

SPATIAL EFFECTS OF RESERVOIRS ON FISH ASSEMBLAGES  
IN GREAT PLAINS STREAMS IN KANSAS, USA

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## ABSTRACT

Reservoirs are important components of modern aquatic ecosystems that have negative impacts on native aquatic biota both up- and downstream. We used a landscape-scale geographic information system (GIS) approach to quantify the spatial effects of 19 large reservoirs on upstream prairie fish assemblages at 219 sites in Kansas, USA. We hypothesized that fish assemblage structure would vary with increasing distance from a reservoir and that the abundance of reservoir fishes in upstream reaches would decline with distance from a reservoir. Ordination of sample sites showed variation in fish assemblage structure occurred primarily across river basins and with stream size. Variance partitioning of a canonical ordination revealed that the pure effect of reservoir distance explained a small but significant (6%;  $F = 4.90$ ,  $P = 0.002$ ) amount of variability in fish assemblage structure in upstream reaches. Moreover, reservoir species catch per unit of effort (CPUE) significantly declined with distance from a reservoir, but only in fourth- and fifth- order streams ( $r^2 = 0.32$ ,  $P < 0.001$  and  $r^2 = 0.49$ ,  $P < 0.001$ , respectively). Finally, a multivariate regression model including measures of stream size, catchment area, river basin, and reservoir distance successfully predicted CPUE of reservoir species at sites upstream of Kansas reservoirs ( $R^2 = 0.45$ ,  $P < 0.001$ ). Overall, we found significant upstream effects of reservoirs on Kansas stream fish assemblages, which over time has led to a general homogenization of fish assemblages because of species introductions and extirpations. However, characteristic reservoir species are present throughout these systems and the importance of spatial proximity to reservoirs is probably dependent on the availability of suitable habitat (e.g. deep pools) in these tributary streams. Copyright © 2005 John Wiley & Sons, Ltd.

KEY WORDS: reservoirs; introduced species; stream fish assemblages; spatial effects; Great Plains; Kansas; upstream

## INTRODUCTION

Dams and their associated impoundments are prevalent features on the modern landscape. Seventy-seven per cent of all major rivers in the northern hemisphere are impounded or diverted for irrigation (Dynesius and Nilsson, 1994). In North America, nearly every major river basin contains an impoundment (Benke, 1990), and large reservoirs (>800 ha surface area) occupy all major basins in Kansas (KDHE, 1996).

Detrimental effects of dams on downstream fish assemblages have been well documented in recent decades. Dams alter physical habitat by causing channel degradation, substrate entrainment, and streambank erosion (Williams and Wolman, 1984; Kondolf, 1997), which lead to habitat simplification and a reduction of native fish species diversity (Berkman and Rabeni, 1987). Changes in thermal regimes below dams have been implicated in the extirpation of stenothermal fish species in these habitats (Vanicek *et al.*, 1970; Holden and Stalnaker, 1975; Edwards, 1978). Dams also alter spatiotemporal patterns of discharge that are important in structuring stream fish assemblages (Poff and Allan, 1995). Unnatural patterns in streamflow variability below dams can reduce diversity of lotic fishes (Cushman, 1985; Bain *et al.*, 1988) and facilitate the establishment of introduced species (Marchetti and Moyle, 2001; Propst and Gido, 2004).

Reservoirs also can affect structure of upstream fish assemblages. For example, piscivorous sportfish stocked into reservoirs (i.e. *Micropterus* spp., *Sander* spp., and *Morone* spp.) can migrate into nearby streams (Martinez *et al.*, 1994) and potentially have negative effects on native fish assemblages through direct predation or predator avoidance (Matthews *et al.*, 1994). Reservoirs also provide habitat for large-bodied omnivores such as *Ictiobus*

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spp. (Stephens, 1986; Gido and Matthews, 2000), which might move into tributary streams and compete for invertebrate prey or alter ecosystem function in these streams.

In the Great Plains, reservoirs have been implicated in the extirpation (Winston *et al.*, 1991; Lienesch *et al.*, 2000) or decline (Luttrell *et al.*, 1999; Wilde and Ostrand, 1999) of native fishes in stream networks upstream of impoundments. In general, species richness of macrohabitat generalists (Herbert and Gelwick, 2003) and centrarchids (Fritz, 1968; Taylor *et al.*, 2001) increases upstream of impoundments in this region. These studies suggest that the construction of dams favours fishes with particular life history traits such as large body size and piscivory, whereas other fishes that are obligate dispersers with semibouyant eggs are at a disadvantage above impoundments (Winston *et al.*, 1991; Luttrell *et al.*, 1999). There is also evidence to suggest that the spatial proximity of reservoirs influences the abundance of introduced species above reservoirs. Gido *et al.* (2004) showed a constraint envelope effect (Brown, 1995), with the maximum number of introduced species occurring at sites near dams in the Great Plains. Although this relationship was weak, it appeared that other factors, such as the species pool of the focal reservoir, constrained introduced species richness at sites in close proximity to reservoirs.

Quantifying the abundance and distribution of facultative reservoir species (species that are stocked into or occur at high abundances in reservoirs) in adjoining streams has important conservation implications. If reservoirs only have localized effects on native fish assemblages, many areas in close proximity to reservoirs may become targets for conservation. This is particularly important in the Great Plains where a large proportion of public lands occur around reservoirs. Thus, we used a landscape-scale geographic information system (GIS) approach to investigate the spatial effect of proximity to a reservoir on upstream fish assemblage structure in Kansas streams. Our objectives were to: (1) investigate gradients in fish assemblage structure in streams upstream of 19 reservoirs; (2) characterize the relative influence of distance to a reservoir as compared to other environmental factors that could structure the fish assemblages upstream of these reservoirs; and (3) quantify the effect of reservoir distance on the abundance of facultative reservoir species at upstream sites. We hypothesized that fish assemblages above Kansas reservoirs are structured along a gradient of stream size, catchment area, and distance from a reservoir, due to both longitudinal processes and spatial effects of the reservoir. Specifically, we predicted that the abundance of reservoir fishes in upstream reaches will decline as distance from a reservoir increases.

## STUDY AREA

Streams above 19 reservoirs (> 800 ha surface area) were selected for this study (Figure 1). Reservoirs ranged in surface area from 836 ha to 6676 ha (Table I). Sample streams were located within the Great Plains ecoregion (Omernik, 1987) in five major river basins in Kansas, corresponding to National Resource and Conservation Service (NRCS) level 4 Hydrologic Unit Codes (HUC; Table I). Primary land uses in this region were agriculture (72%) and grass/rangelands (25%); urban, forest and water uses constituted approximately 1% of the area (USGS, 1994).

