Influence of spatial positioning within stream networks on fish assemblage structure in the Kansas River basin, USA

Darren J. Thornbrugh and Keith B. Gido

Abstract: We found that riverine confluences had localized effects (within 20 km) on stream fish assemblages of the Kansas River basin. The majority of variation in fish assemblages occurred from east to west and along a stream size gradient. After controlling for the influences of longitude and stream size, distance of sample sites from streams accounted for a small proportion of taxonomic variability. However, species richness was significantly higher and assemblage structure was different in tributary stream segments directly connected to larger-ordered streams, suggesting that the effects of spatial position within this stream network were greatest in close proximity to tributary–mainstem confluences. Fish collections from three intensively sampled tributaries also indicated an abrupt change in species assemblages between mainstem river sites and tributary sample sites above confluences, followed by a gradual taxonomic change with increasing distance up to 20 km from the confluence. Changes in fish assemblages were associated with the reduced abundance of adult stream species near the confluence with the mainstem, rather than the occurrences of riverine species in the tributary.

Résumé : Les confluences des cours d’eau ont des effets bien localisés (sur une distance de moins de 20 km) sur les peuplements de poissons d’eau courante dans le bassin versant de la rivière Kansas. La plus grande partie de la variation dans les peuplements de poissons se produit d’est en ouest et suivant un gradient de taille des cours d’eau. Une fois qu’on a tenu compte des influences de la longitude et de la taille des cours d’eau, la distance entre le point d’échantillonnage et les cours d’eau d’ordre ≥ 5 explique un petit pourcentage de la variabilité taxonomique. Cependant, la richesse spécifique est significativement plus élevée et la structure du peuplement différente dans les sections de tributaires qui sont reliées directement à des cours d’eau d’ordre supérieur, ce qui indique que les effets de la position spatiale dans le réseau hydrographique sont maximaux près des confluences des tributaires et du cours principal. Des récoltes de poissons dans trois tributaires fortement échantillonnés montrent aussi un changement abrupt dans les peuplements de poissons entre les sites du cours principal de la rivière et les sites d’échantillonnage des tributaires en amont de la confluence, suivi d’un changement taxonomique graduel en fonction de la distance pouvant se manifester jusqu’à 20 km de la confluence. Les changements dans les peuplements de poissons s’expliquent par une abondance réduite d’espèces adultes de ruisseau près de la confluence avec le cours principal plutôt que par la présence d’espèces de rivière dans le tributaire.

Introduction

Stream fish assemblages are influenced by the availability of aquatic habitats across a variety of spatial scales and the ability of individuals to move among those habitats (Schlosser 1982; Angermeier and Winston 1998; Grossman et al. 1998). Accordingly, measures of local fish assemblage structure are often predicted by the species composition of the surrounding drainage basin, as well as the position of that locality within the drainage (Osborne and Wiley 1992; Matthews and Robison 1998; Schaefer and Kerfoot 2004). Such spatial dependencies of fish populations and communities among stream habitats (e.g., streams of different size or basins with different geology) have been conceptualized by several authors. Recently, Fausch et al. (2002) developed

the riverscapes perspective, which posits that dendritic stream networks cannot be viewed in the context of disjunct parts but should be considered in their entire interconnected network architecture. Campbell-Grant et al. (2007) further emphasized the importance of the structure of dendritic networks in shaping biotic assemblages and highlighted the importance of movement among branches and the heterogeneity of habitats associated with a branch–node structure. These studies are important because they conceptualize how regional factors operating at spatial scales of tens to hundreds of kilometres can influence local assemblage structure, which is typically measured at spatial scales of <0.5 km. Despite this increasing recognition that landscape and stream network architecture influence fish assemblages, empirical data on the relative importance of
Spatial positioning of a habitat within a dendritic stream network and its connectivity to other habitats is limited (Benda et al. 2004a; Lowe et al. 2006; Campbell-Grant et al. 2007). Below, we review studies that address these issues and describe an experiment to test their importance in a prairie stream network.

Physical structuring of stream habitats and associated changes in biota are best documented along gradients of stream size (Horwitz 1978; Vannote et al. 1980; Matthews 1998). However, because dendritic stream networks include abrupt transitions in stream size at tributary confluences, these habitats are likely important in mediating the exchange of biota among branches of these networks (Benda et al. 2004b; Lowe et al. 2006; Campbell-Grant et al. 2007). Whereas some species may favor habitats that vary with stream size, it is likely that many stream organisms move among tributary and mainstem habitats at different life stages for resource use and refugia (Schlosser and Angermeier 1995; Fausch et al. 2002). Landscape complementation or supplementation may occur around these tributary confluences because desired resources (e.g., food, spawning habitat, refugia) in different habitat patches are in close proximity, thus allowing for larger populations to be supported, increased species richness, and potentially longer persistence of species (Dunning et al. 1992). According to the above-mentioned studies, we predict that dispersal patterns of stream fishes should vary along gradients of stream size and movement through confluence zones should be influenced by stream network architecture (Figs. 1a and 1b).

We define confluence zones as sections of tributary streams within the floodplain or an adjoining river that has a notably different habitat than sections further upstream of the confluence. These tributary habitats near mainstem rivers typically have lower gradient and wider channels that result in a reduction in the transport of sediment and wood (Benda et al. 2004a).

