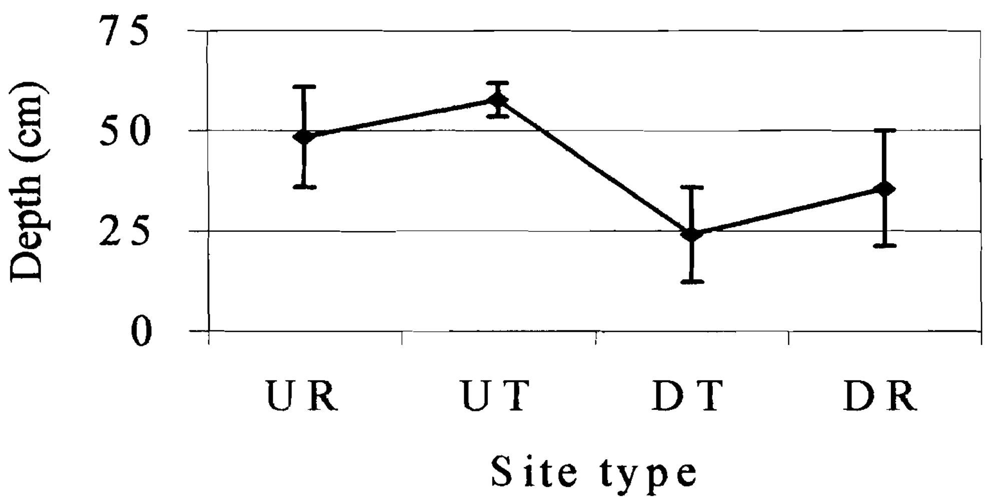
Habitat or physicochemical variable	Upstream reference ($N = 21$)	Upstream treatment ($N = 19$)	Downstream treatment ($N = 24$)	Downstream reference ($N = 24$)
Depth (cm)	48.4 (13.1)	57.7 (4.4)	24.0 (12.4)	35.5 (15.1)
Velocity (m/s)	0.24 (0.15)	0.05 (0.08)	0.42 (0.27)	0.32 (0.15)
Substrate compaction	1.9 (0.2)	2.3 (0.3)	2.8 (0.4)	1.7 (0.3)
Geometric mean	10.83 (0.88)	11.79 (0.76)	63.80 (29.34)	11.50 (1.04)
Fredle index	1.13 (1.23)	2.00 (1.17)	54.55 (35.43)	2.03 (1.17)
Clay/silt (< 0.06 mm)	20.0 (61)	11.5 (6.7)	4.1 (5.4)	14.8 (7.2)
Sand (0.06 – 1 mm)	5.0 (2.4)	3.3 (1.4)	2.8 (2.3)	5.4 (3.2)
Gravel (2 – 15 mm)	41.7 (3.4)	38.4 (6.9)	24.5 (6.4)	42.6 (6.9)
Pebble (16 – 63 mm)	33.0 (6.7)	37.1 (5.7)	22.7 (7.6)	37.1 (6.6)
Cobble (64 – 256 mm)	0.3 (0.8)	7.2 (1.9)	4.3 (2.7)	0.1 (0.2)
Boulder (> 256 mm)	0.0 (0.0)	2.5 (2.6)	1.0 (2.0)	0.0 (0.0)
Bedrock (solid bottom)	0.0 (0.0)	0.0 (0.0)	40.7 (6.1)	0.0 (0.0)
Temperature (°C)	14.9 (9.9)	15.0 (9.5)	15.5 (10.8)	15.3 (10.8)
Dissolved oxygen (mg/L)	8.9 (2.3)	8.3 (2.3)	10.0 (2.5)	9.4 (2.2)
pH	8.0 (0.1)	8.0 (0.1)	8.0 (0.2)	7.9 (0.2)
Alkalinity (mg/L)	171.5 (49.2)	176.0 (58.8)	176.0 (54.4)	179.6 (65.3)
Hardness (mg/L)	239.6 (46.6)	244.2 (42.5)	237.3 (51.1)	230.1 (51.0)
Carbon dioxide (mg/L)	10.1 (3.3)	10.8 (3.9)	9.6 (3.5)	10.4 (4.1)
Ammonia (mg/L)	0.01 (0.03)	0.02 (0.04)	0.02 (0.04)	0.03 (0.05)
Orthophosphate (mg/L)	0.05 (0.06)	0.05 (0.03)	0.04 (0.04)	0.05 (0.05)
Chloride (mg/L)	8.9 (4.2)	9.1 (4.7)	9.3 (5.6)	9.4 (4.6)
Sulfate (mg/L)	28.2 (7.3)	28.8 (9.8)	26.9 (7.0)	27.3 (8.4)
Chlorophyll *a* (*u*g/L)	678.4 (708.8)	680.0 (521.6)	535.1 (574.4)	421.0 (393.3)
POC (mg/L)	170.1 (97.0)	164.6 (81.3)	179.7 (91.3)	166.3 (74.7)
Turbidity (NTU)	35.9 (35.8)	31.1 (21.8)	40.6 (47.6)	40.5 (40.9)

Table 3. Analysis of variance results [F (P-values)] for habitat and physicochemical variable comparisons. Asterisks (*) indicate significant sequential Bonferroni-adjusted P-values.

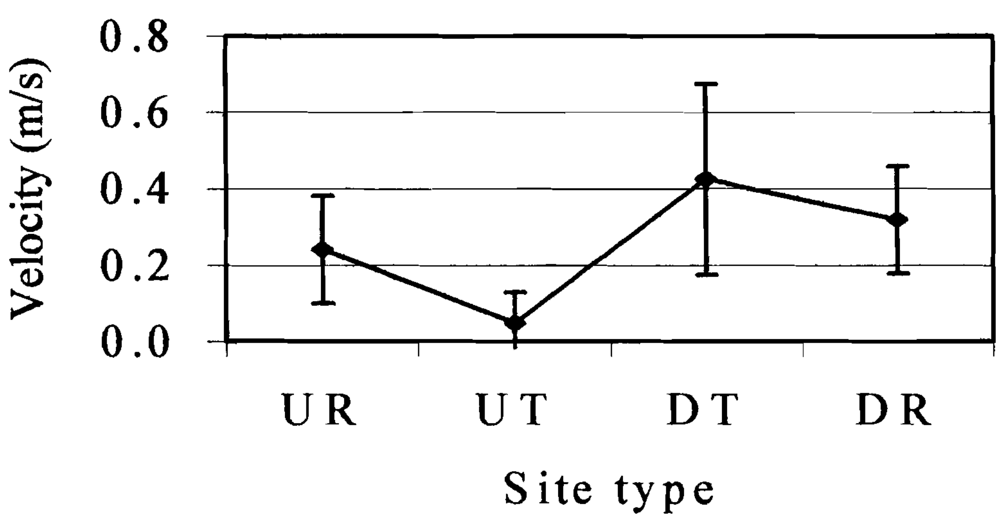
Habitat or physicochemical variable	Site type $df_{3,27}$	Dam $df_{1,27}$	Month $df_{11,27}$
Depth (cm)	57.16 (< 0.0001)*	12.12 (0.002)*	9.93 (< 0.0001)*
Velocity (m/s)	29.64 (< 0.0001)*	1.43 (0.24)	10.27 (< 0.0001)*
Substrate compaction	99.77 (< 0.0001)*	57.82 (< 0.0001)*	2.31 (0.04)
Geometric mean	129.24 (< 0.0001)*	89.65 (< 0.0001)*	0.84 (0.61)
Fredle index	22.06 (< 0.0001)*	13.92 (0.0009)*	0.79 (0.65)
Clay/silt (< 0.06 mm)	22.86 (< 0.0001)*	3.35 (0.08)	1.15 (0.36)
Sand (0.06 – 1 mm)	5.83 (0.003)*	0.25 (0.62)	4.00 (0.002)*
Gravel (2 – 15 mm)	85.85 (< 0.0001)*	44.16 (< 0.0001)*	5.14 (0.0003)*
Pebble (16 – 63 mm)	26.09 (< 0.0001)*	40.66 (< 0.0001)*	1.78 (0.11)
Cobble (64 – 256 mm)	54.08 (< 0.0001)*	95.64 (< 0.0001)*	1.55 (0.17)
Boulder (> 256 mm)	8.14 (0.0005)*	14.68 (0.0007)*	1.67 (0.14)
Bedrock (solid bottom)	425.25 (< 0.0001)*	336.98 (< 0.0001)*	0.76 (0.67)
Temperature (°C)	0.45 (0.72)	1.44 (0.24)	282.71 (< 0.0001)*
Dissolved oxygen (mg/L)	1.70 (0.11)	0.05 (0.88)	12.24 (< 0.0001)*
pH	1.55 (0.22)	0.73 (0.40)	0.82 (0.62)
Carbon dioxide (mg/L)	0.35 (0.79)	0.13 (0.73)	3.71 (0.003)
Ammonia (mg/L)	0.42 (0.74)	0.26 (0.62)	2.75 (0.02)
Orthophosphate (mg/L)	1.61 (0.21)	1.00 (0.33)	33.79 (< 0.0001)*
Chloride (mg/L)	0.16 (0.92)	0.18 (0.67)	12.30 (< 0.0001)*
Sulfate (mg/L)	2.54 (0.08)	11.83 (0.002)	38.11 (< 0.0001)*
Chlorophyll *a* (ug/L)	1.38 (0.27)	2.53 (0.12)	11.47 (< 0.0001)*
POC (mg/L)	0.68 (0.57)	2.67 (0.11)	7.50 (< 0.0001)*
Turbidity (NTU)	1.90 (0.15)	1.60 (0.22)	16.29 (< 0.0001)*