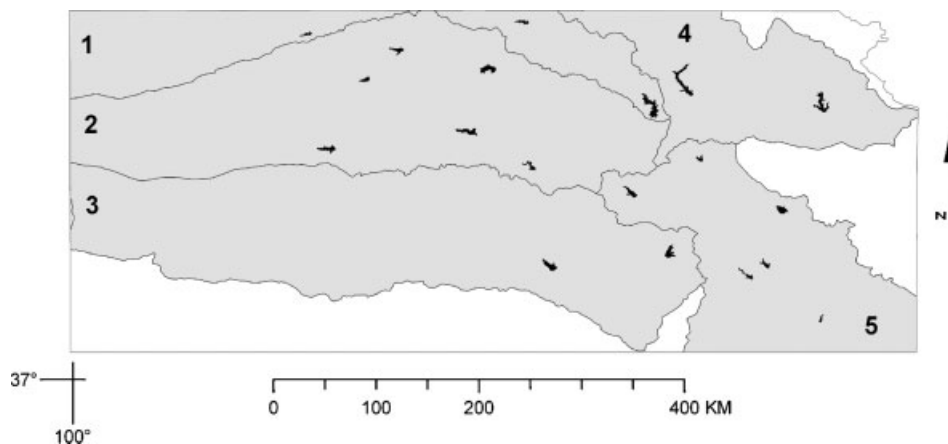


Figure 1. Map of the 19 reservoirs analysed in this study and their location in the state of Kansas, USA. Shaded areas are river basins (USGS 4-digit hydrologic units). 1, Republican; 2, Smoky Hill; 3, Middle Arkansas; 4, Kansas; 5, Neosho-Verdigris

Table I. List of Kansas reservoirs used to evaluate their effects on upstream fish assemblage structure. Surface area, the year impounded, the number of sites upstream from each reservoir, the major river basin, and the upstream watershed area are included for each reservoir

	Surface area (ha)	Year of impoundment	Number of sites	River basin	Watershed area (ha)
Cedar Bluff	2705	1950	7	Smoky Hill	391 302
Cheney	3904	1964	13	Middle Arkansas	251 214
Clinton	3068	1977	7	Kansas	422 635
Council Grove	1060	1964	4	Neosho-Verdigris	292 438
El Dorado	3061	1981	2	Middle Arkansas	252 016
Elk City	1359	1966	6	Neosho-Verdigris	182 050
Fall River	1055	1948	5	Neosho-Verdigris	222 983
John Redmond	3025	1964	20	Neosho-Verdigris	292 438
Kanapolis	1529	1948	11	Smoky Hill	800 044
Keith Sebelius	836	1964	2	Republican	266 858
Kirwin	1977	1955	3	Smoky Hill	359 655
Marion	2488	1967	4	Neosho-Verdigris	243 785
Milford	6676	1967	27	Republican	6 449 000
Perry	4733	1969	33	Kansas	299 658
Toronto	1127	1960	3	Neosho-Verdigris	308 686
Tuttle Creek	6257	1959	50	Kansas	2 490 000
Waconda	4058	1969	12	Smoky Hill	1 282 545
Webster	1402	1956	4	Smoky Hill	301 110
Wilson	3390	1964	6	Smoky Hill	500 679

## MATERIALS AND METHODS

Fish assemblages from 219 sites were sampled by the Kansas Department of Wildlife and Parks (KDWP) during statewide summer surveys between 1995 and 2003. Their sampling protocol followed that of the United States Environmental Protection Agency's (EPA) Environmental Assessment and Monitoring Program (Lazorchak *et al.*, 1998). At each site, a reach 40 times the average wetted width of the stream (minimum 150 m and maximum 300 m) was sampled with a combination of straight and bag seines (4.7 mm mesh) and a DC-pulsed backpack electrofishing unit. Upstream and downstream ends of the site were blocked with nets (4.7 mm mesh). One pass was made from downstream to upstream with the electrofishing gear, and one pass was made upstream to downstream seining suitable habitats. Fishes were identified to species and each site was georeferenced for entry into a GIS point data layer.

Fish abundances were standardized to catch per unit of effort (CPUE) prior to analyses. Electrofishing and seining effort (seconds) were pooled for each site and CPUE was calculated as the number of each species collected at each site per hour of sampling effort.

Landscape-scale environmental habitat variables were generated from multiple GIS layers using ArcGIS 8.2 software (ESRI, 2002) and tested for their relationships with gradients in fish assemblage structure. Streams within this study area were delineated from a digital map of Kansas streams, based on the 1:100 000 National Hydrography Dataset (USGS, 1997). Variables were chosen to represent factors that have been linked to fish-assemblage structure, including stream size and position in the catchment (Sheldon, 1968; Osborne and Wiley, 1992; Zorn *et al.*, 2002) and surficial geology of the reach (Matthews and Robison, 1998; Nelson *et al.*, 1992; Mandrak, 1995). Stream valley segments (segment of stream from one confluence to the next) were classified by Strahler stream order (Strahler, 1957) as a measure of stream size, link magnitude (Shreve, 1967) as a measure of catchment area, and gradient (m/km). Each segment also was assigned a surficial geology class (silt, clay, loam, etc.) taken from the NRCS State Soil Geographic database (STATSGO). Reservoirs selected for this study were represented digitally from a GIS polygon layer of Kansas water bodies (Surface Waters Information Management System; Kansas Department of Health and Environment), developed from the EPA's RF3 digital cartographic hydraulic database. Major river basins were defined from a data set of digital hydrologic unit boundaries (HUC;

USDA, 1993). Each basin was represented by a unique HUC. Basins were considered at the HUC-4 level in this study.

The closest distance (in kilometers along a respective tributary stream) to a downstream reservoir was measured for each site in ArcGIS 8.2. Using GIS tools, each site was linked to a valley segment, and the environmental attributes for that valley segment were appended to the fish abundance information for those sites. Sites also were classified as to the HUC-4 river basin in which they were located (Table I).

We used unimodal multivariate analysis tools to explain patterns in variability in fish assemblage structure upstream of Kansas reservoirs. Distribution and abundance patterns of fishes (and other organisms) across large spatial scales are often unimodal in response to environmental variables, thus traditional linear multivariate techniques are often inappropriate for such analyses (ter Braak and Verdonschot, 1995).

