

## RESEARCH ARTICLE

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# Influence of a high-head dam as a dispersal barrier to fish community structure of the Upper Mississippi River

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## Abstract

In river systems, high-head dams may increase the distance-decay of fish community similarity by creating nearly impermeable dispersal barriers to certain species from upstream reaches. Substantial evidence suggests that migratory species are impacted by dams, and most previous studies in stream/river networks have focused on small streams and headwaters. Here, we assess whether a high-head dam (Lock and Dam 19; LD 19) on a large river, the Upper Mississippi River (UMR), substantially alters fish community structure relative to variability expected to occur independent of the dam's effect as a fish dispersal barrier. Using fish catch per unit effort data, we modelled the distance-decay function for the UMR fish community and then estimated the similarity that would be expected to occur across LD19 and compared it with measured similarity. Measured similarity in the fish community above and below LD19 was close to the expected value based on the distance-decay function, suggesting LD19 does not create an abrupt transition in the fish community. Although some migratory fish species no longer occur above LD19 (e.g., skipjack herring, *Alosa chrysochloris*), these species do not occur in high abundance below the dam and so do not drive variation in fish community structure. Instead, much of the variation in species structure is driven by the loss/gain of species across the latitudinal gradient. Lock and Dam 19 does not appear to be a clear transition point in the river's fish community, although it may function as a meaningful barrier for particular species (e.g., invasive species) and warrant future attention from a management perspective.

## KEYWORDS

dispersal barrier, fish community structure, high-head dam, Lock and Dam 19, Upper Mississippi River

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## 1 | INTRODUCTION

Changes in species presence and abundance across spatial gradients cause a decay in the similarity of communities with geographic distance, known in the literature as the distance-decay function (Morlon et al., 2008; Soininen, McDonald, & Hillebrand, 2007). Put simply, similarity in community structure between any two sites decreases as the physical distance between those sites increases because of (a) changing environmental conditions, (b) dispersal barriers, and (c) ecological drift and/or organisms' limited dispersal abilities (Soininen et al., 2007). Dispersal barriers can limit the range of certain species and create abrupt transitions in community structure (Araújo et al., 2013; Martinez, Chart, Trammell, Wullschleger, & Bergersen, 1994), potentially creating clear boundaries for management action. Humans strongly influence dispersal barriers, both by circumventing barriers (Rothlisberger, Finnoff, Cooke, & Lodge, 2012) and by creating new ones (Mammoliti, 2002).

Dam construction is one of the most fundamental impacts humans can have on natural river systems (Dynesius & Nilsson, 1994). By creating a barrier to movement, dams often eliminate migratory species from habitats above the dam (e.g., skipjack herring [*Alosa chrysochloris*], paddlefish [*Polyodon spathula*], lake sturgeon [*Acipenser fulvescens*], ebony shell [*Fusconaia ebena*], and blue catfish [*Ictalurus furcatus*]; Gehrke, Gilligan, & Barwick, 2002; Fullerton et al., 2010; Wilcox, 1999), which decreases the similarity of communities above and below the dam. Even non-migratory fish that do not lose habitat directly may be affected by dam construction (Araújo et al., 2013), which often create impounded areas that were not previously present in the river network. These impounded areas foster non-native species that become established and expand to upstream and downstream reaches (Gao, Zeng, Wang, & Liu, 2010; Mammoliti, 2002; Martinez et al., 1994; Santucci, Gephard, & Pescitelli, 2005). Independent of their ability to function as a barrier to species dispersal, dams may eliminate flood plain habitats (Koel, 2004), alter flow regimes (Galat & Lipkin, 2000), increase open water surface area, and impound sediment, altering habitat availability and structure immediately above the dam (Bhowmik & Adams, 1989).

Few studies have explored the causes and drivers of the distance-decay function in large rivers. In Soininen et al.'s (2007) review of published distance-decay relationships, none were from the main stem of large river systems. Most previous studies in stream/river networks have focused on small streams and headwaters (e.g., Hitt & Angermeier, 2008; Datry, Pella, Leigh, Bonada, & Hugueny, 2016, but see Araújo et al., 2013; Vitorino Júnior, Fernandes, Agostinho, & Pelicice, 2016). The Upper Mississippi River (UMR) is a large river that extends 1,070 km from St. Anthony Falls, Minnesota, downstream to St. Louis, Missouri. Reaches between Minneapolis, Minnesota, and Clinton, Iowa, lie within the Driftless Area, an area unaffected by Pleistocene glaciation (Fremling, 2005). These reaches have the greatest habitat diversity due to steep forested slopes, bluffs, and rock cliffs preventing agricultural and urban development and thus encouraging natural flood plain habitat development (Theiling et al., 2000). In southern reaches, channelization and agricultural development have greatly simplified habitat structure reducing connectivity and