Spatial positioning within a stream network can affect immigration and extinction risk (Fagan 2002; Campbell-Grant et al. 2007). For example, fishes in prairie rivers have greater colonization probabilities from surrounding habitats in downstream sites and higher extinction risks in upstream or more isolated sites (Gotelli and Taylor 1999; Franssen et al. 2006). Small adventitious streams (site 3 in Fig. 1b) may be isolated from other tributaries if there is little movement of fishes through large rivers, resulting in lower species richness in these streams. Colonization opportunities are also influenced by proximity to unique habitats. For example, Hitt and Angermeier (2008) concluded that proximity to mainstem river confluences influenced tributary fish assemblage structure in mid- to large stream sites (i.e., basin areas > 1000 ha) and extended up to 20 stream km (skm) from the confluence. However, assemblages at sites on the smallest streams (i.e., basin areas < 1000 ha) were not related to stream network topology. Within medium streams (i.e., basin area 1000 ha – 5000 ha), proximity to a confluence increased total species richness, river species richness, catostomid species richness, and cyprinid species richness for up to 20 skm, but this effect was greatest near mainstem rivers. Smith and Kraft (2005) also found that confluence link (watershed size of stream segments immediately downstream of sites) was a significant predictor of fish assemblage structure in the Beaverkill–Willowemoc watershed in New York. Similarly, Falke and Gido (2006a) showed that confluence sites between streams and reservoirs (i.e., stream sites within the floodplain of the reservoir) had higher total nonnative and reservoir species richness than sites 4–16 km upstream of those confluences, suggesting a localized effect of reservoirs. Close proximity to a large river also can influence variability of stream fish assemblages, as sites closer to interface zones were found to be more temporally variable in an adventitious Illinois stream than sites more distant to those interfaces (Schaefer and Kerfoot 2004). Gorman (1986) presented arguments that fish assemblages on tributary streams within close proximity to larger mainstem streams may be strongly influenced by the discontinuity in the stream continuum and the adventitious nature of the streams spatial position in the stream network. This adventitious nature of some streams is an ideal example of mixed-habitat patches within close proximity to mainstem rivers (Dunning et al. 1992).

Our study focused on patterns of fish species richness, abundance and size structure in prairie streams in relation to proximity to mainstem rivers (i.e., stream order ≥ 5th), and the connectance to streams of different sizes. We defined proximity as distance (along the stream channel) between a sample site on a tributary and the junction of that...
tributary with a mainstem river. Associations between proximity and fish assemblage structure were tested at both large (up to 200 km) and small (up to 20 km) spatial scales. At larger spatial scales (across stream segments), fish assemblages within tributaries are predicted to diverge from mainstem river assemblage with increasing distance from the mainstem as a result of decreasing probabilities of biotic exchange (i.e., network dispersal; Fig. 1a). However, biotic exchange may attenuate rapidly as stream size decreases and habitat (e.g., shallow riffle depth) limits movement. Within stream segments connected to mainstem rivers, we predicted that there would be an abrupt change in fish assemblage structure between tributary sites and sites on mainstem rivers because of rapid changes in habitat in the confluence zones. Finally, we predicted that headwater tributaries (site 1 in Fig. 1b) would have fewer riverine species and overall lower species richness than mainstem tributaries (site 3 in Fig. 1b) because of reduced biotic exchanges with mainstem rivers (Osborne and Wiley 1992).

Considering the physical and ecological processes associated with stream networks, we hypothesize that stream fishes exhibit the following movement patterns: (i) limited movement — fishes are restricted to large rivers or small streams because of habitat or resource limitation; (ii) confluence exchange — fishes move between large or small streams and confluences but do not move through confluence boundaries; and (iii) network dispersal — fishes move through confluence zones but the probability of moving
Fig. 3. Number of species collected at sites as a function of basin area for eastern (Big Blue and Kansas basins) and western (Republican and Smoky Hill basins) portions of the Kansas River basin, as well as several tributaries to the Missouri River (Lower Missouri–Blackwater and Missouri–Nishnabotna). Least-squared regression lines are drawn for significant relationships.

away from a habitat (e.g., from large river into tributary) declines with distance. If confluence exchange is prevalent, fish assemblages should vary among streams that are connected to different-sized streams (e.g., sites 1 and 3 in Fig. 1b). If network dispersal is prevalent, we would expect fish assemblage structure to vary at headwater tributary stream sites that occur at different stream distances from mainstem rivers (e.g., sites 1 and 2 in Fig. 1b). Because juvenile fishes can have different habitat preferences than adults (Schlosser 1995), we also expect patterns of movement to vary among species, as well as among size classes.

