Convergence of fish communities from the littoral zone of reservoirs

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SUMMARY

1. Understanding factors that regulate the assembly of communities is a main focus of ecology. Human-engineered habitats, such as reservoirs, may provide insight into these assembly processes because they represent novel habitats that are subjected to colonization by fishes from the surrounding river basin or transported by humans. By contrasting community similarity within and among reservoirs from different drainage basins to nearby stream communities, we can test the relative constraints of reservoir habitats and regional species pools in determining species composition of reservoirs.

2. We used a large spatial database that included intensive collections from 143 stream and 28 reservoir sites within three major river basins in the Great Plains, U.S.A., to compare patterns of species diversity and community structure between streams and reservoirs and to characterize variation in fish community structure within and among major drainage basins. We expected reservoir fish faunas to reflect the regional species pool, but would be more homogeneous that stream communities because similar species are stocked and thrive in reservoirs (e.g. planktivores and piscivores), and they lack obligate stream organisms that are not shared among regional species pools.

3. We found that fish communities from reservoirs were a subset of fishes collected from streams and dominant taxa had ecological traits that would be favoured in lentic environments. Although there were regional differences in reservoir fish communities, species richness, patterns of rank abundance and community structure in reservoir communities were more homogonous across three major drainage basins than for stream communities.

4. The general pattern of convergence of reservoir fish community structure suggests their assembly is constrained by local factors such as habitat and biotic interactions, and facilitated by the introduction of species among basins. Because there is a reciprocal transfer of biota between reservoirs and streams, understanding factors structuring both habitats is necessary to evaluate the long-term dynamics of impounded river networks.

Keywords: community assembly, community structure, environmental filters, homogenization, introduced species

Introduction

A main focus of community ecology is to understand factors that regulate the assembly of communities across space and time (Weiher & Keddy, 1999). The experimental defaunation of natural habitats or monitoring of colonization of newly created habitats can aid in understanding assembly rules (e.g. Simberloff

& Wilson, 1969; Capone & Kushlan, 1991; Rodriguez, 1994; Arrington, Winemiller & Layman, 2005). Unfortunately, many such experimental studies are limited by spatial and temporal scale or are not well replicated (Schindler, 1987; Samuels & Drake, 1997; Chase, 2003). Large-scale changes to ecosystems by humans may provide insight into factors structuring communities at larger spatial scales. For example, species invasions have been used to test patterns of community saturation across large geographic regions (Ross, 1991; Sax, Stachowicz & Gaines, 2005). Human-engineered habitats, such as reservoirs, may also provide insight into rules governing the assembly of communities because they represent novel habitats (sensu Hobbs *et al.*, 2006) with relatively well-known colonization pools from surrounding rivers and streams or through human transport. Moreover, reservoirs are highly replicated within and among drainage basins that represent distinct zoogeographical boundaries. We propose that reservoir ecosystems can be used to test if fish communities that differ in regional species pools converge towards a similar community type in these novel habitats.

The convergence or divergence of communities has been tested across a variety of spatial and temporal scales (Samuels & Drake, 1997; Chase, 2003). Tests of convergence at evolutionary time scales have focused on variation in community structure (e.g. ecological traits among community members) among continents (Orians & Paine, 1983; Schluter, 1986). Tests focused at ecological time scales have manipulated initial community composition or the sequence of colonization and followed trajectories of community development (Drake, 1991; Sommer, 1991; Matthews & Marsh-Matthews, 2006). Characterizing the development of reservoir communities provides a test of community assembly by tracking the dependence of these communities on species present in the surrounding streams and the sequences of species colonizing these habitats.

The assembly of reservoir fish communities can be conceptualized under the framework of environmental filters (Smith & Powell, 1971; Tonn, 1990) that includes: (i) a species pool filter; (ii) an environmental filter and (iii) a biotic interactions filter. The regional species pool for reservoirs is probably greater than that of streams because species colonize from tributary streams as well as from intentional and unintentional species introductions that include exotic species

from other regions (Moyle, 1986; Havel, Lee & Vander Zanden, 2005; Fig. 1). Once fishes are transported to a reservoir, their ecological traits must match the environment in order to establish a reproducing population. Heterogeneous environments within reservoirs can support diverse fish communities (Matthews, Gido & Gelwick, 2004). For example, habitats vary longitudinally, allowing reservoirs to be classified into three distinct zones: riverine, transitional and lentic (Thornton, Kimmel & Payne, 1990). Shallow littoral habitats in reservoirs have the highest potential to maintain populations of native riverine species (Fernando & Holčík, 1991). Major challenges for fishes in reservoirs are that littoral zones vary in exposure to wind-waves from the ends to the mouth of coves (Lienesch & Matthews, 2000) and fluctuating water levels (Ploskey, 1986; Cohen & Radomski, 1993; Irz *et al.*, 2002). Assuming species are able to find suitable physical and chemical habitat in reservoirs, they also must avoid negative species interactions. Although not well studied and difficult to document, there are examples of competitive exclusion within reservoirs (e.g. McComas & Drenner, 1982). In addition, piscivore abundance in reservoirs can be high, limiting the occurrence of susceptible prey species (Nobel, 1986; Paller, 2005). Although some fluvial specialists cannot complete their entire life cycle because of these limiting factors, many fishes may use reservoirs as temporary staging areas (e.g. Herbert & Gelwick, 2003).