Correspondence analysis (CA) was used to summarize variability in fish assemblage structure across sites. CA is a multivariate ordination technique useful in analysing a species by sample matrix (Gauch, 1982). Axes gradient lengths provide a measure of faunal turnover, and sample scores four standard deviations apart should have few species in common (Gauch, 1982; ter Braak, 1995). Rare species (< 0.5% relative abundance across all samples) were excluded from these analyses because they are more likely to occur randomly in samples and not represent true differences in assemblage structure across space or time. Species abundance data were square-root transformed and scaling was focused on inter-sample distances using Hill's scaling.

Canonical correspondence analysis (CCA) was used to detect relationships between environmental variables (stream size, catchment area, gradient, surficial geology, river basin, and reservoir distance) and spatial variation in the fish assemblage structure. Rare species (< 0.5% relative abundance) were excluded from analysis as described above. CCA is a modification of CA that selects a linear combination of environmental variables to maximize the dispersion of species scores (ter Braak, 1995). This analysis produces a diagram with vector arrows that represent the relative importance of environmental factors in describing variation in the fish assemblage. Monte Carlo simulations (500 iterations) were used to test whether eigenvalues from the CCA were significantly greater than those generated from a randomized matrix. We used a variance partitioning procedure (Borchard *et al.*, 1992) to estimate the variation explained by reservoir distance as compared to the five other environmental variables. Variance partitioning splits the variation explained by the CCA into separate components: a pure spatial component (reservoir distance), a pure environmental component (stream size, catchment area, gradient, surficial geology and river basin), and the spatial component of environmental influence (overlap between spatial and environmental components). The environmental matrix was subdivided into two matrices, one with reservoir distance serving as a covariate, the other with stream size, catchment area, gradient, surficial geology, and river basin as covariates. Prior to CCA analysis, variables were checked for multicollinearity, and variables with variable inflation factors (VIF) > 10 were deleted from analysis (ter Braak and Šmilauer, 2002). CA and CCA were performed using CANOCO ver. 4.5 software (ter Braak and Šmilauer, 2002).

Both non-native piscivorous and native species are typically abundant in Great Plains reservoirs. Facultative reservoir species were defined as those that typically occur, or are stocked, in reservoirs and may only require streams for a portion of their life history. These species were classified by a combination of field collections (J. Falke, unpublished data), and a review of species accounts from reservoirs in this region (Eberle *et al.*, 2000; Gido *et al.*, 2002a) (Table II).

Linear regression was used to test the association between facultative reservoir species CPUE and distance from a reservoir using SPSS for Windows ver. 11.0 (SPSS, 2001). Separate regressions were conducted for streams with different Strahler orders to control for the effects of stream size. Abundances of facultative reservoir species at each site were pooled to give a total CPUE for these species at each site.

Multiple regression was used to predict the CPUE of facultative reservoir species as a function of environmental conditions (stream size and catchment area) and spatial factors (reservoir distance and river basin). A previous study (K. Gido and J. Falke, unpublished data) showed that among 25 landscape level variables, catchment area and stream size were among the most important predictors of stream fish assemblage structure in the Big Blue River basin (a subset of the data used in this study). We expected a possible unimodal pattern in facultative reservoir species CPUE with respect to both stream size and catchment area, due to the large spatial extent of our analyses and potential for these species to occur at greatest abundance in streams of intermediate size. Thus, we included a quadratic function of each variable (stream size and catchment area) in the model. We were also

Table II. List of facultative reservoir species, species codes (first three letters of genus and species epithet), relative abundance (proportion among facultative reservoir species), and number of sites occupied

Species	Species code	Relative abundance (%)	Number of sites occupied
<i>Aplodinotus grunniens</i>	APLGRU	4.20	46
<i>Carpiodes carpio</i>	CARCAR	6.08	79
<i>Cyprinus carpio</i>	CYPCAR	6.14	105
<i>Dorosoma cepedianum</i>	DORCEP	36.53	58
<i>Ictalurus punctatus</i>	ICTPUN	19.26	122
<i>Ictiobus bubalus</i>	ICTBUB	0.34	19
<i>I. cyprinellus</i>	ICTCYP	0.23	7
<i>Lepisosteus osseus</i>	LEPOSS	0.48	25
<i>L. platostomus</i>	LEPPLA	0.07	6
<i>Lepomis macrochirus</i>	LEPMAC	8.61	90
<i>Micropterus salmoides</i>	MICSAL	6.87	114
<i>Morone chrysops</i>	MORCHR	1.06	22
<i>Notropis atherinoides</i>	NOTATH	5.78	16
<i>Pimephales vigilax</i>	PIMVIG	0.94	20
<i>Pomoxis annularis</i>	POMANN	1.23	50
<i>P. nigromaculatus</i>	POMNIG	0.11	6
<i>Pylodictis olivaris</i>	PYLOLI	1.93	46
<i>Sander vitreus</i>	SANVIT	0.14	5

interested in variability in the facultative reservoir species pool among river basins, so a binary variable coded for each river basin was included in order to control for biogeographic effects across this large study area. An information-theoretic approach was used to find the most parsimonious set of independent variables to predict facultative reservoir species abundance (Burnham and Anderson, 1998). First, a set of *a priori* candidate models was selected that contained sets of explanatory variables that were of biological significance. Multiple regression analysis was then performed using facultative reservoir species CPUE as the dependent variable and the sets of explanatory environmental variables as independent variables using SPSS. Akaike's information-criterion (AIC) was used to select the best approximating model by comparing each of the candidate models simultaneously. The AIC scores were adjusted for bias due to a small sample size ( $AIC_c$ ), and Akaike weights ( $w_i$ ) were calculated. Thus, the model with the lowest  $AIC_c$  and the highest  $w_i$  was considered the best model.

Lastly, relative abundances of individual species were tested for correlation with the distance to a reservoir (km) at each respective site using Pearson's product moment correlation ( $r_p$ ). Relative abundance was calculated as the number of individuals of each species at a site divided by the total number of individuals of all species collected at the respective site. This analysis was conducted to reveal positive or negative relationships between individual species abundances and increasing distance from a reservoir.

## RESULTS

The distances of the 219 sample sites above the 19 reservoirs ranged from 0.6 km to 275.4 km ( $\bar{x} = 71.0$  km,  $SE \pm 4.0$ ). A total of 162 358 individuals, representing 56 species, were represented in these collections. *Cyprinella lutrensis* was the most abundant species, representing 33.7% of the total number of individuals, followed by *Notropis stramineus* (11.4%) and *Camptostoma anomalum* (8.0%) (Table III). *Cyprinella lutrensis* was also collected at the highest proportion of sites (91.4%), followed by *Lepomis cyanellus* (86.4%) and *Notropis stramineus* (73.6%).