Materials and methods

Study area

We evaluated the influence of proximity and connectance to mainstem rivers on stream fish assemblages at two spatial scales: basin-wide surveys and targeted sampling of three tributaries of the Kansas River (Kansas, USA). The Kansas River basin covers 156,286 km² and includes the Smoky Hill and Republican rivers as main tributaries in western Kansas and the Big Blue and Delaware rivers in the east. In addition, we included a few tributaries of the Missouri River in the Missouri–Nishnabotna and Lower Missouri subregions (e.g., level 2 HUCs) in our basin-wide study because they represented similar habitats to those in the nearby Kansas River basin (Fig. 2; Seaber et al. 1994). Hereafter, these Missouri tributaries and the Kansas River Basin proper are collectively referred to as the Kansas basin. This region contains seven EPA level III ecoregions (Omernik 1987), with land cover primarily comprised of grasses (49%) and agriculture (46%), with a small proportion of the basin forested (<3%) and the remainder urban, water, wetlands, or barren lands (US Geological Survey (USGS) 2006a). Streams at the collection sites ranged from 1st to 8th order (Strahler 1957), and basin area of study reaches ranged from 0.3 to 116,978 km². Twenty major reservoirs with surface areas between 399 ha and 5911 ha occurred within the study area along with numerous smaller impoundments.

Three local tributaries of the Kansas River were targeted to evaluate fine-scale variation in fish assemblage structure along a gradient of increasing distance from their confluence with the mainstem (Clarks Creek, McDowell Creek, and Wildcat Creek; Fig. 2). Five 150 m reaches within the first 20 skm of the Kansas River on each of the three study streams were sampled along with two reaches on the mainstem Kansas River (Fig. 2). Land cover in the three study basins was dominated by grasslands (68%–81%) and agriculture (14%–24%), with the remainder comprised of shrub, forest, urban, water, and wetlands (USGS 2006a). McDowell Creek and Wildcat Creek were similar in basin area, mean width, mean depth, and substrates. Clarks Creek had a basin area approximately twice that of McDowell Creek and Wildcat Creek, and as such, it also had a greater mean width and depth than the other two streams.

Experimental design

Fish sampling

Collections at 413 localities made by the Kansas Department of Wildlife and Parks (KDWP) during their annual stream monitoring and assessment program between 1995 and 2006 were used in our analyses (Fig. 2). These records did not include sites within 20 skm upstream of reservoirs because those sites may have been influenced by reservoir fish assemblages (Falke and Gido 2006b). The KDWP sampling protocol followed that of the US Environmental Protection Agency’s (EPA) Environmental Monitoring and Assessment Program (EMAP; Lazorchak et al.1998). Each sample reach was 40 times the average wetted width of the stream (reach length range: 150–300 m). Sites were sampled using a combination of straight and bag seines (4.7 mm mesh) and pulsed-DC backpack electrofishing. One upstream pass was made with the electrofishing gear, and one downstream pass was made seining all suitable habitats. Fishes were identified to species, and each site was georeferenced with a geographical positioning system (GPS). Vouchers were deposited at the University of Kansas or Fort Hays State University Natural History Museums.

Fishes also were collected at the 17 sites in three tributa-
ries and the mainstem Kansas River using similar methods over three seasons in 2006 and 2007: 6–12 July (summer), 21 August – 9 October (fall), and 11 May – 21 June (spring). Species with notable length classes were separated into small and large size classes. For most taxa (e.g., cyprinids and darters), the size classes represented juveniles (typically, <30 mm total length, TL) and adults (>30 mm TL), whereas in other taxa (e.g., catostomids and ictalurids), the large size class (>60 mm TL) represented adults and subadults (hereafter referred to as adults).

**Habitat**

Stream habitat was quantified at a variety of spatial scales. Stream segments, classified as units of stream between tributary confluences that ranged in length from 0.1 skm to 33.4 skm, were quantified from a stream network derived from a modified version of the national hydrography data set (NHD; USGS 2006b) using ArcGIS 9.2 software (ESRI 2006). Strahler stream order and basin area for stream segments were used to quantify stream size and spatial position within a drainage network. Downstream order (dorder) and distance from the mainstem were used to quantify downstream stream size and downstream spatial position within a drainage network and connectivity to other habitats (Table 1). For the Kansas basin, the mainstem river was defined as ≥5th-order stream and distances were calculated as the distance (skm) between the collection site and the nearest mainstem stream segment. At the basin scale, Universal Transverse Mercator easting coordinates represented an east to west gradient of precipitation, land use, and geography that correspond to changes in fish assemblage structure (Metcalf 1966).

Habitat quantification at the three local tributary sites and the mainstem Kansas River was similar to the EPA-EMAP physical habitat protocol (Lazorchak et al. 1998). At each collection site, width measurements were collected along 10 transects that represented the area sampled, except for Kansas River sites, which only had five transects due to homogeneous habitat. Depth, width, and substrate were quantified along 10 transects in the sampling site. Depth and dominant substrate were recorded every metre. Proximity to the Kansas River was measured from the NHD as the distance (skm) from each sampling site to the Kansas River.

**Data analyses**

**Relations between fish assemblages, stream size, and season**

As a first step in our analysis, we quantified patterns of assemblage structure across a gradient of stream size (i.e.,...
Table 2. Number of fish collected and their relative abundance, percentage of total individuals, and occurrences across 17 sample sites and three seasons from three tributaries of the Kansas River (Clarks, McDowell, and Wildcat creeks).