Figure 3. (a) Mean depth, (b) velocity, and (c) substrate compaction (± standard deviation) per site type (UR = upstream reference; UT = upstream treatment; DT = downstream treatment; DR = downstream reference) in the Neosho River, Lyon County, Kansas, November 2000 to October 2001.

a


75
50
25
0
Depth (cm)
UR
UT
DT
DR
Site type

b


0.8
0.6
0.4
0.2
0.0
Velocity (m/s)
UR
UT
DT
DR
Site type

c

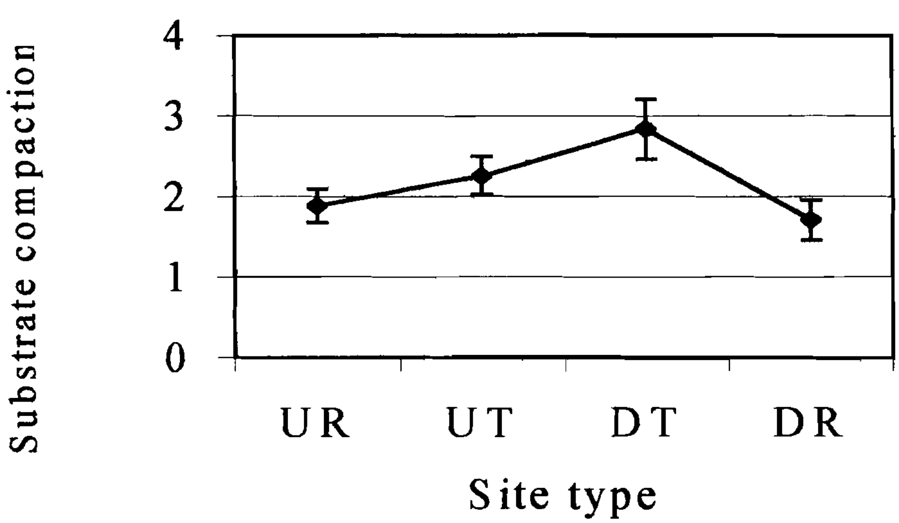

4
3
2
1
0
Substrate compaction
UR
UT
DT
DR
Site type

Table 4. Main effects interactions from three-way analysis of variance [*F* (*P*-values)] for habitat and physicochemical variables. Asterisks (*) indicate significant sequential Bonferroni-adjusted *P*-values.

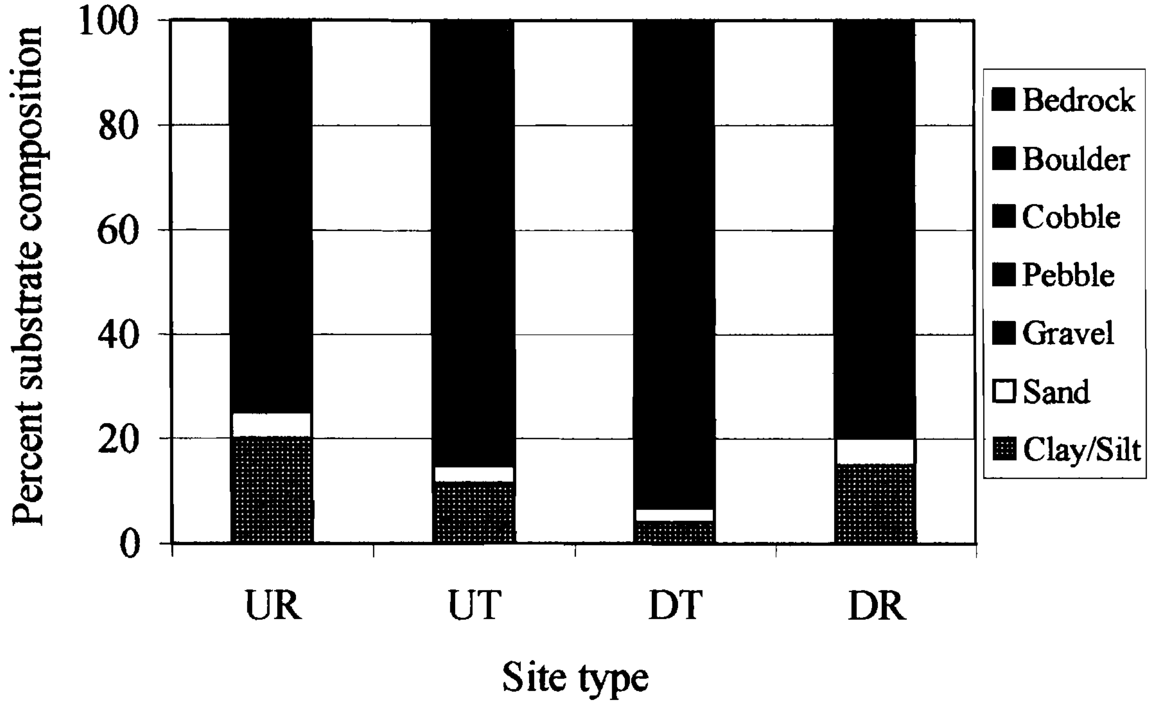
Habitat or physicochemical variable	Site type*Dam $df_{3,27}$	Dam*Month $df_{11,27}$	Site type*Month $df_{31,27}$
Depth (cm)	13.22 (< 0.0001)*	0.91 (0.55)	1.40 (0.19)
Velocity (m/s)	10.21 (0.0001)*	0.53 (0.87)	1.26 (0.27)
Substrate compaction	73.84 (< 0.0001)*	1.93 (0.08)	1.45 (0.17)
Geometric mean	133.20 (< 0.0001)*	1.10 (0.39)	1.00 (0.52)
Fredle index	23.11 (< 0.0001)*	1.08 (0.41)	0.99 (0.52)
Clay/silt (< 0.06 mm)	8.17 (0.0005)*	1.90 (0.08)	2.05 (0.03)
Sand (0.06 – 1 mm)	8.09 (0.0005)*	0.42 (0.93)	0.53 (0.95)
Gravel (2 – 15 mm)	115.55 (< 0.0001)*	1.58 (0.16)	2.38 (0.01)
Pebble (16 – 63 mm)	29.03 (< 0.0001)*	0.63 (0.79)	1.14 (0.37)
Cobble (64 – 256 mm)	50.83 (< 0.0001)*	1.64 (0.14)	0.78 (0.75)
Boulder (> 256 mm)	5.49 (0.002)*	1.39 (0.24)	0.95 (0.56)
Bedrock (solid bottom)	429.43 (< 0.0001)*	1.00 (0.47)	0.94 (0.57)
Temperature (°C)	0.46 (0.71)	0.50 (0.88)	0.97 (0.54)
Dissolved oxygen (mg/L)	2.17 (0.12)	1.41 (0.23)	1.04 (0.46)
pH	0.75 (0.53)	2.54 (0.02)	0.77 (0.76)
Alkalinity (mg/L)	0.91 (0.45)	3.37 (0.005)	1.95 (0.04)
Hardness (mg/L)	0.52 (0.67)	3.06 (0.009)	0.97 (0.53)
Carbon dioxide (mg/L)	1.57 (0.22)	1.30 (0.28)	0.77 (0.76)
Ammonia (mg/L)	0.43 (0.73)	1.27 (0.30)	2.32 (0.01)
Orthophosphate (mg/L)	1.37 (0.27)	1.25 (0.30)	1.86 (0.05)
Chloride (mg/L)	1.15 (0.35)	0.92 (0.54)	0.64 (0.89)
Sulfate (mg/L)	0.76 (0.53)	5.15 (0.003)	1.42 (0.18)
Chlorophyll a (ug/L)	1.40 (0.26)	2.59 (0.02)	2.13 (0.02)
POC (mg/L)	1.56 (0.22)	0.91 (0.54)	0.79 (0.74)
Turbidity (NTU)	1.00 (0.41)	0.96 (0.51)	1.11 (0.40)

3 and Site 7 differed in depth and velocity, partly as a result of periods of no flow at Site 7 in December 2000 and August 2001. Also, because of differences in substrate between Site 3 and Site 7, there were differences in substrate compaction between the two sites.

Downstream treatment sites had a higher substrate geometric mean and fredle index compared to reference sites and downstream treatment sites (Table 2). Downstream treatment sites had a lower percentage of clay/silt, sand, gravel, and pebble, and a higher percentage of bedrock than reference sites and upstream treatment sites (Figure 4). Upstream treatment sites and downstream treatment sites had a higher percentage of cobble than reference sites, and upstream treatment sites had a higher percentage of boulder than reference sites (Figure 4). Site type*dam interactions occurred for all substrate variables as a result of differences between upstream treatment sites and between downstream treatment sites. Site 6 had more cobble and boulder than Site 2, but Site 2 had more clay/silt than Site 6. Site 7 had substrate comprise predominantly of gravel and pebble, whereas Site 3 had substrate comprised predominantly of bedrock.

Thirteen of the 15 physicochemical measured variables were included in analyses (Table 2; see Tiemann et al. 2002 for values of variables for each collection); free acidity and nitrate were invariable in the 88 samples. MANOVA for physicochemical variables showed a significant difference by month ($\lambda < 0.00000001$; n = 82; $P < 0.0001$), but not by site type ($\lambda = 0.23$; n = 82; $P = 0.82$) or dam ($\lambda = 0.41$; n = 82; $P = 0.18$). There was a significant dam*month ($\lambda = 0.0007$; n = 82; $P = 0.03$) interaction, but not a site type*dam ($\lambda = 0.13$; n = 82; $P = 0.30$) or site type*month ($\lambda = 0.000004$; n = 82; $P = 0.40$) interaction. None of the 13 variables differed significantly among site types or between

Figure 4. Mean substrate composition scores per site type (UR = upstream reference; UT = upstream treatment; DT = downstream treatment; DR = downstream reference) in the Neosho River, Lyon County, Kansas, November 2000 to October 2001.