Eighteen facultative reservoir species (13 775 individuals) were represented in these collections (Table II). *Dorosoma cepedianum* was the most abundant facultative reservoir species, and represented 36% of facultative reservoir species collected, followed by *Ictalurus punctatus* (19%) and *Lepomis macrochirus* (9%).

Ordination showed major changes in fish assemblage structure across river basins and longitudinally in streams upstream of Kansas reservoirs. The first CA axis accounted for 14.7% of the variation in fish assemblage structure across the 219 sample sites and had a gradient length of 3.5 standard deviations (Figure 2), indicating an almost

Table III. Pearson's product-moment correlation ( $r_p$ ) between individual species abundance and distance to a reservoir (km), significance ( $p$ -value), abundance (Total), total abundance of each species divided by sum total abundance of all species  $\times 100$  (Rel. abun.), and percentage of samples that contained each species (% of collections)

Species with positive correlations							Species with negative correlations						
Code	Species	$r_p$	$p$	Total	Rel. abun	% of collections	Code	Species	$r_p$	$p$	Total	Rel. abun	% of collections
PIMTEN	<i>Pimephales tenellus</i>	0.31	0.00	706	0.20	6.82	POMANN	<i>Pomoxis annularis</i>	-0.01	0.98	170	0.17	22.73
MINMEL	<i>Minytrema melanos</i>	0.22	0.00	6	0.00	2.27	MOXMAC	<i>Moxostoma macrolepidotum</i>	-0.01	0.92	228	0.13	10.00
MOXERY	<i>Moxostoma erythrurum</i>	0.18	0.01	221	0.07	11.36	NOTFLA	<i>Noturus flavus</i>	-0.02	0.82	415	0.23	23.64
PIMPRO	<i>Pimephales promelas</i>	0.17	0.01	7661	7.21	70.91	LEPHUM	<i>Lepomis humilis</i>	-0.02	0.82	856	0.93	37.73
NOTVOL	<i>Notropis volucellus</i>	0.16	0.01	139	0.05	3.18	CARCAR	<i>Carpoides carpio</i>	-0.02	0.74	837	0.53	35.91
CYPLUT	<i>Cyprinella lutrensis</i>	0.15	0.03	61693	33.73	91.36	CAMANO	<i>Campostoma anomalum</i>	-0.03	0.62	15229	7.97	72.27
PHEMIR	<i>Phenacobius mirabilis</i>	0.13	0.06	3072	1.65	56.82	CYPCAR	<i>Cyprinus carpio</i>	-0.05	0.47	846	0.84	47.73
LEPMEG	<i>Lepomis megalotis</i>	0.13	0.06	705	0.30	14.55	PIMNOT	<i>Pimephales notatus</i>	-0.05	0.47	7303	3.42	55.45
MICPUN	<i>Micropterus punctulatus</i>	0.12	0.07	75	0.03	7.27	NOTPER	<i>Notropis percobromus</i>	-0.05	0.44	460	0.28	3.18
LYTUMB	<i>Lythrurus umbratilis</i>	0.09	0.18	1740	1.06	18.64	LEPCYA	<i>Lepomis cyanellus</i>	-0.06	0.39	4379	5.33	86.36
PERPHO	<i>Percina phoxocephala</i>	0.09	0.19	845	0.37	10.91	ETHNIG	<i>Etheostoma nigrum</i>	-0.06	0.35	144	0.07	5.91
AMEMEL	<i>Ameiurus melas</i>	0.09	0.20	1136	1.74	49.09	SANVIT	<i>Sander vitreus</i>	-0.06	0.35	19	0.01	2.27
LEPOSS	<i>Lepisosteus osseus</i>	0.08	0.27	66	0.04	11.36	POMNIG	<i>Pomoxis nigromaculatus</i>	-0.07	0.34	15	0.01	2.73
ETHSPE	<i>Etheostoma spectabile</i>	0.05	0.44	4434	2.62	47.27	SEMATR	<i>Semotilus atromaculatus</i>	-0.07	0.33	7239	5.91	57.73
AMENAT	<i>Ameiurus natalis</i>	0.04	0.55	509	0.89	42.27	ICTCYP	<i>Ictiobus cyrinellus</i>	-0.07	0.33	31	0.08	3.18
FUNNOT	<i>Fundulus notatus</i>	0.03	0.71	180	0.12	8.64	CYPCAM	<i>Cyprinella camura</i>	-0.06	0.33	1459	0.67	5.45
APLGRU	<i>Aplodinotus grunniens</i>	0.02	0.74	581	0.29	20.91	NOTDOR	<i>Notropis dorsalis</i>	-0.07	0.31	805	0.32	5.45
ICTBUB	<i>Ictiobus bubalus</i>	0.02	0.78	47	0.03	8.64	NOTATH	<i>Notropis atherinoides</i>	-0.07	0.28	796	0.38	7.27
HYBPLA	<i>Hybognathus placitus</i>	0.00	0.95	90	0.06	2.27	PHOERY	<i>Phoxinus erythrogaster</i>	-0.08	0.24	87	0.02	2.27
LEPPLA	<i>Lepisosteus platostomus</i>	0.00	0.98	9	0.01	2.73	LEPMAC	<i>Lepomis macrochirus</i>	-0.08	0.23	1186	0.96	40.91
ETHCRA	<i>Etheostoma cragini</i>	0.00	0.98	289	0.20	4.55	CATCOM	<i>Catostomus commersonii</i>	-0.08	0.23	297	0.29	19.55
							MICSAL	<i>Micropterus salmoides</i>	-0.07	0.20	946	1.23	51.82
							NOTEXI	<i>Noturus exilis</i>	-0.10	0.18	392	0.18	6.36
							NOTSTR	<i>Notropis stramineus</i>	-0.10	0.17	20279	11.39	73.64
							GAMAFF	<i>Gambusia affinis</i>	-0.10	0.13	1238	1.07	18.64
							ICTPUN	<i>Ictalurus punctatus</i>	-0.10	0.12	2653	1.56	55.45
							FUNZEB	<i>Fundulus zebrinus</i>	-0.10	0.12	1879	1.01	10.45
							PIMVIG	<i>Pimephales vigilax</i>	-0.11	0.11	129	0.08	9.09
							LUXCOR	<i>Luxilus cornutus</i>	-0.11	0.10	605	0.24	6.82
							PYLOLI	<i>Pylodictis olivaris</i>	-0.11	0.09	266	0.17	20.91
							LABSIC	<i>Labidesthes sicculus</i>	-0.12	0.08	1216	0.58	11.82
							NOTCRY	<i>Notemigonus crysoleucas</i>	-0.13	0.05	59	0.06	11.82
							PERCAP	<i>Percina caprodes</i>	-0.13	0.05	513	0.28	19.09
							MORCHR	<i>Morone chrysops</i>	-0.15	0.03	146	0.07	10.00
							DORCEP	<i>Dorosoma cepedianum</i>	-0.19	0.00	5032	2.83	26.36