<table>
<thead>
<tr>
<th>Species</th>
<th>Scientific name</th>
<th>Species code</th>
<th>Total abundance</th>
<th>Relative abundance</th>
<th>Summer</th>
<th>Fall</th>
<th>Spring</th>
</tr>
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<tr>
<td>Yellow bullhead</td>
<td>Ameiurus natalis</td>
<td>AMENAT</td>
<td>1 &lt;0.0</td>
<td>1</td>
<td>1</td>
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<td></td>
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<tr>
<td>Freshwater drum</td>
<td>Aplodinotus grunniens</td>
<td>APLGRU</td>
<td>68 0.1</td>
<td>1</td>
<td>19</td>
<td>4</td>
<td>48</td>
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<tr>
<td>Central stoneroller</td>
<td>Campostoma anomalum</td>
<td>CAMANO</td>
<td>2 112 2.2</td>
<td>885</td>
<td>1 193</td>
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<td>34</td>
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<td>River carpsucker</td>
<td>Carpiodes carpio</td>
<td>CARCAR</td>
<td>681 0.7</td>
<td>608</td>
<td>26</td>
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<td>47</td>
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<tr>
<td>White sucker</td>
<td>Catostomus commersonii</td>
<td>CATCOM</td>
<td>23 &lt;0.0</td>
<td>20</td>
<td>6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Common carp</td>
<td>Cyprinus carpio</td>
<td>CYPARC</td>
<td>102 0.1</td>
<td>32</td>
<td>7</td>
<td>4</td>
<td>63</td>
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<tr>
<td>Red shiner</td>
<td>Cyprinella lutrensis</td>
<td>CYPLUT</td>
<td>46 973 48.8</td>
<td>13 54 16</td>
<td>20 950</td>
<td>17</td>
<td>12 178</td>
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<td>Gizzard shad</td>
<td>Dorosoma cepedianum</td>
<td>DORCEP</td>
<td>693 0.7</td>
<td>63</td>
<td>577</td>
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<td>Johnny darter</td>
<td>Etheostoma nigrum</td>
<td>ETHNIG</td>
<td>599 0.6</td>
<td>339</td>
<td>236</td>
<td>14</td>
<td>24</td>
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<tr>
<td>Orangemouth darter</td>
<td>E. spectabile</td>
<td>ETHSPE</td>
<td>1 562 1.6</td>
<td>541</td>
<td>745</td>
<td>12</td>
<td>276</td>
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<tr>
<td>Western mosquitofish</td>
<td>Gambusia affinis</td>
<td>GAMAFF</td>
<td>5 237 5.4</td>
<td>1 387</td>
<td>3 641</td>
<td>17</td>
<td>209</td>
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<tr>
<td>Channel catfish</td>
<td>Ictalurus punctatus</td>
<td>ICTPUN</td>
<td>113 0.1</td>
<td>51</td>
<td>52</td>
<td>11</td>
<td>10</td>
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<tr>
<td>Green sunfish</td>
<td>Leptosyn hynemus</td>
<td>LEPHY</td>
<td>227 0.3</td>
<td>55</td>
<td>51</td>
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<td>121</td>
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<tr>
<td>Orangespotted sunfish</td>
<td>L. humilis</td>
<td>LEPHUM</td>
<td>3 330 3.5</td>
<td>164</td>
<td>2 446</td>
<td>17</td>
<td>720</td>
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<td>LEPMAC</td>
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<td>2 59</td>
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<td>124</td>
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<td>Largemouth gar</td>
<td>Lepisosteus osseus</td>
<td>LEPOS</td>
<td>67 0.1</td>
<td>61</td>
<td>1</td>
<td>1</td>
<td>5</td>
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<tr>
<td>Common shiner</td>
<td>Luxilus cornutus</td>
<td>LUXCOR</td>
<td>232 0.2</td>
<td>19</td>
<td>77</td>
<td>8</td>
<td>136</td>
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<td>Redfin shiner</td>
<td>Lythrurus unbratilis</td>
<td>LYTUMB</td>
<td>3 889 4.0</td>
<td>3 146</td>
<td>1 991</td>
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<td>Microperostom dolomieu</td>
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<td>13</td>
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<td>Spotted bass</td>
<td>M. punctatus</td>
<td>MICPUN</td>
<td>64 0.1</td>
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<td>Largemouth bass</td>
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<td>MCSAL</td>
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<td>White bass</td>
<td>Morone chrysops</td>
<td>MORCHR</td>
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<td>—</td>
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<td>Shorthead redhorse</td>
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<td>MOXMAC</td>
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<td>NOTATH</td>
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<td>Golden shiner</td>
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<td>Slender madtom</td>
<td>Noturus exilis</td>
<td>NOTEXI</td>
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<td>N. flavus</td>
<td>NOTFLA</td>
<td>662 0.7</td>
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<td>Carmine shiner</td>
<td>Notoperc percolomis</td>
<td>NOTPER</td>
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<td>1 209</td>
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<td>4 246</td>
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<td>Sand shiner</td>
<td>N. stramineus</td>
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<td>1 795</td>
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<td>1</td>
<td>1</td>
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<tr>
<td>Bluntspade minnow</td>
<td>Pimephaeus notatus</td>
<td>PIMNAT</td>
<td>9 499 9.4</td>
<td>801</td>
<td>1 415</td>
<td>17</td>
<td>1 833</td>
</tr>
</tbody>
</table>
basin area) within the Kansas River basin using regression analysis. This characterization was a necessary step because it allowed us to identify species that showed an affinity for mainstems or tributary habitats. For analyses of fish assemblage structure, rare fish species (i.e., occurring at <5% of sample sites) were excluded because they can mask variation in the more abundant species in the assemblage. In addition, we reduced the influence of extreme high abundances with log(\(x + 1\)) transformations. To characterize relationships among sites, we calculated a matrix of assemblage dissimilarities among sites using a Bray–Curtis index and visualized gradients of fish assemblage composition with a principal coordinates analysis (PCoA).