Whereas much ecological research in reservoirs has focused on population dynamics of sport fishes, few studies have evaluated variation within and among entire reservoir fish communities. As such, it is not clear if reservoir communities converge toward a similar suite of species across regions, or if the local species pool determines the community within these habitats. Variation in temperature, surface area, basin area, depth and productivity are drivers of fish community structure among reservoirs (Godinho, Ferreira & Portugal e Castro, 1998; Irz *et al.*, 2002; Carol *et al.*, 2006; Han, Fukushima & Fukushima, 2008). Variation among reservoirs also can be attributed to age (e.g. Irz *et al.*, 2002), as new impoundments undergo a predictable increase in productivity followed by a gradual decline as nutrients from inundated vegetation and soils are depleted (Kimmel & Groeger, 1986). Irz, Argillier & Oberdorff (2004) found that native fish diversity in reservoirs in France

Fig. 1 Conceptual model of processes influencing assembly of reservoir and stream fish communities. Arrows represent vectors of dispersal for fish species; movement by fluvial specialists indicated by black arrows and habitat generalists by grey arrows. Human assisted transport includes movement of species within the continent as well as exotic species from outside the continent. Habitat filters are represented by horizontal dashed lines. Line thickness reflects the strength of the vector.
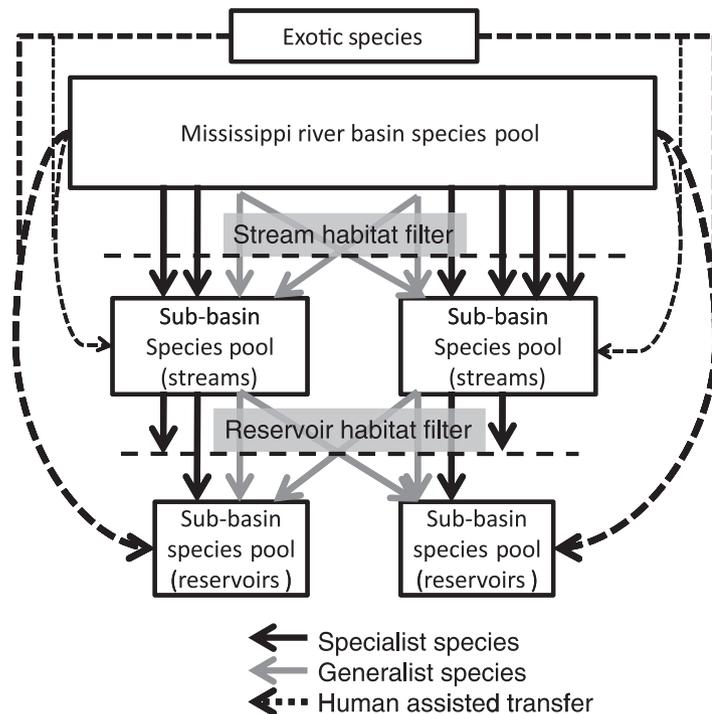
was positively correlated with regional richness, but in a complementary study (Irz *et al.*, 2006) the same authors found no difference in mean local species richness among lakes, reservoirs and rivers. Han *et al.* (2008) also found a positive association between total species richness and exotic species richness in Japanese reservoirs, and that more exotic species also tended to occur near developed areas, suggesting human transport was an important factor determining the presence of exotic fishes. In general, the importance of abiotic factors influencing reservoir fish communities is well documented (e.g. Matthews *et al.*, 2004), but the importance of regional species pools in structuring these communities is equivocal.

We used a large spatial database that included fish community and habitat data collected within three major river basins in the Great Plains of the U.S.A. to contrast factors driving assembly of fish communities in streams with those in littoral habitats of reservoirs. Our main objectives were to (i) compare patterns of species diversity and community structure between streams and reservoirs and (ii) characterize variation in fish community structure within and among major drainage basins. We expected reservoir communities to be more homogeneous across basins than stream communities because reservoirs limit the colonization

and success of obligate stream organisms that are not shared among basins (Fig. 1). In addition, reservoirs are more suitable for lentic specialists (e.g. planktivores and piscivores), and the probability of these species being shared among basins is greater because introductions are associated with sport fisheries. Alternatively, reservoirs may serve as temporary habitat for many stream fishes that require fluvial habitats to complete their life cycles. Thus, variation in species pools of stream fishes among drainage basins also may be reflected in reservoir communities.

Methods

Study area

Fish community records for 28 reservoirs located in the Great Plains portions of the Missouri, Arkansas and Red River basins were compiled for this analysis. We only selected reservoirs in which the littoral zone had been sampled in at least three different years to adequately characterize the fish assemblage. Characteristics of size and age of reservoirs varied considerably within basins (Table 1). Surface areas of these reservoirs ranged from 1085 to 41 728 ha and construction date ranged from 1937 to 1981. In addition,

	Missouri	Arkansas	Red
Reservoir			
Drainage area (km^2)	5358 (8021)	26 049 (42 443)	8582 (17 415)
Longitude	−96.74 (1.61)	−96.37 (1.11)	−96.35 (1.34)
Latitude	38.84 (0.51)	36.45 (0.79)	34.24 (0.44)
Dam height (m)	42 (9)	35 (11)	41 (19)
Surface area (km^2)	67.7 (59.2)	92.7 (106.4)	80.4 (88.3)
Conservation pool volume (m$^3 \times 10^6$)*	260.5 (125.8)	594.4 (817.0)	1025.0 (1,363.9)
Year of construction	1968 (8)	1959 (12)	1960 (18)
Rarified richness	19.8 (2.8)	25.9 (5.1)	26.4 (7.2)
Streams			
Drainage area (km^2)	4245 (7,479)	9668 (15 188)	8608 (15 210)
Longitude	−97.46 (1.94)	−98.13 (1.77)	−96.79 (1.80)
Latitude	39.20 (0.43)	37.22 (1.02)	34.21 (0.42)
Rarified richness	12.3 (4.0)	15.7 (7.4)	27.8 (10.1)

Table 1 Mean (SD) physical characteristics and rarified species richness for reservoirs and streams in the Missouri, Arkansas and Red river basins in the Great Plains, U.S.A.

*Conservation pool volume is the storage used to meet authorized purposes of each reservoir (e.g. water supply, water quality, navigation and recreation).

stream fish community data from 143 locations in the same river basins were used to contrast community structure between reservoirs and streams. The spatial extent of our study region included strong gradients of rainfall (decreasing mean annual precipitation from east to west) and temperature (decreasing mean annual temperature from south to north). Fish diversity generally tracked precipitation and temperature, as fish communities are generally more diverse in warmer regions with greater rainfall (Gido, Schaefer & Pigg, 2004).