increasing fragmentation (Theiling et al., 2000). The longitudinal extent of the UMR allows for considerable variability in climate: Average annual precipitation is 34% higher (St. Louis: 41.0 cm, Minneapolis: 30.6 cm), air temperature is 78% higher (St. Louis: 13.9°C, Minneapolis: 7.8°C), and water temperature is 41% higher (St. Louis: -3.0°C, Minneapolis: -5.1°C) in St. Louis compared with Minneapolis (w2.weather.gov/climate; Theiling et al., 2000).

A total of 29 navigational locks with accompanying dams have been constructed in the UMR to create a waterway suitable for commercial and recreational boat traffic (U.S. Army Corps of Engineers, 2015). The lock and dam structures break the UMR into 28 navigational "pools," although the term "pool" here refers to the reach of river between lock and dam structures, not a habitat type (often there is very little impounded area associated with these lock and dam structures; U.S. Army Corps of Engineers, 2015). During high flow, 27 of these dams are "open" and do not pose any meaningful barrier to fish passage (Theiling & Nestler, 2010). However, open conditions at most dams occur less than 25% of the time (Theiling & Nestler, 2010), so the dams do appear to have reduced longitudinal connectivity to riverine biota (Fremling, 2005; Wilcox, Stefanik, & Kelner, 2004).

Unlike the other 27 UMR dams, Lock and Dam 19 (LD19) and the Upper St. Anthony Falls Dam are high-head dams (>11 m) where fish passage is only possible through the lock chamber (Coker, 1929; Theiling & Nestler, 2010; Wilcox et al., 2004). Concerns about the impact of LD19 on fish communities in the UMR have been longstanding (see review in Wilcox et al., 2004), and the presumption is that some migratory species such as the skipjack herring, no longer occur above LD19 because of the dam's presence. However, Chick, Pegg, and Koel (2006) used a distance-decay analysis to conclude that although upstream and downstream pools in the UMR had differing fish communities, fragmentation due to the navigation system as a whole did not appear to create abrupt changes in the fish community structure across the UMR.

In this study, we used electrofishing data from 11 UMR pools to characterize the distance-decay relationship in the UMR main-stem fish community. Although this relationship was previously observed by Chick et al. (2006), sampling in this past study was limited for Pools 19 and 20 and slightly skewed towards pools occurring above LD19 (eight of 14 pools). Chick et al. (2006) interpreted a strong distance-decay in similarity to be evidence itself of the weak impact of the navigation dams on fish community structure. Here, we also model this distance-decay relationship to predict similarities between Pools 19 and 20 (on either side of LD19). If LD19 has a big impact on community structure, then we would expect Pools 19 and 20 to be less similar than the distance-decay relationship would imply.

## 2 | MATERIALS AND METHODS

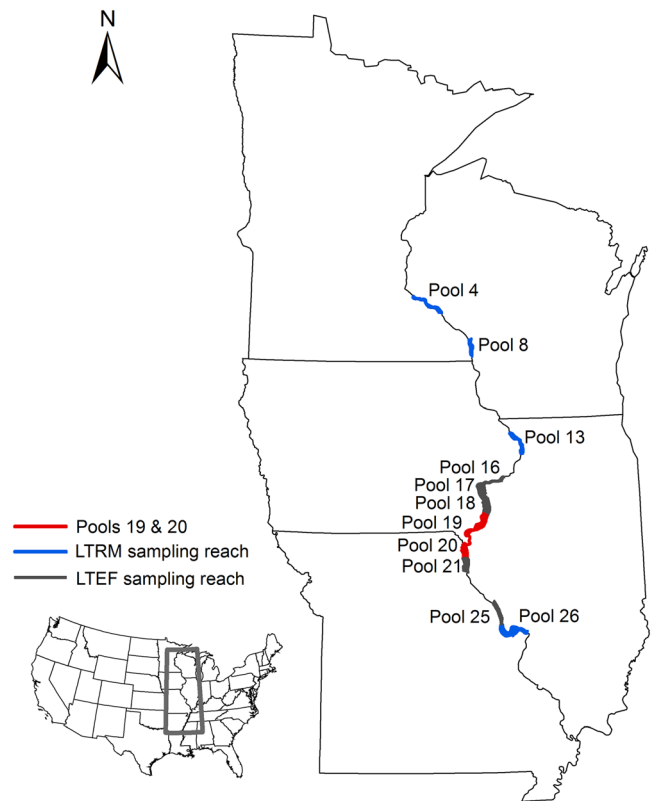
### 2.1 | Study area

Pool 19 is the longest pool in the UMR (74.5 km of total 1,070 km) and is geomorphically diverse. The lower half of the pool is