Percent substrate composition
100
80
60
40
20
0
UR
UT
DT
DR
Site type
Bedrock
Boulder
Cobble
Pebble
Gravel
Sand
Clay/Silt

dams, and all variables except pH, carbon dioxide, and ammonia differed among months (Table 3). There were no significant interactions for any of the main effects (Table 4). A seasonal trend in temperature and dissolved oxygen was evident during the study. Surface temperatures ranged from 0° C in December through February to 32° C in July and August, and dissolved oxygen concentrations ranged from 5 mg/L in August and September at Site 2 (upstream treatment) to 17 mg/L in December at Site 3 (downstream treatment).

Benthic Invertebrates

In 88 samples, I collected 11,594 individual benthic invertebrates representing 12 orders, belonging to 25 families, plus the nematode order Rhabditida, which was not identified to family (Table 5; see Tiemann et al. 2002 for abundance of individual taxa for each collection). Of the 26 taxa collected, 23 were sufficiently common to be retained for multivariate analysis and individual ANOVAs (Table 5). Aquatic insects comprised 94.9% of the benthic invertebrates. The most abundant family was Chironomidae, which accounted for 64.0% of all benthic invertebrates collected and was the most numerous taxon collected at all site types (Table 6). Non-insect benthic invertebrates, including Tubificidae (tubifex worms) and Astacidae (crayfish), comprised 5.1% of the individuals.

MANOVA for benthic invertebrate abundance indicated significant effects by site type ($\lambda = 0.000006$; n = 88; $P < 0.0001$), dam ($\lambda = 0.01$; n = 88; $P = 0.001$), and month ($\lambda < 0.00000001$; n = 88; $P < 0.0001$). There were a significant site type*dam ($\lambda = 0.0002$; n = 88; $P = 0.004$), dam*month ($\lambda = 0.00000002$; n = 88; $P = 0.01$) and site

Table 5. Benthic invertebrate taxa collected in the Neosho River from November 2000 to October 2001. Asterisks (*) indicate taxa that occurred in < 5% of samples and were excluded from MANOVA and individual ANOVA abundance analyses.

Taxon	Common name
Order Ephemeroptera	Mayflies
Potamanthidae	
Baetidae	
Heptageniidae	
Order Plecoptera	Stoneflies
Perlidae	
Order Trichoptera	Caddisflies
Limnephilidae	
Hydropsychidae	
Order Odonata	Dragonflies and damselflies
Lestidae	
Gomphidae	
Order Coleoptera	Beetles
Carabidae	
Dytiscidae	
Gyrinidae	
Order Hemiptera	True bugs
Corixidae	
Belostomatidae	
Nepidae*	
Order Diptera	Flies
Chironomidae	
Chaoboridae	
Culicidae	
Simuliidae	
Ceratopogonidae*	
Order Oligochaeta	Segmented worms
Tubificidae	
Order Rhynchobdellida	Leeches
Glossphonidae	
Order Heterodonta	Clams
Corbiculidae	
Order Gastropoda	Snails
Lynmaeidae	
Order Decapoda	Crayfish and shrimp
Astacidae	
Palaemonidae*	
Order Rhabditida	Roundworms

Table 6. Mean benthic invertebrate abundance per square meter (standard deviation) by site type in the Neosho River from November 2000 to October 2001. *N* is the number of samples per site type.

Benthic invertebrates	Upstream reference ($N = 21$)	Upstream treatment ($N = 19$)	Downstream treatment ($N = 24$)	Downstream reference ($N = 24$)
Potamanthidae	0.23 (0.03)	0.22 (0.00)	0.06 (0.02)	0.40 (0.03)
Baetidae	1.38 (0.42)	0.40 (0.21)	0.24 (0.13)	1.94 (0.29)
Heptageniidae	4.43 (0.85)	1.75 (1.14)	0.96 (0.19)	4.18 (0.13)
Perlidae	0.64 (0.11)	1.39 (0968)	0.14 (0.04)	0.72 (0.04)
Limnephilidae	0.01 (0.00)	0.04 (0.00)	0.03 (0.00)	0.10 (0.03)
Hydropsychidae	6.52 (0.50)	1.66 (1.05)	2.71 (0.91)	6.75 (0.10)
Gomphidae	0.00 (0.00)	0.12 (0.00)	0.00 (0.00)	0.00 (0.00)
Lestidae	0.00 (0.00)	0.95 (0.01)	0.00 (0.00)	0.00 (0.00)
Carabidae	0.75 (0.06)	0.15 (0.08)	0.31 (0.02)	1.11 (0.00)
Dytiscidae	1.98 (0.56)	0.26 (0.16)	0.64 (0.31)	1.86 (0.12)
Gyrinidae	0.73 (0.22)	0.13 (0.07)	0.15 (0.01)	0.74 (0.05)
Corixidae	0.00 (0.00)	0.12 (0.03)	0.00 (0.00)	0.01 (0.00)
Belostomatidae	0.00 (0.00)	0.18 (0.01)	0.01 (0.00)	0.04 (0.00)
Chironomidae	26.78 (2.91)	34.57 (6.45)	17.29 (3.96)	33.71 (0.46)
Chaoboridae	0.73 (0.06)	0.48 (0.05)	0.31 (0.08)	0.65 (0.07)
Culicidae	0.00 (0.00)	1.15 (0.34)	0.03 (0.00)	0.00 (0.00)
Simuliidae	0.87 (0.35)	0.65 (0.27)	1.38 (0.66)	1.04 (0.05)
Tubificidae	0.77 (0.11)	1.20 (0.40)	0.35 (0.11)	0.76 (0.09)
Glossphonidae	0.00 (0.00)	0.29 (0.10)	0.03 (0.00)	0.00 (0.00)
Corbiculidae	0.18 (0.00)	0.00 (0.00)	0.03 (0.00)	0.90 (0.23)
Lynmaeidae	0.00 (0.00)	0.34 (0.09)	0.32 (0.13)	0.00 (0.00)
Astacidae	0.29 (0.01)	1.69 (0.84)	0.86 (0.00)	0.22 (0.02)
Rhabditida	0.07 (0.03)	0.24 (0.09)	0.08 (0.04)	0.21 (0.13)
Total mean abundance	46.35 (6.23)	48.05 (12.39)	25.92 (6.60)	55.36 (1.83)

type*month ($\lambda < 0.00000001$; n = 88; $P < 0.0001$) interactions. Differences in habitat between the two upstream treatment sites and between the two downstream treatment sites led to the site type*dam interaction. Site 6 had more benthic invertebrates than Site 2, and Site 7 had more than Site 3. Step-down ANCOVA indicated that Culicidae (F = 40.84; df = 60, 27; $P < 0.0001$), Lestidae, (F = 7.48; df = 3, 33; P = 0.0002), Chironomidae (F = 9.62; df = 3, 32; $P < 0.0001$), and Heptageniidae (F = 9.86; df = 3, 1; $P < 0.0001$) contributed significantly to variation in abundance among site types. Culicidae and Chironomidae (Diptera) and Lestidae (Odonata) had significantly higher abundances at upstream treatment sites, and Chironomidae had significantly lower abundance at downstream treatment sites compared to other site types. Heptageniidae (Ephemeroptera) had significantly higher abundance in upstream reference and downstream reference sites compared to other site types. Correlation analysis indicated benthic invertebrate abundance was positively correlated with % pebble substrate and negatively correlated with % bedrock substrate (Table 7).

Individual ANOVAs indicated that abundance of 12 of the 23 taxa were significantly different among site types (Table 8). Of the three families of Ephemeroptera collected in my study, Baetidae and Heptageniidae differed significantly among site types, but Potamanthidae did not (Table 8). As with heptageniids, there were significantly more baetids in upstream reference and downstream reference sites compared to upstream treatment and downstream treatment sites. None of the Ephemeroptera varied between dams or among months (Table 8). There was a significant site type*dam interaction for Heptageniidae, but not for Potamanthidae or Baetidae (Table 9). There were no dam*month or site type*month interactions for these

Table 7. Results of Pearson's correlation analysis [r (P-values)] between benthic invertebrate abundance, species richness, evenness, and %EPT, with significant habitat variables plus fish abundance. Asterisks (*) indicate significant sequential Bonferroni-adjusted P-values. Number of observations for each variable is 88.

Variable	Benthic invertebrate abundance		Species Richness		Evenness		%EPT	
Depth	-0.07	(0.54)	0.15	(0.16)	-0.06	(0.57)	-0.05	(0.65)
Velocity	-0.25	(0.02)	0.11	(0.31)	0.35	(0.001)	0.10	(0.38)
Substrate compaction	-0.28	(0.008)	-0.08	(0.48)	-0.15	(0.18)	-0.002	(0.98)
Clay/silt	0.15	(0.16)	0.14	(0.19)	0.12	(0.27)	-0.08	(0.48)
Sand	-0.14	(0.19)	0.29	(0.07)	0.25	(0.02)	-0.002	(0.98)
Gravel	0.32	(0.003)	-0.02	(0.83)	-0.11	(0.32)	-0.08	(0.49)
Pebble	0.46	(< 0.0001)*	-0.12	(0.26)	-0.07	(0.54)	0.08	(0.46)
Cobble	-0.07	(0.54)	0.06	(0.58)	-0.03	(0.80)	0.09	(0.40)
Boulder	-0.06	(0.56)	0.05	(0.63)	-0.11	(0.30)	-0.04	(0.72)
Bedrock	-0.32	(0.0003)*	-0.03	(0.80)	0.02	(0.83)	0.02	(0.88)
Fish abundance	-0.05	(0.64)	0.005	(0.96)	0.17	(0.11)	0.17	(0.12)

Table 8. Analysis of variance results [F (P-values)] for individual benthic invertebrate taxon abundance, species richness, evenness, and %EPT comparisons. Asterisks (*) indicate significant sequential Bonferroni-adjusted P-values.