Fish collections

Fish surveys from Oklahoma reservoirs were conducted by the Oklahoma Department of Environmental Quality (ODEQ) between 1977 and 1994. Fishes were collected by seining 100–200 m of shoreline habitat for approximately 1 h. Collections from Kansas reservoirs were part of long-term monitoring conducted by the Kansas Department of Wildlife and Parks (KDWP) between 1980 and 2005. These surveys included numerous sampling gears, but we limited our analyses to fishes collected with beach seines with dimensions 15.2 × 1.8 m and a mesh size of 6.4 mm. Data from three additional reservoirs were taken from Strakosh (2006), and were collected by multiple-pass backpack electrofishing of littoral habitats in six coves per reservoir over a 4-year period.

Fish occurrence and abundance data from streams came from standardized surveys by the ODEQ and

the KDWP. The ODEQ collections included 34 sites, sampled between 1977 and 1994 using a standardized sampling effort for each collection. Twenty seine hauls, 10 m in length, were taken at each site with a 3 × 1.5 m (4.7 mm mesh) heavy leaded seine for approximately 1 h sampling per site. Thus, we had both species incidence and abundance data; abundance was standardized as the number of fish collected along 200 m of stream in 1 h of sampling. When more than one sample was taken at a site in the same year, abundance of each species was averaged for the year and species were considered present if recorded during any of the visits. Although species abundance may be quite variable between June and August due to spawning and recruitment, we felt an average of these samples would be most comparable with other sites that were only sampled once, typically during July. Specimens were preserved in 10% formalin and representative collections from 1992 to 1994 are archived at the Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma, U.S.A.

Fish surveys of Kansas streams included 99 sites visited between 1995 and 2001 as part of KDWP annual surveys. The sampling protocol followed that of the United States Environmental Protection Agency's Environmental Monitoring and Assessment Program (Lazorchak, Klemm & Peck, 1998). At each sample site, a reach that was 40 times the average wetted width of the stream channel (minimum 150 m and maximum 300 m) was sampled with a combination of straight

and bag seine (4.7 mm mesh) hauls and a single pass with a DC-pulsed backpack electrofishing unit. Voucher specimens were preserved and archived at the Sternberg Museum of Natural History (Fort Hays, Kansas) or the Kansas Museum of Natural History (Lawrence, Kansas).

In reservoirs and larger rivers, collections made with seines and backpack electrofishing units as the sole sampling methods are biased towards small-bodied fishes that occur near shore. Large-bodied fishes that occur in mid-channel or off-shore habitats or that were able to avoid capture were probably underestimated in our sampling (Utrup & Fisher, 2006), although we did catch many juveniles of such species. Moreover, in some of the larger river sites, by sampling less than 300 m of shoreline, rare species that would have been caught with greater sampling effort may have been missed (e.g. Angermeier & Smogor, 1995). These sampling limitations limit our conclusions to spatial and temporal patterns of relatively common, small-bodied fishes.

Data analysis

Comparisons of community structure between reservoirs and streams. Contrasting fish community structure between reservoir littoral zones and streams allowed us to characterize the use of reservoir habitats by fishes from their surrounding drainage basin. We first quantified associations between species richness and drainage basin area for each of the three major river basins. Because sampling gear and effort varied across sites and states, we calculated a rarefaction estimate of species richness (Gotelli & Entsminger, 2008). Rarefaction estimates were based on the random selection of a set number of individuals ($N = 1000$ for this study) from a given collection and calculating the expected number of species if only that number of individuals was collected at all sites. Because rarified richness values can mask variation attributed to environmental conditions rather than sampling effort, we also calculated the average species richness per sample and ran our statistical analyses with both data sets. Because results were comparable, we only present analyses on rarified species richness.

Second, we developed species rank-abundance curves based on the proportion of sites occupied and mean relative abundance of species across sites for streams and reservoirs in each major river basin.

Both linear and nonlinear models were evaluated and the slope of the best model was compared between reservoirs and streams, and across basins.

Finally, we characterized community similarity with both quantitative and qualitative similarity indices among sites using Bray–Curtis and Jaccard's similarity indices. Non-metric multidimensional scaling (NMDS; based on Bray–Curtis similarities) was used to visualize differences among samples in ordination space. Species loadings for each NMDS axis were determined by correlation coefficients between a species' relative abundance and axes scores. Species which showed a relatively strong association ($r > 0.40$ or $r < −0.40$) with axes scores were used to describe patterns of variation along those axes.

An indicator species analysis (Dufrene & Legendre, 1997) was used to identify species that were most representative of stream and reservoir habitats. Indicator values are calculated as the product of the relative frequency and relative average abundance with habitat types. Indicator values range from 0 to 100 (an abundant species with perfect fidelity to a habitat), with their significance judged via a permutation procedure. NMDS and indicator species analyses were conducted using ʀ version 2.6 (http://www.r-project.org) (R Development Core Team, 2007).

Variation in fish community structure within and among major drainage basins. We used a series of regression models and constrained ordination to test the relative importance of habitat structure and regional species pools in regulating fish community structure in reservoir littoral zones. We conducted similar analyses with stream fish communities as a baseline from which to compare patterns of variation observed for reservoir communities. An information-theoretic approach (Burnham & Anderson, 2002) was used to find the most parsimonious set of independent variables to predict rarified species richness in reservoirs and streams within our study area. Two sets of candidate models (predicting stream and reservoir species richness) containing sets of explanatory variables of biological significance were selected *a priori* and analysed independently. Covariates incorporated into the reservoir models included aspects of reservoir size (dam height and surface area; Table 1), shoreline development index (McMahon, Zale & Orth, 1996),

and drainage basin area to reflect variation in habitat structure among reservoirs independent of spatial location. We also included longitude in the reservoir models to reflect gradients in precipitation, which decreases from east to west. We included occurrence in one of the three major drainage basins as a categorical variable in candidate models to reflect differences likely attributed to differences in regional species pools among basins. For stream richness models, we included drainage basin area and longitude as covariates to reflect major habitat gradients as well as major drainage basin to reflect regional species pools. 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. All models were analysed using PROC REG in SAS (version 9.1; SAS Institute, Inc. 2003).