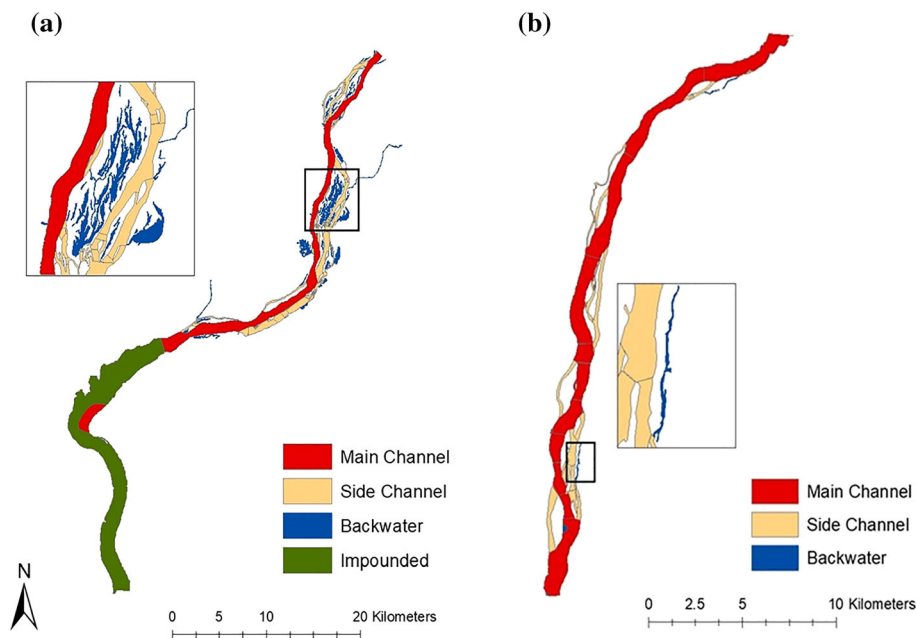
characterized by great width (over 2.5 km below Fort Madison, Iowa), lacustrine habitat with low current velocities, static water levels, and extensive (6,800 ha) shallow-water areas with floating-leaved vegetation. The upper portion of the pool is riverine with extensive side channels and shallow backwaters. Pool 20 (35.2 km) is characterized as straight, narrow, and riverine with high current velocities, lotic conditions, sparse vegetation, and limited off-channel or lacustrine habitat. Pool 20 consists of mostly main channel (80.4%) habitat, followed by side channel (19%) habitat, and a small percentage of backwater (0.6%) habitat (Figure 1). Pool 19 has proportionally less main channel (29.3%) and side channel (17.4%) habitat than Pool 20, in addition to more backwater (5.6%) and impounded habitats (47.7%; Figure 1).

## 2.2 | Data collection

Many sites in the UMR are regularly monitored by government agencies and universities, and descriptions of those sites can be found in Ratcliff, Gittinger, O'Hara, and Ickes (2013) and Fritts et al. (2017). Monitoring of the fish communities in the UMR has been conducted by the U.S. Army Corps of Engineer's Upper Mississippi River Restoration (UMRR) programme's Long Term Resource Monitoring (LTRM) element. From 1994 to present, four pools in the UMR have been subject to annual monitoring three times a year (Ratcliff et al., 2013): Pools 4, 8, 13, and 26 (Figure 2). Since 2009, the Illinois Natural History Survey's Long Term Electrofishing (LTEF) programme, designed to evaluate spatial and temporal trends in fish populations throughout the Illinois River, expanded their fisheries monitoring to the UMR to include Pools 16–21 and 25 (Fritts et al., 2017;



**FIGURE 2** Map of the Upper Mississippi River showing the four Long Term Resource Monitoring (LTRM) regional trend areas: Pools 4, 8, 13, and 26 and Long Term Electrofishing (LTEF) sampling pools: Pools 16 to 21 and 25 used to compare fish assemblages. Pools 19 and 20 are included with LTEF sampling but are designated separately here to emphasize our sampling efforts in 2013 and 2014 [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