Benthic invertebrates	Site type $df_{3,27}$	Dam $df_{1,27}$	Month $df_{11,27}$
Potamanthidae	3.35 (0.03)	1.67 (0.21)	3.02 (0.009)
Baetidae	10.75 (< 0.0001)*	2.39 (0.13)	0.84 (0.60)
Heptageniidae	21.67 (< 0.0001)*	0.23 (0.64)	3.49 (0.004)
Perlidae	7.14 (0.001)	8.61 (0.007)	4.76 (0.0005)*
Limnephilidae	0.79 (0.65)	2.51 (0.12)	0.79 (0.65)
Hydropsychidae	18.30 (< 0.0001)*	1.46 (0.24)	4.91 (0.0004)*
Gomphidae	7.17 (0.001)	5.96 (0.02)	0.84 (0.60)
Lestidae	26.00 (< 0.0001)*	1.24 (0.27)	2.67 (0.02)
Carabidae	19.13 (< 0.0001)*	0.17 (0.68)	9.54 (< 0.0001)*
Dytiscidae	5.36 (0.005)	0.13 (0.72)	2.15 (0.05)
Gyrinidae	12.31 (< 0.0001)*	3.60 (0.07)	7.99 (< 0.0001)*
Corixidae	11.71 (< 0.0001)*	0.04 (0.84)	4.01 (0.002)
Belostomatidae	5.56 (0.004)	0.64 (0.43)	0.27 (0.99)
Chironomidae	25.30 (< 0.0001)*	0.68 (0.78)	18.01 (< 0.0001)*
Chaoboridae	1.04 (0.39)	0.00 (0.98)	4.48 (0.0007)*
Culicidae	40.84 (< 0.0001)*	2.19 (0.15)	10.04 (< 0.0001)*
Simuliidae	0.31 (0.82)	0.00 (1.00)	2.80 (0.01)
Tubificidae	3.60 (0.03)	0.58 (0.45)	1.84 (0.10)
Glossphonidae	19.70 (< 0.0001)*	6.57 (0.02)	3.05 (0.009)
Corbiculidae	10.43 (< 0.0001)*	3.54 (0.07)	0.88 (0.51)
Lynmaeidae	6.30 (0.002)	1.15 (0.29)	1.31 (0.27)
Astacidae	8.57 (0.0004)*	6.53 (0.02)	2.54 (0.02)
Rhabditida	0.52 (0.67)	0.31 (0.58)	1.02 (0.46)
Species richness	0.74 (0.54)	0.09 (0.77)	3.96 (0.002)
Evenness	8.37 (0.0004)*	3.29 (0.08)	8.44 (< 0.0001)*
%EPT	23.36 (< 0.0001)*	8.08 (0.008)	4.98 (0.0003)*

Table 9. Main effects interactions from three-way analysis of variance [F (P-values)] for individual benthic invertebrate taxon abundance, species richness, evenness, and %EPT. Asterisks (*) indicate significant sequential Bonferroni-adjusted P-values.

Benthic invertebrates	Site type*Dam $df_{3,27}$		Dam*Month $df_{11,27}$		Site type*Month $df_{31,27}$	
Potamanthidae	2.42	(0.09)	0.67	(0.75)	0.62	(0.90)
Baetidae	3.23	(0.04)	1.05	(0.43)	0.84	(0.69)
Heptageniidae	13.23	(< 0.0001)*	1.84	(0.10)	2.29	(0.02)
Perlidae	14.77	(< 0.0001)*	0.38	(0.95)	0.66	(0.87)
Limnephilidae	0.40	(0.75)	1.10	(0.40)	0.75	(0.78)
Hydropsychidae	3.01	(0.05)	0.78	(0.66)	1.15	(0.36)
Gomphidae	0.53	(0.66)	1.58	(0.16)	2.96	(0.003)
Lestidae	2.49	(0.08)	0.37	(0.96)	0.54	(0.95)
Carabidae	0.85	(0.50)	0.98	(0.49)	1.27	(0.26)
Dytiscidae	0.28	(0.84)	1.00	(0.47)	3.13	(0.002)
Gyrinidae	0.40	(0.76)	0.75	(0.69)	0.67	(0.86)
Corixidae	6.39	(0.002)	0.78	(0.66)	2.29	(0.004)
Belostomatidae	0.43	(0.73)	2.16	(0.05)	1.03	(0.47)
Chironomidae	3.10	(0.04)	0.85	(0.59)	10.65	(< 0.0001)*
Chaoboridae	1.48	(0.24)	0.76	(0.67)	1.06	(0.45)
Culicidae	3.66	(0.02)	0.68	(0.75)	1.37	(0.21)
Simuliidae	9.92	(0.0001)*	0.83	(0.61)	3.56	(0.0006)*
Tubificidae	1.62	(0.21)	1.44	(0.21)	0.62	(0.90)
Glossphonidae	1.70	(0.19)	0.80	(0.64)	0.97	(0.54)
Corbiculidae	6.76	(0.002)	0.38	(0.95)	0.78	(0.75)
Lynmaeidae	1.11	(0.36)	0.74	(0.69)	1.19	(0.32)
Astacidae	5.96	(0.003)	0.82	(0.62)	0.90	(0.62)
Rhabditida	1.29	(0.30)	0.82	(0.62)	2.84	(0.004)
Species richness	0.51	(0.68)	0.38	(0.95)	0.94	(0.57)
Evenness	4.65	(0.01)	0.94	(0.52)	1.17	(0.34)
%EPT	11.51	(< 0.0001)*	0.76	(0.68)	1.20	(0.32)

three families (Table 9). Perlidae, the only family of Plecoptera collected, differed significantly among months but not among site types or between dams (Table 8). Upstream treatment sites had significantly more perlids than downstream treatment sites, but neither differed significantly from reference sites. There were significantly more perlids in late spring and early summer (April through July) than other months. There was a site type*dam interaction for perlids but not a dam*month or site type*month interaction (Table 9). Hydropsychidae, one of the two families of Trichoptera collected in my study, varied significantly among site types and months but not between dams (Table 8). There were significantly more hydropsychids in upstream and downstream reference sites compared to upstream and downstream treatment sites, and significantly more hydropsychids were collected in fall and winter than spring and summer. Limnephilidae, the other trichopteran family, did not vary among site types, between dams, or among months (Table 8). There were no significant main effects interactions for either of these families (Table 9).

Benthic invertebrate species richness did not differ significantly among site types or between dams but did differ significantly among months (Table 8). Mean benthic invertebrate species richness varied from 2.4 in upstream reference sites and 3.5 in upstream treatment sites to 4.1 in downstream treatment sites and 2.4 in downstream reference sites. There was higher species richness in spring and summer than winter and fall. There were no significant interactions between main effects for species richness (Table 9). Species richness was not correlated with fish abundance or any habitat variable (Table 7).

Evenness differed significantly among site types and months but not between dams (Table 8). Mean benthic invertebrate evenness varied from 0.55 in upstream reference sites and 0.40 in upstream treatment sites to 0.44 in downstream treatment sites and 0.53 in downstream reference sites. Tukey's test indicated that upstream treatment sites had lower evenness than upstream reference and downstream reference sites, but downstream treatment sites did not differ from upstream reference or downstream reference sites. There were no significant interactions between main effects for evenness (Table 9). Evenness was not correlated with fish abundance or any habitat variable (Table 7).

Percent EPT differed significantly among site types, between dams, and among months (Table 8). Mean %EPT varied from 28.5 in upstream reference sites and 24.5 in downstream reference sites to 11.4 in upstream treatment sites and 15.9 in downstream treatment sites. There was significantly higher mean %EPT at reference sites compared to upstream treatment sites (Figure 5). There was significantly higher %EPT at Emporia Dam sites (23.3) than Correll Dam sites (17.5), and spring and fall had higher %EPT than summer and winter. There was a site type*dam interaction but not dam*month or site type*month interactions (Table 9). Percent EPT was not correlated with fish abundance or any habitat variable (Table 7).

Percent similarity index differed significantly by sites ($F = 3.25$; df = 7, 48; $P = 0.007$); mean PSI values between sites ranged from 62% (Site 1 vs. Site 2) to 96% (Site 4 vs. Site 8) (Table 10). Tukey's test indicated that, on average, Site 2, the Correll Dam upstream treatment site, had lower PSIs than all other sites. Percent similarity index did not differ significantly by site type ($F = 2.83$; df = 3, 27; $P = 0.17$); mean site type

Figure 5. Mean %EPT ($\pm$ standard deviation) per site type (UR = upstream reference; UT = upstream treatment; DT = downstream treatment; DR = downstream reference) in the Neosho River, Lyon County, Kansas, November 2000 to October 2001.