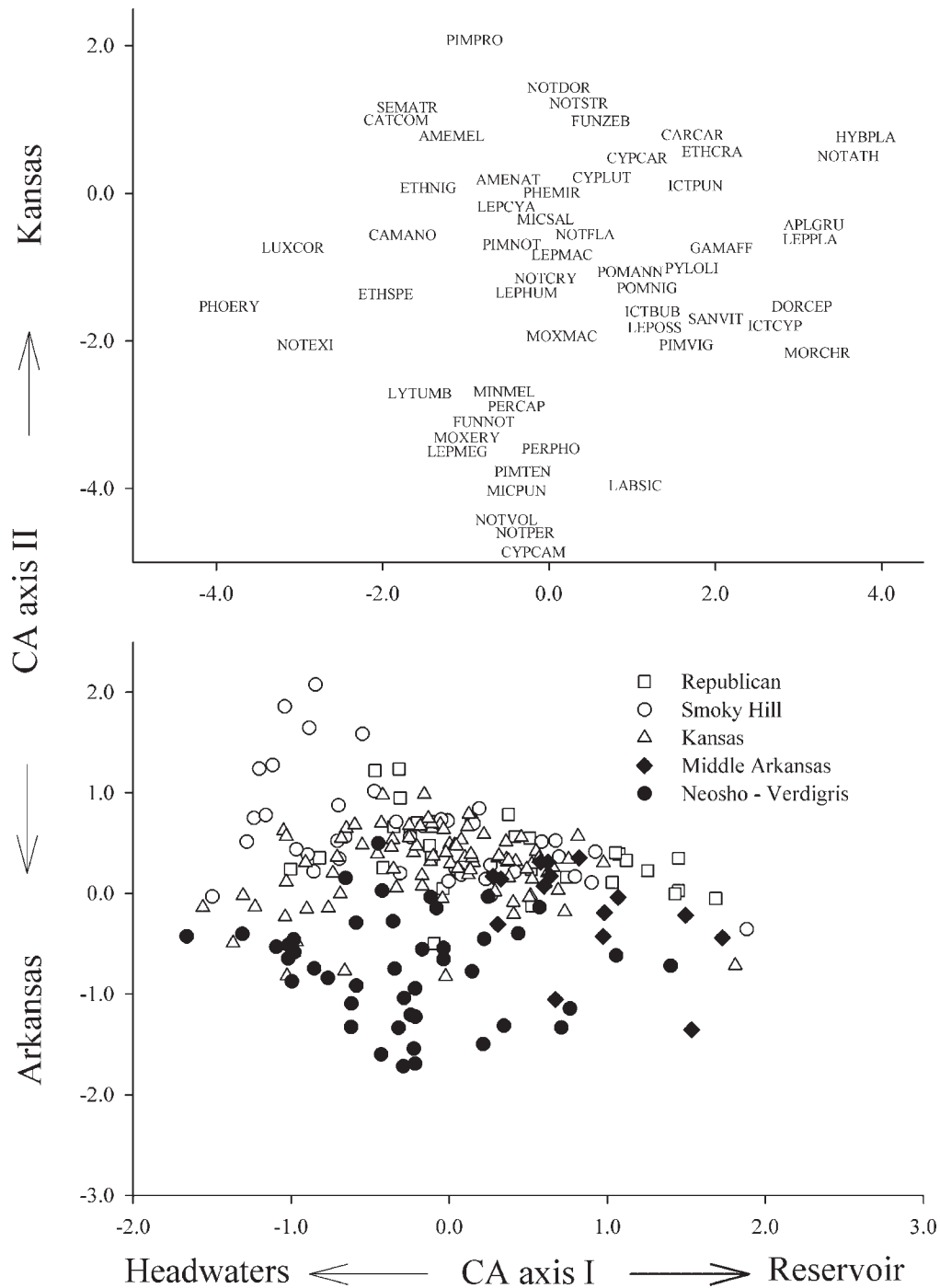


Figure 2. Correspondence analysis of fish community data across 219 sites upstream of reservoirs in Kansas. First and second axes had eigenvalues of 0.327 and 0.300 and explained 14.7% and 13.4% of the variation in community structure, respectively. Top panel shows species scores and lower panel gives sample scores. Species codes are the first three letters of the genus plus the first three letters of the specific epithet, as in Table III. Symbols on the lower plot correspond to river basins, as explained in key