**FIGURE 1** (a) Map of Pool 19 of the Upper Mississippi River showing side channel, main channel, impounded reach, and backwater strata distribution. (b) Map of Pool 20 of the Upper Mississippi River showing side channel, main channel, and backwater strata distribution [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

Figure 2), although these data are limited to main channel border (i.e., shallow water areas along channel edges) sites. Both LTRM and LTEF monitoring follow methods originally developed for the LTRM program (Gutreuter, Burkhardt, & Lubinski, 1995; see more detail below). Data from the LTRM and LTEF programs were obtained from the LTRM online database ([http://www.umesc.usgs.gov/data\\_library/fisheries/fish\\_page.html](http://www.umesc.usgs.gov/data_library/fisheries/fish_page.html)) and from the Illinois Natural History Survey (INHS), Illinois River Biological Station, Havana, IL, USA, personnel, respectively.

To add to the existing network of data, we extensively sampled fish communities in Pools 19 and 20. Although LTEF has been sampling Pools 19 and 20 since 2009, their protocol limits sampling to one main channel site per five river miles. However, LTRM procedures select sites occurring within particular habitat types. Habitat types were identified based on aquatic areas designated by Wilcox (1993). Forty-eight sites (24 main channel and 24 side channel) were selected using a stratified random sampling approach according to LTRM protocol (Gutreuter et al., 1995) to collect fish community samples, for both Pools 19 and 20 in 2013 and 2014. The main channel conveys the majority of the river discharge and in most reaches includes the navigation channel (Figure 1). Side channels are large channels that carry less flow than the main channel (Figure 1). Inaccessible areas, including those with private or no physical access, were omitted from consideration. If insufficient water depth or obstructions were present, the randomly selected site was replaced with the nearest randomly selected alternative site. In Pool 19 during 2013, one randomly selected site was sampled on two separate dates in the same time period, bringing the total for that year to 49 sites (Table 1). In some cases, it was not possible to sample (e.g., flooding, dangerous water conditions, inclement weather, and equipment malfunction) as was the case at some sites in Pool 20 during 2013, bringing the total for that year to only 43 sites (Table 1).

Fish collection methodology generally followed LTRM standardized electrofishing methods described in Gutreuter et al. (1995; <https://www.umesc.usgs.gov/documents/reports/1995/95p00201.pdf>). Each electrofishing run lasted 15 min and spanned a 200-m stretch of shoreline, which was consistent for both main channel and side channel sites. The electrofishing boat was operated by a pilot and two dip netters. Dip netters collected fish as they appeared, regardless of size or species. Fish were placed in a holding tank until the run was completed, and then enumerated, recorded, and released back into the river. Fish were collected three times each year (2013 and 2014; June 15 to July 31, August 1 to September 15, and September 16 to October 31) using new random sites each time interval. Pulsed DC daytime boat electrofishing was used to sample fish using LTRM standardized electrofishing specifications. Power goals from the electrofishing boat and sampling design emulated LTRM protocols to achieve comparable fish catch rates and standardization across all pools in the UMR (Gutreuter et al., 1995). Western Illinois University Institutional Animal Care and Use Committee approval was obtained before commencement of this study (WIU 13-13-r). All fish were acquired and used in accordance with federal, state, and local laws and regulations.

**TABLE 1** Total number of main channel border (MCB) and side channel border (SCB) sites sampled, individuals captured, and species richness for years 2013 and 2014 using data from Long Term Resource Monitoring (LTRM; Pools: 4, 8, 13, 19, 20, and 26) and Long Term Electrofishing (LTEF; Pools: 16, 17, 18, 21, and 25) programmes

Pool	Total fish captured		Species richness		Total sites sampled	
	MCB	SCB	MCB	SCB	MCB	SCB
2013						
4	1,804	1,772	36	40	24	23
8	1,757	2,942	39	42	12	24
13	979	438	36	32	12	6
16	--	--	--	--	--	--
17	--	--	--	--	--	--
18	--	--	--	--	--	--
19	6,064	5,756	54	48	24	25
20	4,624	3,029	41	38	19	24
21	--	--	--	--	--	--
25	--	--	--	--	--	--
26	6,563	3,446	51	34	24	18
2014						
4	4,273	2,565	40	48	24	23
8	1,822	3,884	40	42	12	24
13	1,299	774	36	34	12	6
16	2,256	--	46	--	15	--
17	3,049	--	40	--	12	--
18	1,764	--	37	--	14	--
19	4,190	3,373	52	45	24	24
20	2,023	1,604	37	40	24	24
21	905	--	28	--	12	--
25	1,044	--	42	--	18	--
26	3,108	2,335	38	40	24	18

Note. Long Term Electrofishing data were only analysed for year 2014 and are limited to MCB sites.