To test the associations of drainage basin characteristics (e.g. stream size and reservoir area) with community structure among stream and among reservoir samples, we used canonical correspondence analyses (CCA) based on proportional abundance of species at each site. Eigenvalues and site scores for CCA were calculated using CANOCO software, version 4.5 (ter Braak & Šmilauer, 2002). A forward selection procedure was used to select a subset of independent variables that significantly contributed to the variation in the species data for each scale of analysis. In sequential steps, each variable that explained the greatest amount of added variation to the model was included in a Monte Carlo permutation test (1000 iterations) to evaluate if that variable explained a significant ($P < 0.10$) proportion of the species data. Once a variable failed to explain a significant proportion of the variation, no additional variables were added to the model.

We also contrasted the mean similarity of all pairwise comparisons within and among basins for both reservoir and stream fish communities based on species composition and ecological traits of those species. If reservoir communities are constrained by their habitat and converge towards a similar species composition or ecological traits, we would expect the ratio of mean community similarity among drainage basins to that within basins to be much lower for

reservoirs than streams. We used a Bray–Curtis similarity index to quantify similarity in both species composition and trait composition among sites. Ecological traits for fishes were compiled from Goldstein & Meador (2004) and represented trophic level, mode of locomotion, substrate preference, habitat preference (at two spatial scales) and reproductive strategy. We slightly modified the matrix of Goldstein & Meador (2004) by creating a separate trophic class for omnivores, which included species that were classified as both herbivores/detritivores and insectivores. This classification allowed us to evaluate patterns of distribution and abundance for species with broad diets. Next, we summed the proportional abundance of species possessing each trait to give an abundance weighted value for that trait. We used nonparametric multivariate analysis of variance (NPMANOVA; Anderson, 2001) to directly partition among and within basin variability in Bray–Curtis similarity matrices of community structure and species ecological traits. NPMANOVA provides a test statistic (pseudo F) analogous to Fisher's F-ratio. For our analyses, the pseudo F represents the ratio of similarity among basins to within basins with lower values indicating more homogeneous communities or suites of ecological traits among drainage basins. NPMANOVA was conducted with the adonis function in R version 2.6 (http://www.r-project.org).

Results

Comparisons of community structure between reservoirs and streams

Stream collections included 161 species in contrast to 101 species found in reservoirs (Appendices S1 & S2). All 101 reservoir species also occurred in streams. Rarified species richness ranged from 3 to 51 species across stream sites and between 16 and 37 for reservoir sites (Fig. 2). Mean reservoir and stream species richness was greatest in the Red River basin and least in the Missouri River basin. Variation in species richness across drainage basins was greater in streams (range 3–51 species) than reservoirs (range 16–37). Within these river basins, species richness was not strongly associated with catchment area above the site (Fig. 2).

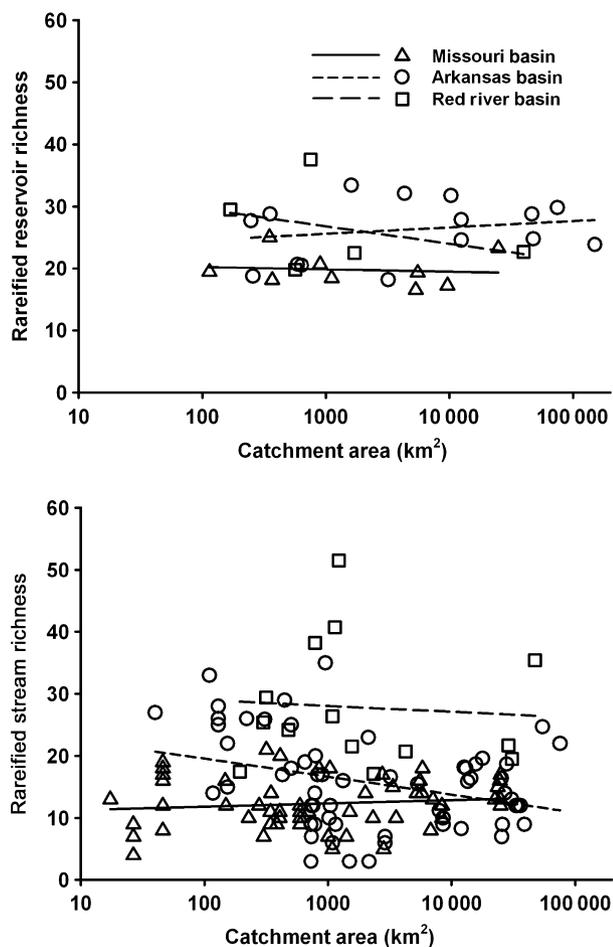The relationship between the per cent of sites occupied and rank abundance for fish species in

Fig. 2 Relationship between drainage basin area and rarified species richness for reservoirs (top panel) and streams (bottom panel) across three river basins in the Great Plains. Shapes represent drainage basins: Triangles = Missouri Basin; circles = Arkansas; squares = Red River.