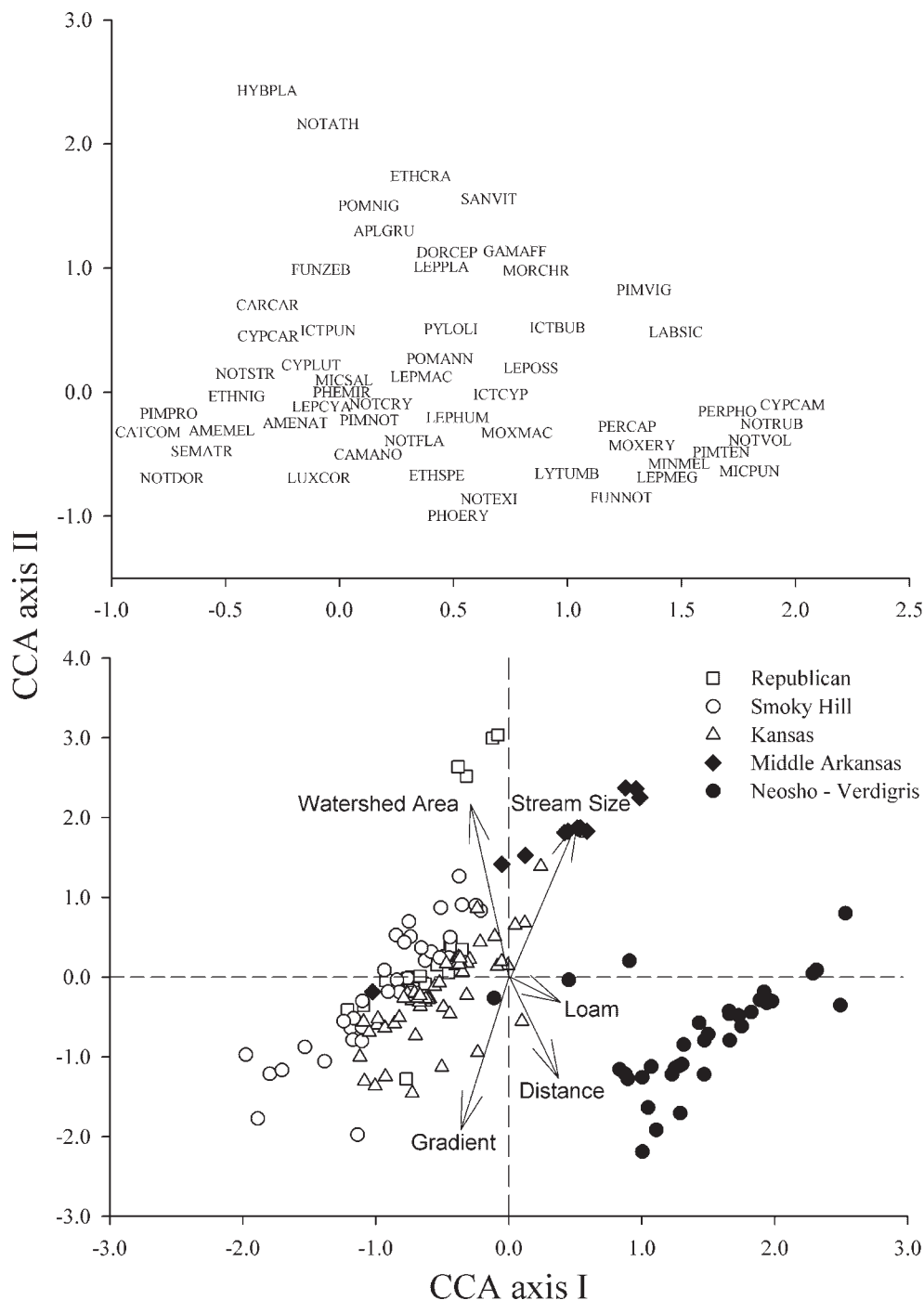


Figure 3. Canonical correspondence analysis of fish community data across 219 sites upstream of reservoirs in Kansas. First and second axes of the ordination had eigenvalues of 0.225 and 0.201, respectively. Top panel shows the species scores and lower panel gives the site scores and environmental correlates. Species codes are the same as in Figure 2. Abbreviations: Gradient, gradient ( $m\ km^{-1}$ ); Loam, loam soil texture class; Distance, reservoir distance (km); Stream Size, Strahler stream order; Watershed Area, Shreve link magnitude. Vector arrows for a categorical river basin variable were removed and site scores are displayed by symbols on the lower plot, as explained in key

complete turnover in species composition between samples located at opposite ends of the ordination. Sites with high Axis I scores were composed of species associated with reservoirs and large rivers (e.g. *Dorosoma cepedianum*, *Morone chrysops*, and *Notropis atherinoides*), while sites with low Axis I scores contained species more characteristic of headwater areas (e.g. *Luxilus cornutus*, *Noturus exilis*, and *Phoxinus erythrogaster*). Sites mainly composed of ubiquitous species were clustered around the centroid (0,0 on Axis I and II, respectively) and included species such as *Lepomis macrochirus*, *Micropterus salmoides* and *Phenacobius mirabilis*. Axis II of the ordination explained 13.4% of the overall variation in assemblage structure and had a gradient length of 3.8 standard deviations. High Axis II scores represented samples collected in the Smoky Hill and Republican River basins, with intermediate scores (approximately  $-1$  to  $1$ ) representing samples collected in the Kansas River basin. Sites located in the Middle Arkansas River basin also had intermediate Axis I scores. Low Axis II scores represented sites located in the Neosho-Verdigris River basin. Species with high Axis II scores represented those characteristic of the Kansas River basin, such as *Pimephales promelas*, *Notropis dorsalis* and *Semotilus atromaculatus*, whereas species with low Axis II scores were more characteristic of the Arkansas River basin (e.g. *Cyprinella camura*, *Notropis percobromus* and *Pimephales tenellus*).

Environmental variables explained 64.3% of the overall variation in the unconstrained assemblage structure (i.e. variation from the indirect gradient analysis) along Axis I and II of the CCA, and confirmed the importance of stream size and river basin in structuring the fish assemblage (Figure 3). Variables included in the CCA analysis after deleting variables with VIF scores  $> 10$  included: reservoir distance (1.21), stream size (2.78), catchment area (2.08), gradient (1.87), loam (1.08), Smoky Hill basin (3.07), Kansas basin (4.75), Middle Arkansas basin (2.19), and Neosho-Verdigris basin (4.10). Eigenvalues from the first two axes of the CCA were significantly different from random (Axis I  $P = 0.002$ , Axis II  $P = 0.002$ ). Stream size, catchment area, gradient, reservoir distance, and river basin explained the most variation in the assemblage structure. Axis I represented a gradient among river basins; sites with lower scores were located in the Republican and Smoky Hill basins. Sites with high Axis I scores were located in the Middle Arkansas and Neosho-Verdigris basins, and included characteristic species such as *Minytrema melanops*, *Pimephales tenellus* and *Notropis vollucellus*. Axis II represented a contrast between sites with high gradient and sites in larger streams. High gradient ( $> 5.0 \text{ m km}^{-1}$ ), small streams were characterized by a headwater fish assemblage, and included species such as *Luxilus cornutus*, *Campostoma anomalum* and *Phoxinus erythrogaster*. Sites in low gradient ( $< 4.9 \text{ m km}^{-1}$ ), larger streams included species such as *Morone chrysops*, *Aplodinotus grunniens* and *Lepisosteus osseus*.