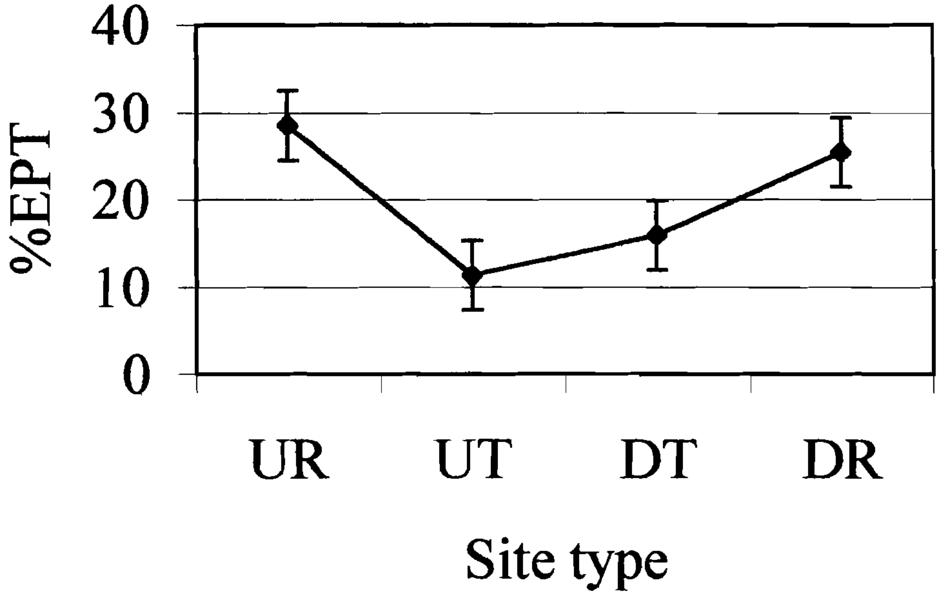

40
30
20
10
0
%EPT
UR
UT
DT
DR
Site type

Table 10. Percent similarity index for benthic invertebrates (B.i.) (bottom diagonals) and fish (top diagonals) abundances between sites, and mean PSI values (standard deviation) by site in the Neosho River from November 2000 to October 2001.

	Site							
Site	1	2	3	4	5	6	7	8
1		66	67	63	70	72	70	62
2	62		60	63	62	61	61	56
3	79	76		76	50	49	73	85
4	93	66	82		65	58	72	79
5	92	65	80	92		88	52	57
6	81	68	82	83	83		54	56
7	84	73	89	87	85	80		73
8	93	68	83	96	93	83	88	
Fish	67	61	65	68	63	62	70	67
	(3.6)	(3.3)	(13.4)	(7.6)	(13.1)	(13.6)	(10.8)	(12.1)
B.i.	84	68	82	86	84	80	83	86
	(10.8)	(4.8)	(3.8)	(10.1)	(9.8)	(5.3)	(5.6)	(9.6)

PSI values varied from 84% at upstream reference sites and 74% at upstream treatment sites to 83% at downstream treatment sites and 86% at downstream reference sites (Table 10).

Fishes

Eighty-eight samples yielded 15,222 fish representing 31 species, 19 genera, and 10 families (Table 11; see Tiemann et al. 2002 for species abundances for each collection). Of the 31 species collected, 21 were sufficiently common to be retained for multivariate analysis and individual ANOVAs (Table 11). Of those retained, eight were cyprinids, one was a catostomid, three were ictalurids, one was a poeciliid, three were centrarchids, four were percids, and one was a sciaenid (Table 11). Eleven species were collected at all eight sites: central stoneroller, *Campostoma anomalum*; red shiner, *Cyprinella lutrensis*; ghost shiner, *Notropis buchanani*; bluntnose minnow, *Pimephales notatus*; bullhead minnow, *Pimephales vigilax*; channel catfish, *Ictalurus punctatus*; orangespotted sunfish, *Lepomis humilis*; bluegill, *Lepomis macrochirus*; orangethroat darter, *Etheostoma spectabile*; logperch, *Percina caprodes*; and slenderhead darter, *Percina phoxocephala*. Red shiner was the most abundant species collected (Table 12), accounting for 47.8% of fish captured.

MANOVA for fish abundance indicated a significant difference by site type ($\lambda = 0.0002$; n = 88; $P < 0.0001$), dam ($\lambda = 0.03$; n =88; $P = 0.001$), and month ($\lambda = 0.00000001$; n = 88; $P < 0.0001$). There were significant site type*dam ($\lambda = 0.001$; n = 88; $P = 0.002$), dam*month ($\lambda = 0.0000004$; n = 88; $P = 0.02$), and site type*month ($\lambda < 0.00000001$; n = 88; $P = 0.0003$) interaction. Differences in habitat between the two

Table 11. Fishes collected in the Neosho River from November 2000 to October 2001. Asterisks (*) indicate species that occurred in < 5% of samples and were excluded from MANOVA and individual ANOVA abundance analyses.

Scientific name	Common name
Family Clupeidae	
*Dorosoma cepedianum**	Gizzard shad
Family Cyprinidae	
Campostoma anomalum	Central stoneroller
*Cyprinella camura**	Bluntface shiner
Cyprinella lutrensis	Red shiner
*Lythrurus umbratilis**	Redfin shiner
Notropis buchanani	Ghost shiner
Notropis stramineus	Sand shiner
Phenacobius mirabilis	Suckermouth minnow
Pimephales notatus	Bluntnose minnow
Pimephales tenellus	Slim minnow
Pimephales vigilax	Bullhead minnow
Family Catostomidae	
*Carpiodes carpio**	River carpsucker
Moxostoma erythrurum	Golden redhorse
Family Ictaluridae	
Ictalurus punctatus	Channel catfish
Noturus flavus	Stonecat
Noturus placidus	Neosho madtom
*Pylodictis olivaris**	Flathead catfish
Family Fundulidae	
*Fundulus notatus**	Blackstripe topminnow
Family Poeciliidae	
Gambusia affinis	Western mosquitofish
Family Moronidae	
*Morone chrysops**	White bass
Family Centrarchidae	
Lepomis cyanellus	Green sunfish
Lepomis humilis	Orangespotted sunfish
Lepomis macrochirus	Bluegill
*Lepomis megalotis**	Longear sunfish
*Micropterus punctulatus**	Spotted bass
Family Percidae	
*Etheostoma flabellare**	Fantail darter
Etheostoma spectabile	Orangethroat darter
Percina caprodes	Logperch
Percina copelandi	Channel darter
Percina phoxocephala	Slenderhead darter
Family Sciaenidae	
Aplodinotus grunniens	Freshwater drum

Table 12. Mean fish abundance per square meter (standard deviation) by site type in the Neosho River from November 2000 to October 2001. *N* is the number of samples per site type.

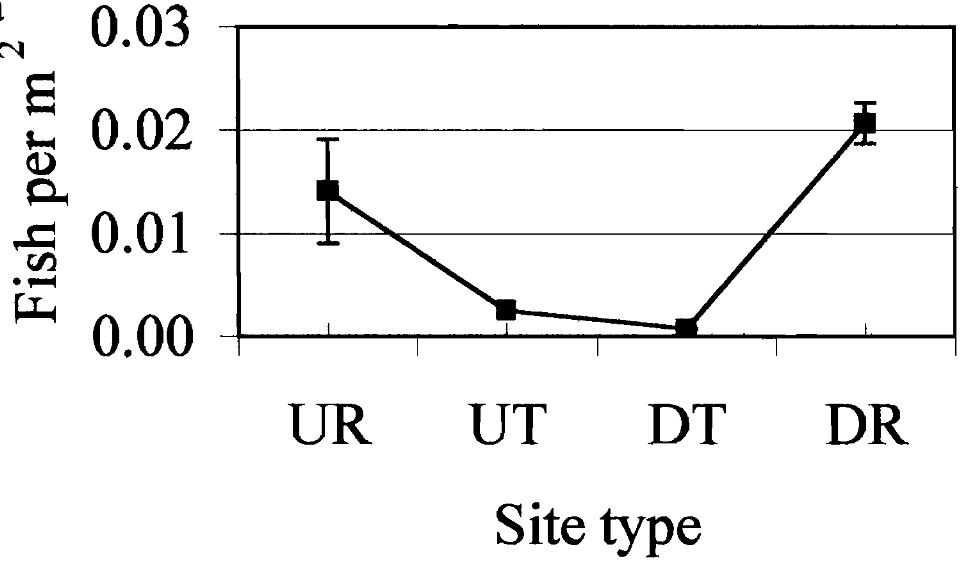
Fish species	Upstream reference (*N* = 21)	Upstream treatment (*N* = 19)	Downstream treatment (*N* = 24)	Downstream Reference (*N* = 24)
Central stoneroller	0.013 (0.008)	0.037 (0.023)	0.028 (0.011)	0.025 (0.000)
Red shiner	0.386 (0.002)	0.454 (0.069)	1.421 (0.031)	1.773 (0.095)
Ghost shiner	0.310 (0.033)	0.333 (0.167)	0.193 (0.005)	0.156 (0.034)
Sand shiner	0.015 (0.009)	0.006 (0.000)	0.006 (0.002)	0.049 (0.031)
Suckermouth minnow	0.019 (0.011)	0.001 (0.000)	0.064 (0.009)	0.027 (0.008)
Bluntnose minnow	0.200 (0.055)	0.321 (0.138)	0.215 (0.061)	0.341 (0.047)
Slim minnow	0.048 (0.032)	0.091 (0.000)	0.020 (0.001)	0.091 (0.035)
Bullhead minnow	0.091 (0.035)	0.057 (0.019)	0.041 (0.008)	0.233 (0.067)
Golden redhorse	0.001 (0.000)	0.003 (0.000)	0.001 (0.000)	0.001 (0.000)
Channel catfish	0.022 (0.003)	0.008 (0.005)	0.014 (0.000)	0.019 (0.008)
Stonecat	0.003 (0.000)	0.000 (0.000)	0.006 (0.001)	0.005 (0.000)
Neosho madtom	0.014 (0.007)	0.003 (0.001)	0.001 (0.000)	0.021 (0.003)
Western mosquitofish	0.006 (0.000)	0.004 (0.001)	0.028 (0.019)	0.000 (0.000)
Green sunfish	0.000 (0.000)	0.009 (0.001)	0.010 (0.003)	0.012 (0.002)
Orangespotted sunfish	0.097 (0.045)	0.331 (0.041)	0.083 (0.027)	0.178 (0.039)
Bluegill	0.005 (0.002)	0.008 (0.001)	0.005 (0.003)	0.003 (0.001)
Orangethroat darter	0.041 (0.028)	0.048 (0.013)	0.133 (0.010)	0.037 (0.021)
Logperch	0.009 (0.002)	0.014 (0.001)	0.023 (0.013)	0.006 (0.002)
Channel darter	0.009 (0.000)	0.013 (0.000)	0.000 (0.000)	0.015 (0.008)
Slenderhead darter	0.007 (0.017)	0.102 (0.046)	0.377 (0.216)	0.095 (0.044)
Freshwater drum	0.000 (0.000)	0.002 (0.000)	0.002 (0.000)	0.002 (0.000)
Total mean abundance	1.367 (0.290)	1.846 (0.520)	2.679 (0.423)	3.093 (0.443)