Fig. 3 Species rank-abundance curves for fish assemblages in streams and reservoirs in three major river basins in the Great Plains. Per cent abundance (*y*-axis) represents the percent of samples sites in which a species occurred.

basin (Table 2). These patterns of similarity can be visualized with NMDS, which showed notable differences between reservoir and stream fish communities in ordination space (Fig. 4). High scores on axis 1 were associated with high relative abundances of red shiner (*Cyprinella lutrensis*) and low scores are associated with high abundances of gizzard shad (*Dorosoma cepedianum*), white bass (*Morone chrysops*), bluegill (*Lepomis macrochirus*) and white crappie (*Pomoxis annularis*). High scores on axis 2 were associated with species that are typically abundant in reservoirs (white bass and gizzard shad), whereas low scores represented stream fish communities with creek chub

streams and reservoirs was best described (r^2-values > 0.94, *P*-values < 0.001) by an exponential decay function ($y = ae^{-bx}$), where *x* is rank abundance of each species and *y* is the per cent of sites occupied by that species. The slope (*b*) of this relationship was more variable among drainage basins for stream fishes than among basins for reservoir fishes (Fig. 3); *b* increased from 0.020 in the Red River to 0.079 in the Missouri River basin for streams, indicating a more even distribution of species abundances in the Red River. In contrast, *b* for reservoirs was similar among drainage basins, only ranging from 0.033 to 0.042.

Mean fish community similarity (based on Jaccard's index) among reservoirs was greater than among streams within the three drainage basins, with the exception of reservoirs and streams in the Red River
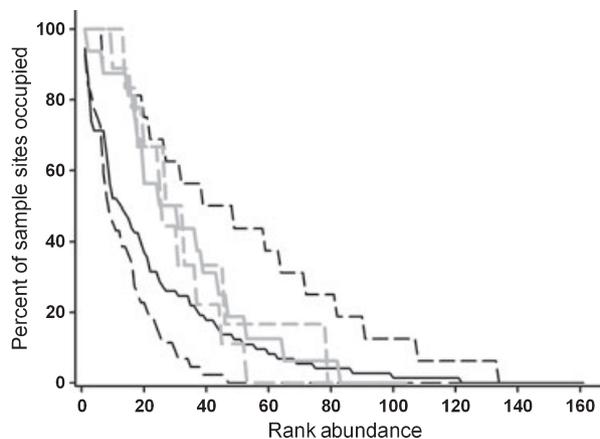
Table 2 Mean similarity of fish assemblages in streams and reservoirs for three drainage basins in the Great Plains

Contrast	Drainage basin	N	Bray–Curtis	Jaccard's
Streams				
Within basins	Missouri	44	39.6	33.0
	Arkansas	73	37.4	29.5
	Red River	16	38.6	39.0
Among basins			32.6	24.6
Reservoirs				
Within basins	Missouri	9	52.7	55.0
	Arkansas	16	50.4	50.1
	Red River	5	46.2	43.6
Among basins			42.7	44.9

Bray–Curtis and Jaccard's similarity indices represent quantitative (based on abundance) and qualitative (based on occurrence) comparisons of assemblage similarity, respectively.
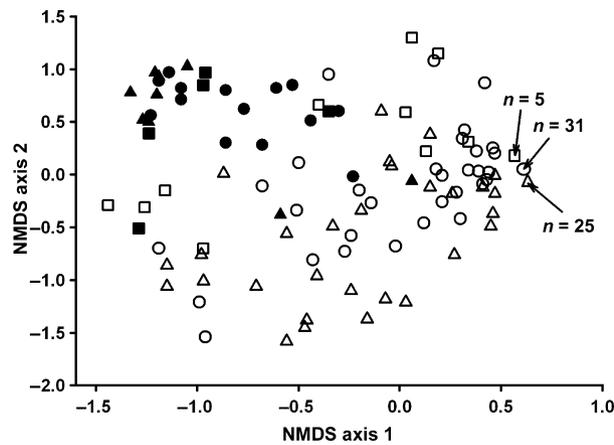
Fig. 4 Non-metric multidimensional scaling (NMDS) used to characterize variation in fish assemblage structure across reservoirs (closed symbols) and streams (open symbols) in the Great Plains, U.S.A. Shapes represent major drainage basins: Triangles = Missouri Basin; circles = Arkansas; squares = Red River. Where there was a high degree of overlap among sites, centroids of multiple points were drawn and the number of sites represented by each centroid is given. This ordination was based on a Bray–Curtis similarity index.

(*Semotilis atromaculatus*), central stoneroller (*Campostoma anamolum*) and orangethroat darter (*Etheostoma spectabile*).

Indicator species analysis showed that 51 of the 161 species had higher indicator values in reservoirs and 35 of those were significant (Appendices S1 & S2). The three dominant indicator species in reservoirs were white crappie, gizzard shad and freshwater drum. There were 110 out of 161 species with higher indicator values in streams but only five were significant [red shiner, sand shiner (*Notropis stramineus*),

fathead minnow (*Pimephales promelas*), suckermouth minnow (*Phenacobius mirabilis*) and creek chub (*S. atromaculatus*)].

Variation in fish community structure within and among major drainage basins

Spatial location, waterbody size and drainage basin accurately predicted rarified species richness in reservoirs and streams. The best model selected by AIC for reservoirs included positive associations between reservoir size (dam height) and longitude, and occurrence outside the Missouri drainage basin ($R^2 = 0.56$; $P < 0.001$). Estimates of the slope of each parameter were significantly different from zero ($P < 0.05$). This model carried 90% of the weight for the set of candidate models (Table 3). No other models had Akaike weights (w_i) greater than 0.10. In summary, species richness in reservoirs was associated both with physical characteristics of the reservoir and the regional species pool as evidenced by the inclusion of river basin identity in regression models.

Species richness in streams was mainly a function of environmental gradients associated with geographic location. Variables in the best stream model indicated increasing richness with increasing longitude, as well as variable richness among river basins ($R^2 = 0.54$, $P < 0.001$; Table 3). Among basins, richness was greatest in the Red River and least in the Missouri River basin. The three models with $w_i > 0.10$ only differed in the inclusion and exclusion of a categorical variable representing each drainage basin. Overall, species richness in reservoirs and streams was influenced by location in the landscape (i.e. river

Table 3 Top multiple linear regression models ($w_i > 0.10$) for predicting species richness in 28 Great Plains reservoirs and 143 streams as determined by Akaike information criterion (AIC) rankings

Model	K	R^2	AIC	AIC_c	w_i
Reservoirs					
Dam height, longitude, Missouri Basin	4	0.56	80.71	98.45	0.90
Global Model	10	0.60	102.16	155.10	–
Streams					
Longitude, Arkansas Basin, Red River Basin	4	0.54	446.50	464.23	0.32
Longitude, Missouri Basin, Red River Basin	4	0.54	446.50	464.23	0.32
Longitude, Missouri Basin, Arkansas Basin	4	0.54	446.50	464.23	0.32
Global Model	6	0.54	453.55	481.55	–

AIC_c, AIC corrected for small sample size; K, number of parameters in the fitted model (including the intercept); ΔAIC_c, difference between the candidate model and the model with the lowest AIC_c.
The Akaike weights (w_i) sum to 1.

basin and longitude, which are associated with trends in precipitation and temperature).