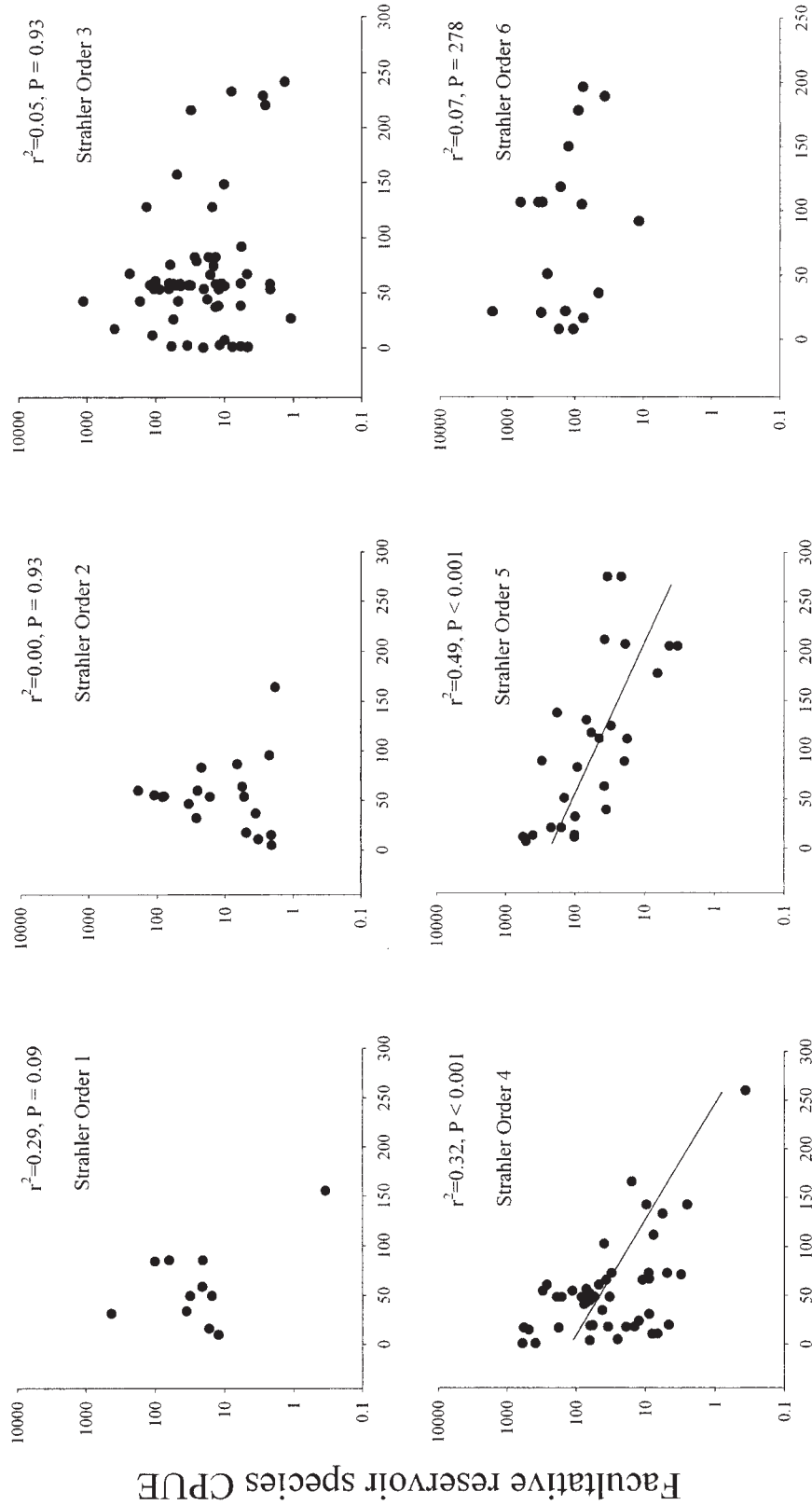
The pure effect of reservoir distance in the CCA explained 6.0% of the overall variation in the unconstrained assemblage structure (i.e. variation from the indirect gradient analysis). The pure environmental component (Strahler order, link magnitude, gradient and geology) explained 93.2% of the overall variation. The spatial component of environmental influence explained 0.8% of the overall variation, indicating little overlap between the spatial and environmental components. Each of the covariate models was significantly different from random ( $P = 0.002$ ; Table IV), suggesting reservoir proximity influences fish assemblage structure independent of other confounding environmental factors.

The spatial component of reservoir distance was an important variable in predicting the abundance of facultative reservoir species CPUE upstream of Kansas reservoirs. Facultative reservoir species CPUE significantly declined

Table IV. Sum of all canonical eigenvalues,  $F$ -values and  $p$ -values from the CCA species–environment variance partitioning procedure

Model*	Sum	$F$	$P$
CCA	0.664	9.84	0.002
Distance	0.619	10.31	0.002
Environment	0.037	4.90	0.002
Overlap	0.008	—	—

\*CCA, full model; Distance, reservoir distance as a covariable; Environment, environmental variables as covariables; Overlap, spatial component of environmental influence.



Reservoir distance (km)

Figure 4. Relationship between log-transformed facultative reservoir species catch-per-unit of effort (CPUE; number of facultative reservoir species sampled per hour; y-axes) at each of 219 sites upstream of Kansas reservoirs and reservoir distance (km; x-axes). Separate graphs are presented for sites on streams with different Strahler stream orders

Table V. Top linear models for predicting reservoir species abundance above 19 Kansas reservoirs as determined by Akaike information criterion (AIC) rankings

Model and parameters	AIC <sub>c</sub>	K	ΣAIC <sub>c</sub>	w <sub>i</sub>
Distance, Strahler order, Strahler order <sup>2</sup> , link magnitude, link magnitude <sup>2</sup> , river basin	655.20	11	0	0.92
Distance, Strahler order, Strahler order <sup>2</sup> , river basin	661.45	9	5.83	0.05
Distance, link magnitude, link magnitude <sup>2</sup> , river basin	663.38	9	7.75	0.02
Distance, Strahler order, link magnitude, river basin	665.59	9	9.11	0.01

AIC<sub>c</sub> is the AIC corrected for small sample size, K is the number of parameters in the fitted model (including the intercept); ΣAIC<sub>c</sub> is the difference between the candidate model and the model with the lowest AIC<sub>c</sub>. The Akaike weights (w<sub>i</sub>) sum to 1.0.

with distance from a reservoir in fourth and fifth- order streams ( $r^2 = 0.32$ ,  $P < 0.001$  and  $r^2 = 0.49$ ,  $P < 0.001$ , respectively; Figure 4).

The best model selected by the AIC included measures of stream size, reservoir distance, hydrologic unit, and quadratic functions of stream size and catchment area (Table V) and explained approximately 45% of the variability in reservoir species CPUE ( $P < 0.001$ ). The Akaike weight ( $w_1 = 0.92$ ) of this model suggests it was approximately 18.4 times more likely to be the best approximating model than the next candidate model ( $w_1 = 0.05$ ).

The relative abundance of nine species at sites upstream of reservoirs was significantly ( $P \leq 0.05$ ) correlated with reservoir distance (Table III). Relative abundances of *Minytrema melanops* and *Pimephales tenellus* showed the highest positive correlation with reservoir distance. *Dorosoma cepedianum* and *Morone chrysops* showed the highest negative correlation, indicating high relative abundances of these species near reservoirs.