upstream treatment sites and between the two downstream treatment sites accounted for the site type*dam interaction. Step-down ANCOVA indicated that orangethroat darter ($F = 14.86$; df = 60, 27; $P < 0.0001$) and suckermouth minnow, *Phenacobius mirabilis*, ($F = 5.96$; df = 3, 72; $P = 0.001$) contributed significantly to the variation in abundance among site types. Abundances of orangethroat darter and suckermouth minnow were higher in downstream treatment areas compared to reference sites (Figure 6). Correlation analysis indicated fish abundance was not correlated with benthic invertebrate abundance or any habitat variable (Table 13), but suckermouth minnow abundances were positively correlated with velocity (Table 14).

Individual ANOVAs indicated that abundance of four of the 21 species (Neosho madtom and slenderhead darter in addition to orangethroat darter and suckermouth minnow) was significantly different among site types (Table 15). Sixty-four Neosho madtoms were collected at seven of the eight sites (never at Site 7), but accounted for only 0.42% of the total catch. Forty-two percent (27) of Neosho madtoms were collected at upstream reference sites and 50% (32) at downstream reference sites, compared to 5% (3) at upstream treatment sites and 3% (2) at downstream treatment sites. Two Neosho madtoms collected at a downstream treatment site (Site 3) that was predominantly bedrock were captured in a pocket of loose gravel that was underwater because of high discharge. Three Neosho madtoms collected at upstream treatment sites were collected after a period of high discharge when these fish might been have washed down from upstream. Neosho madtoms were collected in nine of the 12 months at upstream reference sites and in 10 months at downstream reference sites compared to three months at upstream treatment sites and two months at downstream treatment sites. Neosho

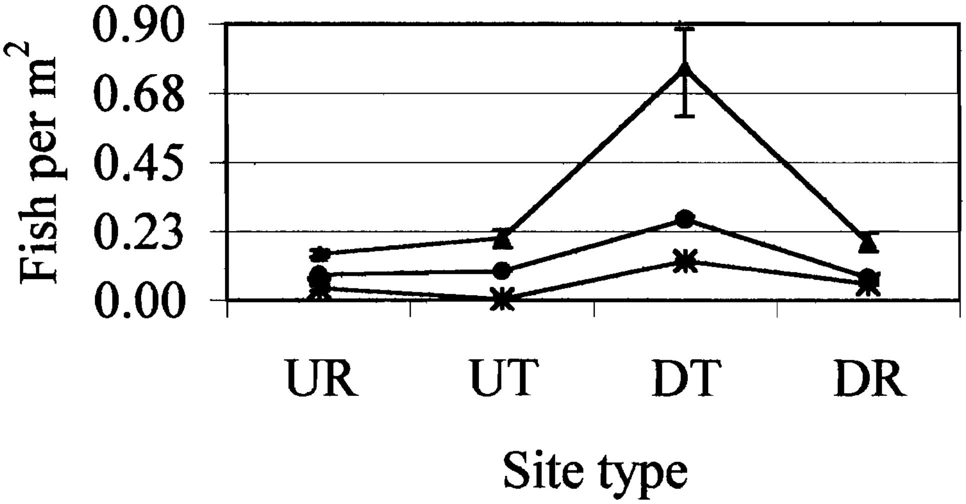
Figure 6. (a) Neosho madtom, and (b) suckermouth minnow (asterisk), orangethroat darter (circle), and slenderhead darter (triangle) abundance (± standard deviation) per site type (UR = upstream reference; UT = upstream treatment; DT = downstream treatment; DR = downstream reference) in the Neosho River, Lyon County, Kansas, November 2000 to October 2001.

a



Fish per m2
0.03
0.02
0.01
0.00
UR
UT
DT
DR
Site type

b



Fish per m2
0.90
0.68
0.45
0.23
0.00
UR
UT
DT
DR
Site type

Table 13. Results of Pearson's correlation analysis [r (P-value)] between fish abundance, species richness, and evenness, with significant habitat variables plus benthic invertebrate (B. i.) abundance. Number of observations for each variable is 88.

Variable	Fish abundance	Species richness	Evenness
Depth	-0.05 (0.65)	0.09 (0.41)	0.24 (0.03)
Velocity	0.10 (0.38)	-0.03 (0.75)	-0.11 (0.33)
Substrate compaction	-0.002 (0.98)	0.02 (0.84)	-0.27 (0.01)
Clay/silt	-0.08 (0.48)	0.14 (0.20)	0.08 (0.48)
Sand	-0.002 (0.95)	0.10 (0.37)	0.19 (0.08)
Gravel	-0.08 (0.49)	0.01 (0.90)	0.28 (0.01)
Pebble	0.08 (0.46)	-0.20 (0.06)	0.23 (0.03)
Cobble	0.09 (0.40)	-0.11 (0.30)	0.02 (0.87)
Boulder	-0.04 (0.72)	0.006 (0.95)	0.04 (0.70)
Bedrock	0.02 (0.88)	0.04 (0.72)	-0.30 (0.006)
B. i. abundance	-0.05 (0.64)	-0.19 (0.09)	0.16 (0.14)

Table 14. Results of correlation analysis [*r* (*P*-value)] between significant fish species' abundances with significant habitat variables plus benthic invertebrate (B. i.) abundance. Asterisks (*) indicate significant sequential Bonferroni-adjusted *P*-values. Number of observations for each variable is 88.

Variable	Neosho madtom	Suckermouth minnow	Orangethroat darter	Slenderhead darter
Depth	-0.26 (0.02)	-0.31 (0.004)	-0.31 (0.003)	-0.10 (0.35)
Velocity	-0.02 (0.84)	0.36 (0.001)*	0.02 (0.87)	0.36 (0.001)*
Substrate compaction	-0.34 (0.001)*	-0.05 (0.68)	0.29 (0.007)	-0.21 (0.05)
Clay/silt	0.03 (0.81)	-0.21 (0.06)	-0.17 (0.12)	-0.22 (0.04)
Sand	-0.03 (0.80)	0.06 (0.57)	-0.25 (0.02)	0.20 (0.06)
Gravel	0.28 (0.01)	-0.01 (0.89)	-0.34 (0.002)	0.16 (0.13)
Pebble	0.22 (0.04)	-0.11 (0.32)	-0.14 (0.21)	0.11 (0.32)
Cobble	-0.24 (0.03)	0.06 (0.59)	0.15 (0.16)	0.16 (0.15)
Boulder	-0.16 (0.15)	-0.12 (0.26)	0.07 (0.54)	0.01 (0.99)
Bedrock	-0.18 (0.10)	0.12 (0.25)	0.28 (0.008)	-0.10 (0.37)
B. i. abundance	0.34 (0.001)*	-0.15 (0.17)	0.25 (0.02)	-0.22 (0.04)

Table 15. Analysis of variance results [F (P-values)] for individual fish species abundance, species richness, and evenness comparisons. Asterisks (*) indicate significant sequential Bonferroni-adjusted P-values.

Fish species	Site type $df_{3,27}$		Dam $df_{1,27}$		Month $df_{11,27}$	
Central stoneroller	1.10	(0.37)	0.81	(0.38)	2.76	(0.02)
Red shiner	4.53	(0.01)	0.75	(0.39)	2.13	(0.05)
Ghost shiner	0.86	(0.47)	2.24	(0.13)	5.82	(< 0.0001)*
Sand shiner	4.00	(0.02)	3.43	(0.08)	0.62	(0.79)
Suckermouth minnow	14.38	(< 0.0001)*	0.21	(0.14)	3.85	(0.002)
Bluntnose minnow	1.24	(0.31)	2.31	(0.65)	2.95	(0.01)
Slim minnow	6.42	(0.002)	42.46	(< 0.0001)*	3.48	(0.004)
Bullhead minnow	4.73	(0.009)	0.10	(0.75)	3.24	(0.006)
Golden redhorse	0.56	(0.65)	1.38	(0.25)	0.88	(0.57)
Channel catfish	2.24	(0.74)	0.26	(0.61)	2.52	(0.02)
Stonecat	0.11	(2.24)	0.10	(0.76)	1.48	(0.20)
Neosho madtom	9.66	(0.0002) *	1.76	(0.20)	0.94	(0.52)
Western mosquitofish	0.93	(0.44)	4.82	(0.04)	2.90	(0.01)
Green sunfish	0.95	(0.42)	1.89	(0.18)	2.49	(0.03)
Orangespotted sunfish	3.73	(0.03)	1.08	(0.31)	1.26	(0.30)
Bluegill	0.65	(0.59)	1.93	(0.18)	2.25	(0.04)
Orangethroat darter	14.86	(< 0.0001)*	11.97	(0.002)	6.89	(< 0.0001)*
Logperch	2.87	(0.05)	0.94	(0.34)	2.14	(0.05)
Channel darter	2.65	(0.07)	14.09	(0.0009)	1.29	(0.28)
Slenderhead darter	9.85	(0.0001)*	9.75	(0.004)	3.13	(0.008)
Freshwater drum	0.24	(0.87)	0.01	(0.91)	0.93	(0.53)
Species richness	2.83	(0.06)	0.42	(0.52)	6.40	(0.0004)*
Evenness	4.83	(0.008)	6.57	(0.02)	0.82	(0.62)

madtom abundance was significantly different among site types, but not between dams or among months (Table 15). Tukey's test indicated lower abundance of Neosho madtoms in upstream treatment sites and downstream treatment sites compared to reference sites (Figure 6). There were no significant interactions between main effects for Neosho madtom abundance (Table 16). Neosho madtom abundance was positively correlated with benthic invertebrate abundance and negatively correlated with substrate compaction (Table 14). Abundance of slenderhead darter also was significantly different among site types (Table 15). Abundance of slenderhead darter was higher in downstream treatment areas compared to reference sites (Figure 6). The only significant interaction between main effects for slenderhead darter was a site type*dam interaction. Slenderhead darter abundance was positively correlated with velocity (Table 14).