### 2.3 | Statistical analyses

Like all collection methods, electrofishing is only effective for sampling a subset of the fish community, so we limited our analyses to species that are either known to be easily captured by electrofishing or are considered common species. Previously published research has shown that electrofishing has power > 0.80 to detect a 20% interannual abundance change in at least one habitat type for 16 species in the UMR (Lubinski, Burkhardt, Sauer, Soballe, & Yin, 2001; Table 2). We term these the "highly catchable" species. We restricted the analyses to either (a) those 16 "highly catchable" species or (b) each species that made up >1% of the catch in any pool, termed the ">1% catch" species (Table 2).

Data from 2013 and 2014 were used in these analyses, but LTEF data analyses were limited to 2014, because we acquired data for only year 2014 from INHS personnel. Similarity in fish community

**TABLE 2** The 16 “highly catchable” species and the 27 species displaying a >1% catch in any given pool of the Upper Mississippi River, USA, and the four letter species code used in Long Term Resource Monitoring (LTRM) data

27 species >1% catch	16 “highly catchable” species	Species codes
	Bigmouth buffalo <i>Ictiobus cyprinellus</i>	BMBF
Black crappie <i>Pomoxis nigromaculatus</i>	Black crappie <i>Pomoxis nigromaculatus</i>	BKCP
Bluegill <i>Lepomis macrochirus</i>	Bluegill <i>Lepomis macrochirus</i>	BLGL
Bullhead minnow <i>Pimephales vigilax</i>	Bullhead minnow <i>Pimephales vigilax</i>	BHMW
Channel catfish <i>Ictalurus punctatus</i>	Channel catfish <i>Ictalurus punctatus</i>	CNCF
Channel shiner <i>Notropis wickliffi</i>		CNSN
Common carp <i>Cyprinus carpio</i>	Common carp <i>Cyprinus carpio</i>	CARP
Emerald shiner <i>Notropis atherinoides</i>	Emerald shiner <i>Notropis atherinoides</i>	ERSN
Freshwater drum <i>Aplodinotus grunniens</i>	Freshwater drum <i>Aplodinotus grunniens</i>	FWDM
Gizzard shad <i>Dorosoma cepedianum</i>	Gizzard shad <i>Dorosoma cepedianum</i>	GZSD
Golden shiner <i>Notemigonus crysoleucas</i>		GDSN
Largemouth bass <i>Micropterus salmoides</i>	Largemouth bass <i>Micropterus salmoides</i>	LMBS
Mimic shiner <i>Notropis volucellus</i>		MMSN
Mississippi silvery minnow <i>Hybognathus nuchalis</i>		SVMW
Orangespotted sunfish <i>Lepomis humilis</i>		OSSF
Pumpkin seed <i>Lepomis gibbosus</i>		PNSD
River carpsucker <i>Carpiodes carpio</i>		RVCS
River shiner <i>Notropis blennioides</i>		RVSN
Rock bass <i>Ambloplites rupestris</i>		RKBS
Shorthead redhorse <i>Moxostoma macrolepidotum</i>	Shorthead redhorse <i>Moxostoma macrolepidotum</i>	SHRH
Silver carp <i>Hypophthalmichthys molitrix</i>		SVCP
	Silver redhorse <i>Moxostoma anisurum</i>	SVRH
Smallmouth bass <i>Micropterus dolomieu</i>	Smallmouth bass <i>Micropterus dolomieu</i>	SMBS
Smallmouth buffalo <i>Ictiobus bubalus</i>	Smallmouth buffalo <i>Ictiobus bubalus</i>	SMBF
Spotfin shiner <i>Cyprinella spiloptera</i>	Spotfin shiner <i>Cyprinella spiloptera</i>	SFSN
Spottail shiner <i>Notropis hudsonius</i>		STSN
Weed shiner <i>Notropis texanus</i>		WDSN
White bass <i>Morone chrysops</i>	White bass <i>Morone chrysops</i>	WTBS
Yellow perch <i>Perca flavescens</i>		YWPH