Canonical correspondence analysis of stream assemblages showed a weak association (explaining only 15.6% of the variation on the first two axes) among fish community structure, geographic coordinates, drainage basin area and basin identity (Fig. 5a). Species associated with sites located within the Missouri River basin included stonecat (*Noturus flavus*), slender madtom (*N. exilis*) and golden shiner (*Notemigonus chrysolucas*). Environmental variables explained a greater proportion of variation (25.2%) in reservoir fish communities on the first two axes (Fig. 5b).
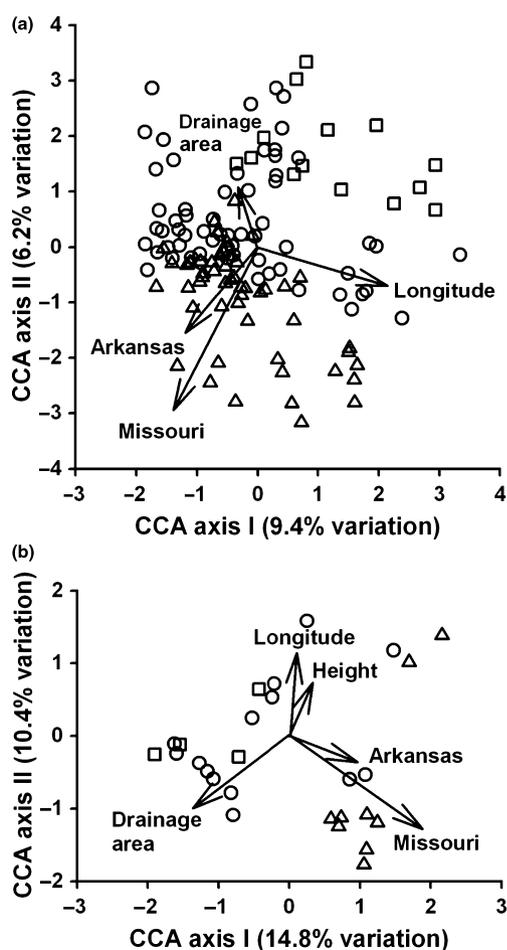
Reservoirs in the Missouri River basin had higher abundances of bluntnose minnow (*Pimephales notatus*), orangethroat darter, black crappie (*Pomoxis nigromaculatus*) and walleye-sauger hybrids (*Sander vitrum × canadensis*), whereas reservoirs within the Red River basin were dominated by inland silverside (*Menidia audens*), ghost shiner (*Notropis buchanani*), common carp (*Cyprinus carpio*), silver chub (*Hybopsis storeriana*) and threadfin shad (*Dorosoma petenense*). These patterns suggest more spatial variability among stream fish communities than among reservoir communities.

Ecological traits of reservoir and stream fish communities were significantly more variable among than within basins (Table 4). However, pseudo *F* values from NPMANOVA were lower in reservoirs than streams, suggesting species in reservoirs were more homogeneous with respect to ecological traits compared to stream species. In general, reservoirs contained a large number of invertivores, planktivores and broadcast spawners, which were mostly restricted to large-river stream habitats in our study basins (Fig. 6).

Discussion

Our analyses contrasted fish communities of streams and reservoirs across three large river basins to

Fig. 5 Canonical correspondence analysis (CCA) used to characterize stream (a) and reservoir (b) fish assemblage structure across three drainage basins in the Great Plains under the constraint of measured environmental gradients. Shapes represent major drainage basins: Triangles = Missouri Basin; circles = Arkansas; squares = Red River. Abbreviations indicate independent variables (Ark, Arkansas River basin; Long, longitude; Lat, latitude; Age, reservoir age).

Table 4 Results of nonparametric multivariate analysis of variance to test whether variability in species and ecological trait data for reservoir and stream fish communities was greater across basins than within basins

Parameter	d.f.	MS	Pseudo *F*	*P*-value
Reservoir (species)				
Basin	2	0.800	3.76	0.001
Residuals	25	0.213		
Total	27			
Stream (species)				
Basin	2	1.265	5.04	<0.001
Residuals	127	0.251		
Total	129			
Reservoir (ecological traits)				
Basin	2	0.203	3.59	0.005
Residuals	25	0.056		
Total	27			
Stream (ecological traits)				
Basin	2	0.328	5.37	<0.001
Residuals	127	0.061		
Total	129			