Fish species richness was significantly different among months, but was not significantly different among site types or between dams (Table 15). Mean species richness varied from 17.9 in upstream reference sites and 16.2 in upstream treatment sites to 16.5 in downstream treatment sites and 13.6 in downstream reference sites. Summer months had higher richness than other seasons. There were no significant interactions between main effects for species richness (Table 16). Species richness was not significantly correlated with benthic invertebrate abundance or any habitat variable (Table 13).

Fish evenness differed significantly among site types, but not between dams or among months (Table 15). Mean evenness varied from 0.67 in upstream reference sites and 0.63 in upstream treatment sites to 0.49 in downstream treatment sites and 0.51 in downstream reference sites. Upstream reference and upstream treatment sites had higher

Table 16. Main effects interactions from three-way analysis of variance [F (P-values)] for individual fish species' abundance, species richness, and evenness. Asterisks (*) indicate significant sequential Bonferroni-adjusted P-values.

Fish species	Site type*Dam $df_{3,27}$	Dam*Month $df_{11,27}$	Site type*Month $df_{31,27}$
Central stoneroller	2.99 (0.05)	0.85 (0.60)	1.15 (0.36)
Red shiner	0.64 (0.59)	1.46 (0.20)	0.82 (0.70)
Ghost shiner	2.51 (0.08)	0.75 (0.68)	1.22 (0.30)
Sand shiner	5.34 (0.005)	0.69 (0.74)	0.89 (0.63)
Suckermouth minnow	4.20 (0.01)	1.31 (0.27)	2.43 (0.01)
Bluntnose minnow	1.64 (0.20)	0.74 (0.69)	0.72 (0.81)
Slim minnow	6.44 (0.002)	1.29 (0.28)	1.23 (0.29)
Bullhead minnow	3.11 (0.04)	0.30 (0.89)	1.80 (0.03)
Golden redhorse	2.98 (0.05)	1.32 (0.27)	1.11 (0.39)
Channel catfish	1.38 (0.27)	0.90 (0.55)	1.19 (0.32)
Stonecat	3.10 (0.04)	0.72 (0.71)	0.93 (0.58)
Neosho madtom	2.78 (0.06)	0.81 (0.62)	0.88 (0.63)
Western mosquitofish	0.83 (0.49)	2.41 (0.03)	0.97 (0.53)
Green sunfish	0.39 (0.76)	1.32 (0.27)	1.40 (0.19)
Orangespotted sunfish	1.08 (0.37)	0.62 (0.80)	0.92 (0.59)
Bluegill	0.45 (0.72)	2.04 (0.06)	0.90 (0.62)
Orangethroat darter	1.97 (0.14)	0.72 (0.71)	4.14 (0.0002)*
Logperch	4.68 (0.009)	0.74 (0.69)	0.89 (0.63)
Channel darter	2.12 (0.12)	1.60 (0.15)	0.79 (0.74)
Slenderhead darter	10.19 (0.0001)*	1.45 (0.21)	1.90 (0.05)
Freshwater drum	0.98 (0.42)	0.32 (0.97)	0.62 (0.90)
Species richness	0.43 (0.74)	1.24 (0.33)	1.75 (0.11)
Evenness	0.20 (0.89)	2.33 (0.04)	1.07 (0.43)

evenness than downstream treatment sites, but only upstream reference sites differed from downstream reference sites. There were no significant interactions between main effects for evenness (Table 16). Evenness was not significantly correlated with benthic invertebrate abundance or any habitat variable (Table 13).

Percent similarity index did not differ significantly by site ($F = 0.38$; df = 7, 48; $P = 0.91$) or by site type ($F = 4.41$; df = 3, 27; $P = 0.08$). Mean PSI values between sites ranged from 49% (Site 3 vs. Site 6) to 88% (Site 5 vs. Site 6) (Table 10), and mean site type PSI values varied from 65% at upstream reference sites and 62% at upstream treatment sites to 66% at downstream treatment sites and 68% at downstream reference sites (Table 10).

Discussion

Any modifications to stream habitat, such as inundation, can have profound effects on the biotic integrity of the stream, including declines in abundance, species richness, and diversity (Neves and Angermeier 1990; Weaver and Garman 1994; Luttrell et al. 1999). Results of my study suggest differences in fish and benthic invertebrate assemblage structure and habitat characteristics, but not physicochemistry, upstream and downstream from two lowhead dams on the Neosho River. Seasonal effects (e.g. spring floods, summer and winter drought, and winter freeze) could account for the significant main effects for habitat and physicochemistry variables. These seasonal effects, in addition to differences in habitat and seasonal movements (e.g. emergence for benthic invertebrates and spawning movements for fishes) could account for the significant main effects for benthic invertebrate and fish abundances.

Habitat and Physicochemistry Variables

As habitat recovers or becomes less affected downstream from a dam, faunal assemblages should become more similar to conditions upstream from the impounded area (Bain et al. 1988). My upstream reference sites and downstream reference sites were more similar to each other, in terms of benthic invertebrate composition, abundance, and evenness, than to either the upstream treatment or downstream treatment sites. Because benthic invertebrates are good indicators of habitat quality (Merritt and Cummins 1996), these results suggest that lowhead dams create habitat that is unfavorable for many aquatic organisms. As water velocity is reduced, a river no longer has the power to carry the sediment in the water column, resulting in increased sedimentation (Kondolf 1997; Wood and Armitage 1997). Upstream treatment sites had lower velocity and higher substrate compaction, suggesting that reduction in velocity led to sedimentation, which reduced or eliminated habitat needed by many fishes, including the Neosho madtom, and many benthic invertebrates, such as the EPT taxa.

Site types also differed in substrate geometric mean and fredle index, indicating that there were differences in substrate composition. Downstream treatment sites had a higher proportion of larger substrate than reference and upstream treatment sites, and a lower proportion of fine substrates (clay/silt, sand, gravel, and pebble). Perhaps this is a result of streambed erosion by "sediment hungry" release waters (Camargo and Voelz 1998) and increased velocity, which suggests that water flowing over these dams might have scoured out the finer substrates, reducing habitat diversity (Baxter 1977; Kondolf 1997). The effect on substrate size composition is typically greatest immediately downstream from a dam, and causes physical scouring of organisms and leaves riverbeds devoid of much of their fauna (Camargo and Voelz 1998). After the Brazos River (Texas) was dammed, the substrate changed from a sand bottom to a predominantly rubble substrate (Ward and Stanford 1983).

Site 7, the site immediately downstream from the Emporia Dam (built to supply Emporia's drinking water supply) had periods of no flow immediately downstream from the dam, suggesting a negative effect of lowhead dams not previously reported. The City of Emporia extracts approximately 30 million liters of water daily (City of Emporia 2001); in December 2000 and August 2001, no water flowed over the dam. During periods of no flow, the gravel bar at Site 7 is exposed, which could allow the gravel to become compacted due to drying of organic material in interstitial spaces, and remain compacted following return to normal water levels (Wildhaber et al. 2000a; Bulger and Edds 2001). As a result, many substrate dwelling fishes, like the Neosho madtom, might be forced into less suitable areas, which could lower their survival rates.

Values of physicochemical variables around these dams were within the range reported by Wildhaber et al. (2000a) and Bulger and Edds (2001) for undammed portions of the Neosho River. Unlike large dams (Baxter 1977), these lowhead dams did not seem to affect physicochemical parameters in the Neosho River. Perhaps these dams do not retain water long enough to cause changes in physicochemistry. The term nutrient trap has been applied to inundated areas because lentic water leads to reduced nutrient availability downstream from dams as a result of increased production by phytoplankton (Baxter 1977). In addition, areas immediately downstream from dams typically experience reductions in productivity as a result of increased scouring (Baxter 1977), which was not the case in my study. There were no significant differences among site types for either chlorophyll *a* or POC, suggesting that, unlike large dams, these lowhead dams do not cause changes in productivity. Some large reservoir dams, especially those with hypolemnetic releases, also cause differences in temperature and dissolved oxygen downstream from the dam (De Jalon et al. 1994), which also did not occur during my study. Neither surface temperatures or dissolved oxygen concentrations varied among site types.

Benthic Invertebrates

Differences in habitat around these lowhead dams were associated with differences in benthic invertebrates. Step-down analysis indicated that two families of Diptera (Culicidae and Chironomidae) and one family each of Odonata (Lestidae) and Heptageniidae (Ephemeroptera) contributed significantly to the variation in benthic invertebrate abundance among site types. These taxa are found in a variety of habitats, but most notably in standing water (Merritt and Cummins 1996), similar to the conditions found at my upstream treatment sites, which might account for their increased abundances in these areas. Chironomidae, however, also were reduced in the downstream treatment sites, which could, among other factors, account for some of the reduced fish abundance. Merritt and Cummins (1996) reported that most aquatic predators feed predominantly on chironomids during some point in their life cycle.