In the three intensively sampled tributaries, we characterized spatial and temporal variation in assemblage structure to evaluate the influence of mainstem rivers within the first 20 km of their confluence. We first tested for differences in fish species richness among three sampling periods (summer, fall, and spring) and streams (Clarks, McDowell, and Wildcat creeks) with analysis of variance (ANOVA). As with the basin-wide analyses, a PCoA was performed to summarize variation in the fish assemblage structure within and among tributaries and among seasons based on a Bray–Curtis dissimilarity matrix. Analysis of similarity (ANOSIM) was used to test for differences in assemblage structure among sample periods and streams. These analyses were conducted using the R statistical package (R Development Core Team 2007).

Relations between fish assemblage structure and distance from mainstem rivers

We used multiple regression models and constrained ordination to test if proximity to mainstem rivers explained a significant amount of variation in assemblage structure, while controlling for longitudinal and stream size gradients within the Kansas River basin. The influence of proximity to mainstem rivers on species richness was made by comparing adjusted \(R^2\) values from models that included stream order and easting (i.e., universal transverse mercator easting coordinates), but differed in the inclusion of proximity to the mainstem river. To evaluate the influence of proximity to a mainstem river on fish assemblage structure, we used a partial constrained analysis of principal coordinates (CAP; Anderson and Willis 2003). CAP is similar to redundancy analysis but allowed us to evaluate the match between environmental variables and variation in fish assemblage structure based on a Bray–Curtis dissimilarity matrix. As in the multiple regression, we controlled for stream order and easting and tested for significance with a permutation test. CAP analyses were performed in the R statistical package version 2.7.2 using the function “capscale” in the vegan library (R Development Core Team 2007). In addition, we ran models with mean abundance of riverine and stream fish as dependent variables to evaluate the use of tributaries by fishes that typically occupy the mainstem river or the avoidance of confluence zones by species that occupy smaller streams. We classified species based on their affinity for stream size (e.g., riverine or stream fishes) using our basin-wide database. Species were classified as riverine if their mean abundance was greater at sites on stream segments \(\geq 5\)th order than at smaller-ordered sites, and classified as stream fish if

### Table 2 (concluded)

<table>
<thead>
<tr>
<th>Species</th>
<th>Scientific name</th>
<th>Total abundance</th>
<th>Sites occupied</th>
<th>Relative abundance</th>
<th>Abundance</th>
</tr>
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<td>Fathead minnow</td>
<td>P. promelas</td>
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<td>1</td>
<td>0.1</td>
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</tr>
<tr>
<td>Bullhead minnow</td>
<td>P. vigilax</td>
<td>3,527</td>
<td>16</td>
<td>3.7</td>
<td>2,624</td>
</tr>
<tr>
<td>White crappie</td>
<td>Pomoxis annularis</td>
<td>88</td>
<td>5</td>
<td>0.1</td>
<td>32</td>
</tr>
<tr>
<td>Flathead catfish</td>
<td>Pylodictis olivaris</td>
<td>10</td>
<td>3</td>
<td>&lt;0.0</td>
<td>8</td>
</tr>
<tr>
<td>Creek chub</td>
<td>Semotilus atromaculatus</td>
<td>47</td>
<td>6</td>
<td>&lt;0.0</td>
<td>4</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>96,340</td>
<td>16</td>
<td></td>
<td>23,886</td>
</tr>
</tbody>
</table>

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Their mean abundance was greatest on streams <5th order. Prior to analyses, normality of habitat variables was tested and non-normal variables were log(x + 1)-transformed to reduce the effects of outliers and heterogeneity of variances.

Regression analysis also was used to quantify the association between fish assemblage structure (richness and abundance of river and stream fishes) and habitat measures with distance from the Kansas River at the three intensively sampled tributaries. In addition, we contrasted dissimilarity of sample sites on each of the three tributaries (Clarks, McDowell, and Wildcat creeks) with that of the Kansas River for all sampling periods using a Bray–Curtis dissimilarity index. Means and standard deviations of Bray–Curtis indices were calculated by combining data from all sampling periods for each site and examined as a function of distance from the mainstem Kansas River.

We separately tested the association in abundance of adults and juveniles of 18 species with distance from the mainstem using regression analyses. We were unable to consider other species because we did not capture both life stages in high enough abundance to conduct the regression analysis. Coefficients of determinations ($r^2$) were used to characterize the deviation in longitudinal structuring between adult and juvenile fishes.