Larger pseudo *F* values indicate greater variation across basins.
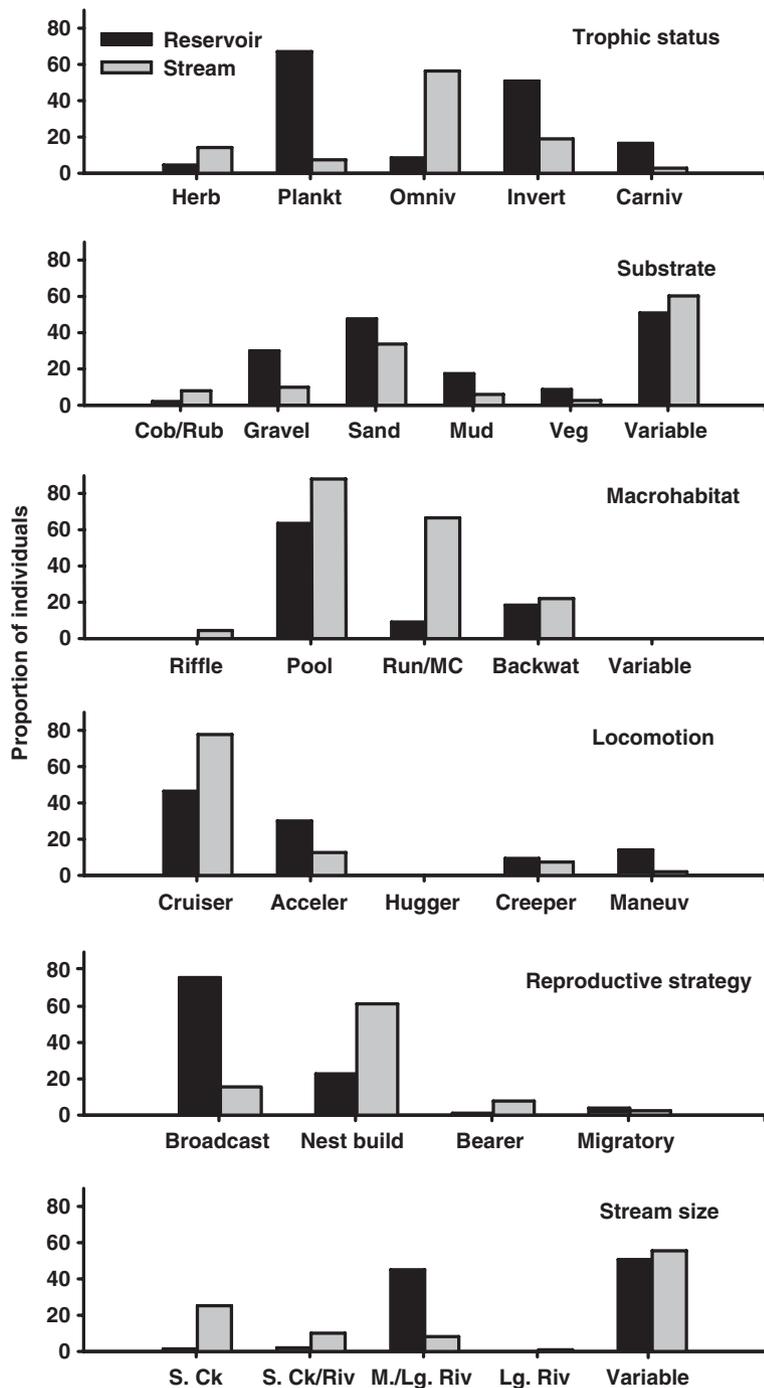
Fig. 6 Ecological traits of fish species occurring in reservoirs and streams in the Great Plains. Bars represent the proportion of individuals in the community that were classified as each ecological trait. Trait categories were slightly modified from Goldstein & Meador (2004) (see text). Abbreviations are as follows (Herbiv, herbivore; Plankt, planktivore; Omniv, omnivore; Invert, invertivore; Carniv, carnivore; Cob/Rub, cobble/rubble; Veg, vegetation; Run/MC, run/main channel; Backwat, backwater; Acceler, accelerator; Maneuv, maneuver; S. Ck, small creek; M. Riv, medium river; Lg. Riv, large river).

evaluate factors associated with the assembly of these communities. We found that the fish communities occupying the littoral zones of 28 reservoirs were a subset of fishes collected from streams. In addition, reservoir communities were more homogeneous across three major drainage basins than were stream communities. Not only did reservoirs across a broad geographic area share similar species,

but their relative abundance and patterns of rank abundance were also similar. Although there were regional differences in reservoir assemblages associated with different species pools within their respective basins, it appears that local factors (e.g. abiotic and biotic interactions, species introductions) may substantially constrain species occurrences in these habitats.

Of the ecological traits evaluated for differences between stream and reservoir communities, it was not surprising that trophic group, reproductive strategy and habitat affinity were associated with success in reservoir environments. These differences in ecological traits between streams and reservoirs are similar to those reported for gradients of stream size, in that reservoir species have traits similar to fishes in large rivers (Aarts & Nienhuis, 2003). For example, we found that carnivorous and planktivorous species were more abundant in reservoirs than streams, presumably because many sport and bait fishes are introduced in these systems. The contrast between broadcast spawning in reservoirs and nest builders in streams is probably a response to differences in sedimentation rates, current velocity and substrate availability. Similarly, the lack of species with a preference for smaller streams is probably a response to high turbidity or the presence of predators in reservoirs, as many small-stream species are small-bodied (Schlosser, 1987), susceptible to predation and do not typically occur in turbid streams. Regardless of the differences in traits of stream and reservoir species, it was interesting to note the diversity of ecological characteristics of reservoir fishes. However, it was not clear whether species with different traits could complete their life cycle in the reservoir or if reservoirs simply served as staging areas and stream habitats were required for critical life stages.

We suggest two main factors that have led to convergence of species richness and community composition in reservoir littoral zones: (i) introduction of a similar suite of species through intentional stocking and unintentional bait bucket introduction and (ii) similar habitat or biotic forces (i.e. environmental filters) in reservoir littoral zones that favour a subset of species that occur in streams (Fig. 1). Not surprisingly, largemouth bass (*Micropterus salmoides*), white crappie and channel catfish (*Ictalurus punctatus*), which are highly valued sportfishes in Oklahoma and Kansas, also were common in a high proportion of reservoirs. Nevertheless, only white crappie accounted for more than 5%, on average, of the total individuals collected from reservoirs. The most numerically dominant taxa were gizzard shad and inland silverside, which are managed as forage fish for these larger predators. Whereas the broad distribution of these species across reservoirs may be due to management programmes, their high numerical

abundance may be attributable to their adaptations for lentic habitats. In addition to sportfish, several species that have high relative abundances in reservoirs also were broadly distributed across stream sites (e.g. red shiner and river carpsucker). The distribution of these species across reservoirs may be due to their ubiquitous distribution or their unique ability to colonize these systems, and their high numerical abundance in reservoirs suggests these habitats have sufficient resources for them to succeed.