## DISCUSSION

We found that fish assemblage structure above Kansas reservoirs was structured along a gradient of stream size and catchment area. In addition, basin zoogeography, and the proximity to reservoirs explained notable variation in assemblage structure. Longitudinal (Huet, 1959; Schlosser, 1990; Edds, 1993; Zorn *et al.*, 2002) and zoogeographic (Cross and Moss, 1987; Hugueny and L  v  que, 1994; Matthews and Robison, 1998) patterns in fish assemblages are well studied in lotic systems. However, we were interested in quantifying the specific effects of reservoirs.

By splitting the variation explained by the environmental variables into spatial and environmental components, we were able to examine the influence of reservoir distance independent of other confounding environmental variables. The spatial component of reservoir distance explained 6% of the variability in fish assemblage structure and also was useful in predicting the CPUE of facultative reservoir species at sites upstream of reservoirs. This suggests that spatial proximity to a reservoir does influence structure of stream fish assemblages; however, this effect is weak overall, and is constrained to fourth- and fifth- order streams.

Facultative reservoir species CPUE decreased linearly with distance from Kansas reservoirs in mid-sized streams (fourth- and fifth- order). Habitat in these streams may be more suitable for facultative reservoir species as most of these species are native to mid-sized streams in their native range (e.g. *Ictiobus cyprinellus*, *Carpionotus carpio*). Smaller streams (first to third order) did not show significant linear relationships with facultative reservoir species abundance at upstream sites, as reservoir fishes were present throughout these streams, regardless of distance. Large-bodied facultative reservoir species may not colonize smaller streams due to unsuitable habitat (e.g. lack of deep pools), and the stochastic nature of environmental conditions of small streams in the Great Plains (Schlosser, 1987; Dodds *et al.*, 2004). Moreover, fishes may be more likely to encounter passage barriers (e.g. bridge crossings or natural waterfalls) in smaller streams. Thus, even though smaller-bodied facultative reservoir species (e.g. *Lepomis macrochirus*, *Micropterus salmoides* and *Pomoxis* spp.) exist in smaller streams above Kansas reservoirs, their populations may originate in the thousands of small impoundments upstream of Kansas reservoirs, as opposed to in the large reservoirs themselves. This may have confounded our analysis in smaller streams.

The abundance of facultative reservoir species at upstream sites was also partially explained by river basin, indicating the variable effects of reservoir distance among river basins. Distribution of native facultative reservoir

species in the Great Plains would explain some of this disparity in effects among basins. For example, *Pimephales vigilax* is native to the Arkansas River basin but it is an invasive species in the Kansas River basin (Cross and Collins, 1995). If reservoirs are facilitating populations of this species, we might expect these effects to be stronger within its native range, where overall habitat conditions may be more suitable. Negative effects of reservoirs on upstream assemblages may also be more noticeable in basins that are initially more species-rich. The potential for competitive interactions between the native fauna and facultative reservoir species may be greater in these systems. The species by reservoir distance correlation analysis indicated that several species native to the Neosho-Verdigris basin (*Pimephales tenellus*, *Minytrema melanops* and *Notropis volucellus*) showed significant positive association with increasing reservoir distance. The Neosho-Verdigris basin is the most species-rich basin in this study area (Cross and Collins, 1995).

Facilitated species introductions and species extirpations as a result of impoundments have led to the homogenization of fish assemblages across North America and the Great Plains (Gido and Brown, 1999; Rahel, 2000; Gido *et al.*, 2004). In this study we found that stream fish assemblage structure at sites upstream of reservoirs showed a high degree of overlap, regardless of major river basin. Some of this homogeneity stems from the glacial history and connectivity of Great Plains streams in Kansas (Cross and Moss, 1987; Cross and Collins, 1995), as many common species are native to both basins (i.e. *Cyprinella lutrensis*, *Lepomis cyanellus*, *Camptostoma anomalum*). Much of this overlap may also result from inter-basin transfers of fishes (e.g. from the Arkansas basin into the Kansas basin; *Notropis atherinoides*, *Pimephales vigilax*), or from within-basin expansion of fishes due to bait bucket introductions (e.g. *Notropis dorsalis*). Finally, the loss of unique species such as *Notropis girardi* in the Arkansas River basin has further increased the similarity of the fauna across river basins. Clearly, the construction of impoundments has exacerbated assemblage homogenization among river basins in Kansas.

The impoundment of rivers in Kansas over the past 40 years has resulted in changes to fish assemblage structure upstream of impoundments, likely due in part to introduced species. Other studies in the Midwest found substantial changes in stream fish assemblages in reservoir systems post-impoundment due to introduced species (Pigg *et al.*, 1998; Taylor *et al.*, 2001; but see Gido *et al.* (2002b) for alternative). Reservoirs may play a large part in this process by providing favourable habitat for introduced species (Fernando and Holčík, 1991; Holčík, 1998), and by serving as a vector for both intentional and unintentional introductions (Moyle, 1986). Thus, over the previous 40 years post-impoundment, these systems may have become saturated by introduced species. This could also explain the lack of linear effects between distance and reservoir fish abundance in smaller streams where facultative reservoir species were found in smaller stream reaches throughout the system from 0 to 250 km upstream of reservoirs.

The results of this study are promising when conservation implications are considered. If spatial effects of reservoirs are confined to short distances upstream (e.g. in first- to third- order streams), we would predict relatively intact native assemblages above reservoirs. Thus, stream reaches upstream of reservoirs with relatively minor anthropogenic impacts could be suitable targets for conservation action (e.g. land acquisition, restocking extirpated species, etc.). However, because little is known about the metapopulation dynamics of streams that are isolated by reservoirs (Winston *et al.*, 1991), caution must be taken before labelling those streams as suitable native fish habitat. For example, if environmental conditions become degraded in these streams, reservoirs may not act as a corridor to suitable refugia for displaced stream fishes. This factor has been implicated in the extirpation of some species that carry out their life history at multiple spatial scales (i.e. those with drifting eggs; Winston *et al.*, 1991; Luttrell *et al.*, 1999).

In conclusion, we found that the upstream effects of reservoirs on Kansas stream fish assemblages declined with distance in mid-sized streams. In smaller streams, smaller bodied facultative reservoir species are ubiquitous throughout upstream basins, regardless of distance, which along with species introductions and extirpations, has exacerbated assemblage homogenization in Kansas. More research into the spatial effects of reservoirs at smaller spatial scales is needed to clarify patterns of facultative reservoir species abundance in nearby streams in order to quantify preferred habitat by these species outside of a reservoir.

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