**Connectivity**

To test the prediction that streams sharing their confluences with larger-order streams would have greater mean species richness and different assemblage structure than streams that shared their confluence with smaller-order tributaries, we evaluated differences in mean species richness, abundances of riverine and stream fishes, and assemblage structure among sites on stream segments with the same stream order, but differing downstream orders, using a one-way ANOVA for richness and ANOSIM for assemblage structure. If the ANOVA results were significant, a post hoc least significant difference (LSD) test was run on the comparison of mean...
Results

Effects of stream size and season on fish assemblage structure

Sixty-eight species of fish representing 39 genera in 14 families were collected from the 413 sites in the Kansas basin. Cyprinids were the dominant family, comprising 84% of the total individuals captured, followed by centrarchids (8%) and percids (4%). The number of sites visited ranged from four in 8th-order streams to 154 in 3rd-order streams. There was a significant increase in the number of fish species with drainage area for both eastern and western portions of the Kansas basin ($P = <0.01$, $r^2 = 0.14$, $r^2 = 0.13$, respectively; Fig. 3). A similar trend was observed for the Missouri tributary sites, but this was not significant ($P = 0.14$, $r^2 = 0.03$).

Local fish assemblage structure also varied with stream size, as characterized with PCoA (Fig. 4; 1st axis eigenvalue, 21.4; 2nd, 13.9; and 3rd, 10.9). The first axis represented a gradient of stream size with sites in larger streams having a positive association with this axis and small streams having a negative association (Fig. 4). Examples of fishes associated with larger streams were *Aplodinotus grunniens*, *Pylodictis olivaris*, and *Dorosoma cepedianum*, and fishes associated with small streams were *Phoxinus erythrogaster*, *Etheostoma spectabile*, and *Luxilus cornutus*. Axis 2 likely represented an east to west gradient because of the large positive loadings of *Fundulus kansae*, a species restricted to western Kansas, in contrast to negative loadings of species such as *Percina caproideus*, which are more abundant in eastern Kansas. Axis 3 was likely a gradient from low to high gradient streams, as inferred by the high loadings of fishes typical of small streams (e.g., *Petenagonon crysoleucus*).

Thirty-nine species of fish representing 29 genera in nine families were collected during the intensive sampling of the three local tributaries (Table 2). Repeated-measures ANOVA indicated that species richness varied by season ($P = 0.03$), with richness generally lower in spring than in summer and fall. There was no significant difference in richness among tributaries or interaction among seasons and tributaries. ANOSIM results indicated that assemblages in McDowell and Clarks creeks were distinct from those in Wildcat Creek (Global $R = 0.192$, $P = 0.08$) and that there were distinct assemblages among the three sample seasons (Global $R = 0.461$, $P = 0.001$). A PCoA (Fig. 5; 1st axis eigenvalue, 1.20; 2nd, 0.82; and 3rd, 0.65) illustrated these differences and indicated a relationship between proximity to the mainstem and assemblage structure. The 1st axis described a gradient of proximity to the Kansas River having a positive association with this axis, whereas streams that are farther from the Kansas River had a negative association with this axis. The species most closely associated with the Kansas River was *A. grunniens*. Fishes having a positive association with axis 1 (i.e., further away from the mainstem) were typical stream species such as *Camposostoma anomalum*, *Notropis percobromis*, *Noturus exilis*, *E. spectabile*, and *E. nigrum*. Fish species that had a negative association with axis 2 occurred in higher abundance in confluence zones (e.g., *Micropterus punctulatus*, *Pimephales promelas*, and *Lepomis macrochirus*), with the one exception being juvenile *P. erythrogaster*, which occurred after a spring flood event downstream of a tributary confluence. The 3rd axis was not associated with proximity to mainstem, rather it described a gradient across sampling periods, with the summer and fall sampling periods having negative associations with
this axis and the spring sampling period having a positive association. Fishes collected in higher abundance in the summer were *Lepisosteus osseus*, *Carpiodies carpio*, and *D. cepedianum*. Fishes that occurred in higher abundance during spring were *P. erythrogaster*, *P. promelas*, and *L. cornutus*.

### Effects of distance from mainstem rivers on fish assemblage structure

Multiple regression models that predicted fish species richness in the Kansas basin indicated that stream order and easting were significantly associated with richness, whereas proximity to a mainstem river explained little additional variation (<2% change in adjusted $R^2$; Table 3). A partial CAP analysis indicated a significant effect of proximity to mainstem rivers after controlling for stream order and easting ($F = 4.36, P = 0.005$). However, proximity only explained 1.1% of the unconstrained variation in fish assemblage structure (full constrained ordination including stream order and easting explained 14.7% of unconstrained variation).

Consistent with this large-scale pattern, fish assemblages changed abruptly between sites on the mainstem Kansas River and those on the three intensively sampled tributary streams. Bray–Curtis dissimilarity of fish assemblages in tributary sites compared with Kansas River sites increased abruptly with distance from the Kansas River. However,
after this abrupt shift in assemblage structure, there was only a slight divergence from the mainstem fish assemblage with increasing distance from the Kansas River (Fig. 6). Fishes driving these changes as distance increased from the Kansas River were stream fishes that were collected only at the sites farthest away. Increases in the abundance of stream fish with distance from the mainstem Kansas River were significant in the summer and fall sampling periods (\(P < 0.01\) and \(P < 0.01\), respectively), but this same pattern was not seen in the spring sampling period (Fig. 7). The relationships between distance from the mainstem Kansas River and abundance of 18 fish species, with both adults and juveniles collected during sampling periods, suggested that adults were more structured along this gradient than juveniles (Fig. 8). Coefficients of determinations (\(r^2\)) describing this relationship ranged from approximately 0.00 to 0.14 with a mean of 0.03 for juvenile fishes and approximately 0.00 to 0.42 with a mean of 0.12 for adults.