A number of abiotic and biotic features of reservoirs could limit the species richness and community structure in littoral zones of reservoirs. Physical (e.g. substrate, water level fluctuations, turbidity, temperature regimes) and chemical (e.g. dissolved oxygen) features of reservoirs likely limit the spawning and recruitment success of many species native to streams. In addition, many native stream-dwelling species may not effectively forage on resources that are more abundant in reservoir environments (e.g. plankton). For example, we found planktivory was a life history trait common among reservoir fishes, but not among obligate stream species. There also is evidence that biotic interactions among fish species can be strong within reservoirs. One of the most abundant species in littoral zones of reservoirs in the Red and Arkansas River basins was the inland silverside, which can competitively displace the native brook silverside because it is a more efficient planktivore (McComas & Drenner, 1982). In addition, piscivore abundance in reservoirs can be high, and, as has been shown in natural lakes (Jackson, Peres-Neto & Olden, 2001) and reservoirs (Godinho *et al.*, 1998), may limit the occurrence of susceptible prey species (e.g. minnows).

The lack of association between basin area and species richness was contrary to other studies that have evaluated patterns of species richness across relatively large spatial scales (Matthews, 1986; Rahel & Hubert, 1991; Gido *et al.*, 2006; Ibanez *et al.*, 2007). The apparent lack of this pattern was probably a result of a strong gradient of decreasing species richness from east to west associated with precipitation and geology, as was shown in a previous survey of stream fish communities in this region (Gido *et al.*, 2002). Thus, small streams in the eastern portion of the three basins had greater species richness than large rivers in the western portions of these basins. Although we cannot discount that sampling efficiency may have resulted in apparently lower richness in

larger rivers, juveniles of many large-bodied species also occurred in our samples. Moreover, we observed similar patterns with non-rarified richness data that integrated species captured over multiple sample trips and increased the probability that rare species were captured.

Slopes of species rank abundance curves for reservoirs were less variable among the three main basins compared to the slopes of those relationships for streams. The observed patterns suggest that littoral zones in reservoirs in the Missouri and Arkansas basins have greater evenness than streams in those basins, whereas littoral zones in reservoirs in the Red River basin have lower evenness than streams in the basin (Fig. 3). Species richness also was more variable among streams in different basins than for reservoirs (Fig. 2). We propose three potential explanations for these patterns. First, littoral habitats may become saturated with species and the threshold for saturation occurs when the regional species pool reaches that observed in the Red River basin. This explanation assumes there have been a greater number of failed invasions in reservoirs of the Red River basin. Second, the increasing regional species pool from north to south may be largely attributed to species that are intolerant of reservoir conditions (e.g. lotic specialists). Although experimentation would be necessary to test the strength of biotic interactions in littoral zones of reservoirs, relative differences in habitat structure (sloping shores versus pool-riffle complexes) and water level fluctuations between reservoirs and streams might amplify species interactions. Finally, convergence of reservoir communities across major drainage basins can partly be attributed to a homogenisation of fish faunas as a result of the general northward invasion of fishes in the region (Gido *et al.*, 2002; Falke & Gido, 2006; Eberle, 2007). Thus, the pattern of greater occurrence of introduced species in reservoirs of the Missouri Basin can be partly attributed to the invasion of several widespread species native to the Arkansas and Red River basins (e.g. western mosquitofish *Gambusia affinis* and bullhead minnow *Pimephales vigilax*) in the more depauperate Missouri River basin. This is consistent with the observation that fish communities from reservoirs in the Red River basin do not typically include species unique to that drainage.

Although our analyses focused on three drainage basins in the Great Plains, convergence of littoral zone fish communities is probably a general pattern in freshwater river systems. For example, Irz *et al.* (2006) also documented local and regional controls of reservoir fish faunas in France. As in our study, they found that reservoir fishes were a subset of those found in rivers and that Jaccard's indices of similarity between streams and reservoirs was 0.38, which was comparable to values we found across the three basins (0.27–0.30). We agree with Irz *et al.* (2006) that reservoir and stream faunas are to some extent dependent on each other and should be considered in catchment-scale management efforts. This is particularly relevant to managing the spread of invasive species, as many species are introduced to reservoirs and subsequently spread to streams (Havel *et al.*, 2005; Johnson, Olden & Vander Zanden, 2008). Knowledge of the extent to which reservoir or stream habitats constrain or facilitate faunal movements is necessary to evaluate the stability of fish populations in highly modified river networks.

Reservoirs are currently a dominant feature of the landscape that provide habitat for many aquatic organisms and provide a number of ecosystem services such as sinks for nutrients and sediment (Downing *et al.*, 2006). This is particularly true in Kansas, U.S.A., where the length of shorelines of impoundments is roughly 25% that of the linear stream habitat in this region (K.B. Gido, unpubl. data). Because littoral zones of reservoirs are similar in many respects to river habitats (Fernando & Holčík, 1991), they may contain high abundances of native stream fishes (e.g. Gido *et al.*, 2002). Given their prevalence in the landscape and potential function as corridors connecting stream habitats, the conversion of natural stream drainage networks into fragmented systems has created ecosystems where communities are composed of species that are not likely to have an evolutionary history of co-occurrence. Following Hobbs *et al.* (2006), we contend that further characterization of these novel ecosystems and their linkages within stream networks deserves attention by managers.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Per cent abundance and occurrence of fish species in reservoirs from three major drainage basins in the Great Plains, U.S.A. Indicator values represent indicator species scores for reservoirs. Significance of indicator values is only given for species with higher indicator values in reservoirs than streams

Appendix S2. Per cent abundance and occurrence of fish species in streams from three major drainage basins in the Great Plains, U.S.A. Indicator values represent indicator species scores for streams. Significance of indicator values is only given for species with higher indicator values in streams than reservoirs

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