Percent similarity indices indicated that sites were similar in benthic invertebrate composition, except for Site 2, the inundated area created by the Correll Dam. Site 2 did not have suitable habitat for many benthic invertebrates. Areas with moderate velocity and loosely compacted substrate containing a higher proportion of gravel and pebble contained a higher abundance of benthic invertebrates. Suitability of habitat, such as stream velocity, substrate composition, and water chemistry, are primary factors governing the colonization of benthic invertebrates, which makes them good indicators of habitat stability and water pollution (Brown and Basinger-Brown 1984; Brown and Brussock 1991; Merritt and Cummins 1996).

Waters (1995) suggested that benthic invertebrate abundance is dependent upon a mixture of heterogeneous gravel, pebble, and cobble. Benthic invertebrate abundance in my study was positively correlated with % pebble substrate and negatively correlated with % bedrock, suggesting that differences in substrate adversely affect benthic invertebrates. Similar to results found in studies of large dams (Boon 1988; De Jalon et al. 1994), the areas immediately upstream and downstream from the dams in my study had lower %EPT compared to reference sites. Benthic invertebrates in the EPT group usually inhabit the surface of stones and the interstitial spaces in gravel, pebble, and cobble (Waters 1995). Most EPT taxa respond negatively to increased siltation and substrate compaction; sedimentation results in a change from a community of EPT to one mainly of chironomids (Waters 1995). In my study, %EPT was negatively correlated with substrate compaction; there was higher %EPT in areas with flow and loosely compacted substrates (references sites), suggesting that lowhead dams limited abundances of these insects. Percent EPT tends to decrease as a result of flow fluctuations and differences in substrate composition caused by dams (De Jalon et al. 1994). Petts (1984) reported that, downstream from reservoirs in England, many species of mayflies either were reduced in numbers or eliminated completely. Boon (1988) suggested that heptageniid mayflies are severely affected upstream from dams due to an increase in siltation and higher algal growth in the impounded waters, which could create unfavorable habitat conditions. Dams, as a result of siltation and scouring, also adversely affect stoneflies, especially perlids (Boon 1988); however, this was not apparent in my study, because perlids (the only family found in my study) did not differ significantly among site types. Caddisflies were lower in areas immediately downstream from the lowhead dams in my study, unlike Spence and Hynes (1971) who reported high densities of caddisflies immediately downstream from reservoirs. One possible reason could be differences in flow; both increased and decreased flow hinder benthic invertebrates living at a site (Boon 1988). Brown and Brussock (1991) found fewer trichopterans in pools compared to riffles, which is similar to the results of my study if considering my upstream treatment sites as pools.

Changes in flow also increase benthic invertebrate drift (De Jalon et al. 1994). Camargo and Voelz (1998) noted a significant decline in benthic invertebrates downstream from the Burgomillodo Dam on the Duraton River (Spain) in response to flow alterations, and reported that water level fluctuations prevent establishment of many benthic invertebrates downstream from dams. Newcombe and MacDonald (1991) suggested that benthic invertebrates inhabiting exposed streambed substrates like bedrock, which predominated my Site 3, are subjected to scouring, making the organisms more susceptible to predation through dislodgment.

Berkman and Rabeni (1987) noted that alterations in flow and increased substrate compaction reduces benthic invertebrate abundance and diversity. Deposition of silt creates compact substrate and decrease living space for benthic invertebrates by reducing interstitial space, causing a reduction in benthic invertebrate abundance. Brown and Brussock (1991) reported that benthic invertebrate assemblages in riffles of gravel bed streams in the Ozark Plateau contained more species and total numbers than did pools. In essence, my upstream treatment sites were pools, in that they were deeper and had lower stream velocity than reference sites. Thus, the lower benthic invertebrate abundance and evenness at upstream treatment sites was predictable.

Species richness of benthic invertebrates was similar among site types, but evenness was higher at upstream reference and downstream reference sites. Benthic invertebrate evenness might have been lower in upstream treatment sites as a result of the reduced velocity and higher substrate compaction, factors that tend to hinder many benthic invertebrates (Merritt and Cummins 1996). Waters (1995) suggested that with low levels of sedimentation, abundance and diversity of benthic invertebrates might decrease as a result of a reduction of interstitial habitat, but species richness might not change. Similar to that found for fishes, higher evenness at reference sites might be attributed to higher habitat diversity, which likely allows for habitation by more species. Although mayflies, stoneflies, and caddisflies were present in downstream treatment sites, their numbers were reduced, which could account for the difference in evenness among site types.

The higher number of invertebrates collected during winter and fall than spring and summer might have been the result of spring and summer emergence of benthic invertebrates, or of flooding that occurred during late spring and early summer. March and June had high precipitation and high discharge from Council Grove Reservoir, and had the lowest number of benthic invertebrates.

Fishes

Differences in habitat and benthic invertebrates were associated with differences in fishes. Many species, including suckermouth minnow and Neosho madtom, are habitat specialists whose abundance varies according to stream velocity and substrate composition (Cross and Collins 1995; Pflieger 1997). Abundances of orangethroat darter and suckermouth minnow (the two species that contributed significantly to the variation in fish abundance), in addition to slenderhead darter also differed among site types. Abundances of suckermouth minnow and slenderhead darter were positively correlated with velocity, and these two species, in addition to orangethroat darter, were most abundant at downstream treatment sites, which had higher velocity compared to other site types. Pflieger (1997) reported that these three species prefer permanent stream velocity, moderate gradients, sites free of silt, and substrate ranging in size from mixed sand to small rubble. The suckermouth minnow, orangethroat darter, and slenderhead darter all live on the bottom of rivers and disturb the substrate in search of food (Pflieger 1997). These species also could be affected by substrate compaction, as seen in the upstream treatment sites, where it would be difficult to agitate the substrate.

Neosho madtom abundance was lower immediately upstream and downstream from lowhead dams. Similar to the results of Fuselier and Edds (1994), Wildhaber et al. (2000a), and Bulger and Edds (2001), Neosho madtoms were collected almost exclusively in areas with shallow water, moderate stream velocities, loosely compacted substrates, and areas high in benthic invertebrate abundance, suggesting that Neosho madtom abundance could have been limited by habitat and food in treatment areas.

Upstream treatment, and at times downstream treatment sites, lacked the stream velocity that Neosho madtoms prefer (Cross and Collins 1995; Pflieger 1997), which might also account for the higher substrate compaction at upstream treatment sites than at upstream reference sites. Stream velocity reductions resulting from flow regulation reduces abundance of benthic invertebrates utilized as food by many fishes (Reiser and White 1990). Neosho madtom abundance was positively correlated with benthic invertebrate abundance, suggesting that food might be a limiting factor for Neosho madtoms in these areas. Wildhaber et al. (2000a) stated that in the Spring River (Kansas), Neosho madtoms might be limited by lower benthic invertebrate abundance, possibly as an indirect result of contaminants limiting the amount of available benthic invertebrates.

Neosho madtom abundance was negatively correlated with substrate compaction. Upstream reference and downstream reference sites contained more loosely compacted gravel and pebble substrate, and less cobble, boulder, and bedrock substrates, than upstream treatment and downstream treatment sites. Substrate compaction of gravel bars does not allow for the clean, loose substrate preferred by Neosho madtoms (Fuselier and Edds 1994; Pflieger 1997). Compaction of substrate might force habitat specialists like the Neosho madtom into less suitable areas where they could experience lower survival rates (Bulger and Edds 2001). Wildhaber et al. (2000a) suggested that larger interstitial spaces in larger substrate (cobble) might not offer as much protection from predators or as much food (benthic invertebrates) for Neosho madtoms as smaller substrate (gravel and pebble).

Fish species richness did not differ significantly among site types, but did vary among months. More species were captured in summer than in other seasons, probably as a result of spawning and the development of young in gravel bar nursery areas (Gelwick 1990). Percent similarity indices indicated that all sites were fairly similar in fish species composition. The least similar sites were Site 3 and Site 6 (downstream treatment vs. upstream treatment), which could be attributed to differences in habitat. The most similar sites were Site 5 and Site 6, the Emporia Dam upstream reference and treatment sites, respectively. The gradient between these two sites was very small (0.07 m/km), suggesting that both were somewhat affected by the backwater of the dam.

Evenness differed among site types; evenness in upstream reference and upstream treatment sites was higher than in downstream treatment and downstream reference sites, but only upstream treatment sites differed significantly from downstream treatment sites. Higher evenness in upstream reference and upstream treatment sites might be attributed to greater habitat heterogeneity. Downstream site types had assemblages dominated by few species (e.g. red shiner and slenderhead darter). As a result of scouring, downstream treatment sites lacked food (benthic invertebrates) and the loosely compacted gravel and pebble needed by many species.

Conclusions

My study contributes to our knowledge of the effects of lowhead dams on riverine habitat, in addition to fish and benthic invertebrate assemblage structure in midwestern rivers. My findings suggest that lowhead dams are associated with differences in habitat immediately upstream from and downstream from these barriers, affecting fish and benthic invertebrate assemblages in ways similar to those reported for large dams. The two lowhead dams in my study appear to have caused significant differences in depth, velocity, substrate compaction, and substrate composition, which have affected benthic invertebrate and fish abundance and evenness, especially for habitat specialists like mayflies, stoneflies, caddisflies, suckermouth minnows, and Neosho madtoms.

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Effects of lowhead dams on fish and benthic invertebrate assemblage structure in the Neosho River, with comments on the threatened Neosho madtom, *Noturus placidus*
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