The most notable association between physical habitat and distance from the Kansas River was in the proportion of coarse substrate (\(r^2 = 0.285\), \(P = 0.040\)), which was generally <40% in the first 2 km of local tributaries and increased to around 70% at sites >2 km from the mainstem (Fig. 9). There was no significant difference in mean depth (range: Clarks Creek, 20.6–16.3 cm; McDowell Creek, 21.1–93.2 cm; Wildcat Creek, 26.2–110.7 cm) or width (range: Clarks Creek, 5.1–52.8 m; McDowell Creek, 4.4–23.0 m; Wildcat Creek, 10.0–21.3 m) with distance from the mainstem (\(P\) values > 0.440).

Effects of connectivity on fish assemblage structure

Not all combinations of joining streams of different orders were represented in the basin-wide data set, thus we only considered network combinations for which we had adequate data to statistically test patterns (i.e., \(N > 4\)). Of those, there was a general trend that stream segments sharing their confluences with larger mainstem tributaries had higher mean species richness than segments that shared their confluence with smaller-order tributaries (Figs. 10a, 10e, 10i). Fish assemblages also differed among streams with different levels of connectivity. Assemblage structure in 1st-order streams was dependent on connection with 2nd-, 3rd-, and 4th-order streams (ANOSIM Global \(R = 0.315\)). This can be visualized by increasing PCoA axis 1 scores for 1st-order sites as the stream order of connecting streams increased (Fig. 10b). Assemblages in sites on 2nd-order streams connected to 3rd-order streams were different than sites on 2nd-order streams connected to 2nd-, 4th-, or 7th-order streams (Global \(R = 0.081\)), and this is reflected with PCoA axis 3 scores (Fig. 10f). Fish assemblages in 3rd-order streams were marginally associated with connection to other streams (Global \(R = 0.064\)), and there was a trend (\(P > 0.059\)) for differences in fish assemblage structure of 3rd-order streams connected to 4th-order streams than those connected to 3rd- or 8th-order streams (Fig. 10j). First-order streams that share their confluences with 3rd- or 4th-order tributaries had significantly (\(P < 0.01\)) higher riverine fish abundance than streams that share their confluences with 2nd-order tributaries (Fig. 10c). Third-order streams that...
share their confluences with 3rd- and 4th-order tributaries had significantly ($P < 0.01$) different abundances of stream fishes (Fig. 10). There was no difference in mean stream fish abundance in 1st- or 2nd-order sites for sites with differing downstream orders.

**Discussion**

By characterizing patterns of assemblage structure at the basin and individual tributary scales, we developed a thorough evaluation of factors influencing local fish assemblage structure in the Kansas River basin. The basin-wide analysis was coarse but gave us a greater number of samples and a wide variety of network combinations (e.g., probability of different-order streams having their confluences with one another) to quantify the influence of connectivity and proximity on fish assemblage structure. When considering both stream segments that shared a confluence with mainstem rivers and those that do not, we only detected a marginal influence of proximity to the mainstem on fish assemblage structure, thus rejecting our hypothesis of network dispersal. However, the significant influence of downstream order on fish assemblage structure in stream segments directly connected to mainstem rivers supports the hypothesis of confluence exchange and a more localized effect of downstream habitats. Moreover, when evaluated at a finer spatial scale (i.e., during intensive sampling of sites in three mainstem tributaries that were <20 km from the confluence), we found fish assemblages at sites near the Kansas River to differ from the mainstem assemblage, but those differences associated with proximity to the source were primarily related to the reduced abundance of small stream fishes near tributary confluences. Combining these analyses suggests a relatively localized exchange of biota (i.e., confluence exchange) between mainstem rivers and their tributaries. This is not to say that periodic events or migrations that are important to the persistence of the species do not occur, but long-term monitoring at a finer temporal scale may be necessary to evaluate the importance of these rare events.

Our results are consistent with previous research that noted an association between fish assemblage structure and the presence of mainstem rivers (Hitt and Angermeier 2006; Hitt and Angermeier 2008) and reservoirs (Falke and Gido 2006b) downstream from sample sites. In these studies, however, downstream habitats had the most notable influence on fish assemblages in medium-sized tributaries. Hitt and Angermeier (2006) suggested that increased fish species richness and increased riverine species richness in 3rd-order and larger tributaries of larger rivers were mediated through microhabitat complexity and channel shape. We found larger differences in assemblage structure of 1st-order streams draining into larger streams and hypothesize that the isolation of these small streams may result in a reduction of obligate small-stream fishes, while allowing the immigration of small-bodied larger river fishes, such as red shiners. The latter is probably the case in the Kansas River basin, as abundance of larger river species also increased as 1st-order streams drained into larger streams.

The presence of riverine fishes in smaller streams above tributary junctions could be associated with reproduction and spawning migrations. Hitt and Angermeier (2008) noted that tributaries were used for nursery and spawning habitat by riverine species such as catostomids and cyprinids, which were higher in abundance and more species-rich in mainstem tributaries than in headwater tributaries. In contrast to this result, abrupt changes in assemblage structure in the intensively sampled tributaries were primarily driven by the lack of small stream fish (e.g., *Luxilus cornutus*, *E. spectabile*, and *C. anomalum*) near mainstem rivers, rather than the presence of large river fishes. The primary exception to this was *P. vigilax*, which generally decreased in abundance with distance from the mainstem river. The absence of small stream species near confluences with mainstem rivers may be due to increased turbidity, changes in habitat (e.g., substrate), or biotic interactions. Indeed, changes in fish assemblage structure coincided with abrupt changes in habitat between mainstem rivers and their tributaries, with the lower portions made up of more homogeneous floodplain habitat types with finer substrates. These deeper homogenous floodplain ecotones also might allow predatory fishes to persist in the assemblage for a short distance in these transitional zones of tributaries and their mainstem. As our data do not show a marked increase in these predatory species, they may not have been sampled effectively.

Within our three intensively monitored tributary streams, we also found a slight decrease in variability and a decrease in dissimilarity to the mainstem with increasing distance from the Kansas River and variability across sampling periods in fish assemblage. Gorman (1986) speculated that the impact of mainstem fish assemblages on adventitious tributaries is probably significant but noted that these influences were probably temporally variable and synchronized with reproductive seasonal pulses of migrant fishes. Schaefer and Kerfoot (2004) provided empirical evidence of greater species diversity and variability in fish assemblages over time at interface sites of Piasa Creek, Illinois, with declining variability and diversity with increasing distance from the mainstem river over their approximate 60 km study area. Our study indicated a high degree of temporal variation in fish assemblage structure among sampling periods that was confounded by variable abundance of juveniles and adults. Moreover, the abundance of adult fishes was more structured along a gradient of distance from the mainstem than juvenile fishes. More randomly distributed juveniles along a longitudinal gradient could indicate that they are more prone to dispersal, which may be necessary to locate suitable rearing habitat (e.g., shallow, predator-free areas; Harvey 1987). Adults, however, may respond to habitat at larger spatial scales (i.e., longitudinal zonation) that is driven by physical habitat (e.g., depth) or biotic interactions.

Ecological characteristics of fish species are likely to mediate their ability to disperse through stream networks. Many of the species that we captured in mainstem rivers that quickly disappeared in collections upstream of tributary confluences were relatively large-bodied as adults (e.g., *A. granniens, P. olivaris*) and may avoid small tributary streams because shallow, clear water may expose them to terrestrial predators (e.g., *Power et al. 1989*). Other common mainstem species such as *N. stramineus* and *Cyprinella lutrensis* are small-bodied but may avoid streams with low turbidity (Cross and Collins 1995). Although these two species can sporadically occur in mainstem tributaries, sometimes in
high abundance, it is not clear why these species are more dominant in turbid mainstem rivers. Nevertheless, they seem to be at a disadvantage compared with other stream minnow species with similar ecological characteristics (e.g., *Lythrurus umbratilis* and *P. notatus*) that are dominant in tributaries. The avoidance of mainstem rivers and potentially confluence zones by tributary specialists is likely related to habitat, particularly turbidity and substrate. For example, many darters and minnow species require coarse substrates to successfully reproduce.

Conservation implications

Quantifying the linkage between habitats within a stream network can help managers evaluate the relative importance of these disjunct habitats when making decisions on the scale at which to conserve stream organisms. Although our results suggest that many prairie stream fish populations are localized and possibly independent from mainstem river habitats during normal conditions, a number of studies have reported the importance of connectance to refugia habitats after a disturbance in small- to medium-order streams (Bayley and Osborne 1993; Sheldon and Meffe 1994; Lonzarich et al. 1998). Recolonization of fish assemblages in lotic systems can be quite rapid (≤1 year; Detenbeck et al. 1992; Bayley and Osborne 1993), but recolonization rate is dependent on distance from source populations (Sheldon and Meffe 1994; Lonzarich et al. 1998) and the presence of barriers (Detenbeck et al. 1992). Most of these studies cited above were in small- to medium-order streams in which fish assemblages are isolated from source populations and fishes were likely more adapted to rapid recolonization due to the frequent disturbances from floods and droughts (Schlosser 1987). Larger tributary fish assemblages are more apt to be recolonized from source populations of fishes that are not adapted to highly stochastic habitats. These mainstem tributary fish assemblages may be more resilient to extinction risk by being less isolated and closer to source pools and rapidly recolonized via emigration as predicted by island biogeography theory (MacArthur and Wilson 1967).

The importance of connectivity and location within a drainage network is likely to vary among species with different ecological characteristics. In the Great Plains, USA, many species that characterize mainstem river assemblages are in need of conservation, but the importance of tributaries to their conservation is not well understood. Given the recent threats to mainstem rivers, tributaries may be important refugia habitat from pulsed disturbance events in mainstem rivers. Likewise, the role of mainstem rivers as corridors for tributary species is also equivocal, but recent studies suggest that these habitats allow connectance of metapopulations and maintenance of allelic diversity (Skalski et al. 2008). Although our results suggest that biotic exchanges such as these may not be sufficient to result in strong shifts in assemblage structure, the temporal scale of our study was not adequate to evaluate the long-term importance of these network linkages. Long-term management and conservation of fishes will require further evaluation of the influence of connectivity in stream networks and how this influences metapopulation dynamics and overall resiliency of stream biota.

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