structure between pools was estimated using the Bray–Curtis Dissimilarity index as implemented in the R package “vegan” (Bray & Curtis, 1957; Dixon, 2003; R Development Core Team, 2014). Dissimilarity is  $1 - \text{similarity}$ , so for clarity, we converted everything to similarity for all data presentation and will refer to similarity hereafter. In the Bray–Curtis similarity index, higher values indicate more similarity (i.e., two communities are more alike). Bray–Curtis similarity between pools was calculated for each year. To minimize differences in fish community due to habitat (which influences electrofishing effectiveness), statistical procedures were performed separately for main channel and side channel habitats. In addition, statistical procedures were not performed separately among sampling time periods. All samples within a pool were standardized for a 15-min sampling run and averaged to generate a pool-specific estimate of CPUE. All data were square root transformed and standardized (using the “wisconsin” standardization) prior to analysis (Dixon, 2003). To assess

how robust our similarity measurements were to small differences in the number of samples collected, we performed resampling on our data at the level of the electrofishing run. For each resampling, 10% of electrofishing runs were discarded randomly, and similarity indices were calculated for all pairwise pool combinations using the remaining data. We repeated this resampling procedure 500 times and then calculated mean and standard deviation of similarity for all site-year combinations. We estimated the correlation between similarities calculated using the different species lists, habitat types, or sampling year to assess whether these differences strongly influenced our conclusions about among-pool variation in fish community structure. That is, if we used the highly catchable species list, did our calculated similarity vary among pool combinations the same way as when we used the >1% catch species list? Pearson's correlation coefficients were calculated using the base R function “cor().”

Similarities were then related to physical distance using a simple linear regression model implemented using a Bayesian framework (McCarthy, 2007). Longitudinal distance was calculated as river km between the midpoint of one pool to the midpoint of another pool (Table S1). Distance and similarity were standardized prior to estimating regressions so that standardized slopes could be calculated (Hair, Anderson, Tatham, & Black, 1998). Priors (Bayesian probability distributions) for the slope were informative to reflect the assumption that sites further apart would be more different than sites closer to each other (although uninformative priors only slightly altered these estimates). We then used this regression to calculate the “predicted” similarity due to distance between Pools 19 and 20. If the actual similarity between Pools 19 and 20 was lower than the predicted similarity, then we considered this evidence that the dam is causing larger than expected impacts to the fish community. Similarities between 19 and 20 were included in the regression, but removal of those similarities did not alter the conclusions; as a result, we have retained them in the regressions. This analysis was undertaken separately for 2013 and 2014 and for side channel and main channel habitats.

### 3 | RESULTS

#### 3.1 | Similarity among pools on the Mississippi River

Calculated similarities in fish assemblages among pools were relatively insensitive to (a) data resampling, (b) choice of species list, (c) analysis year, and (d) habitat type (Table 3). (a) The resampling analysis indicated the mean similarity values calculated from the resampling procedure had a standard deviation (SD) equal to or less than 0.03 (the index ranges from 0 to 1; Table S2–S4). (b) Correlations between similarity calculated with the two species lists were high (Pearson's  $r = .96$  for main channel habitats and  $r = .93$  for side channel habitats). (c) Correlations between similarity calculated with 2013 and 2014 data were identical between years for main channel habitats ( $r = .79$  for both species lists) and comparable between years for side channel habitats ( $r = .89$  for >1% catch,  $r = .80$  for highly catchable). (d) Correlations between similarity calculated with main channel and side channel data were comparable between habitats ( $r = .86$  for >1% catch,  $r = .81$  for highly catchable) (Table 3).

**TABLE 3** Pearson correlation coefficients ( $r$ ) between Bray–Curtis similarity index values calculated using two different species lists (>1% catch or highly catchable species), years (2013 and 2014), and habitat types (main channel or side channel) using data from Long Term Resource Monitoring (LTRM; Pools: 4, 8, 13, 19, 20, and 26) and Long Term Electrofishing (LTEF; Pools: 16, 17, 18, 21, and 25) programmes

Association	Habitat	Species list	$r$
>1% catch versus highly catchable	Main channel	—	.96
	Side channel	—	.93
2013 versus 2014	Main channel	>1% catch	.79
	Main channel	Highly catchable	.79
	Side channel	>1% catch	.89
	Side channel	Highly catchable	.80
Main channel versus side channel	—	>1% catch	.86
	—	Highly catchable	.81

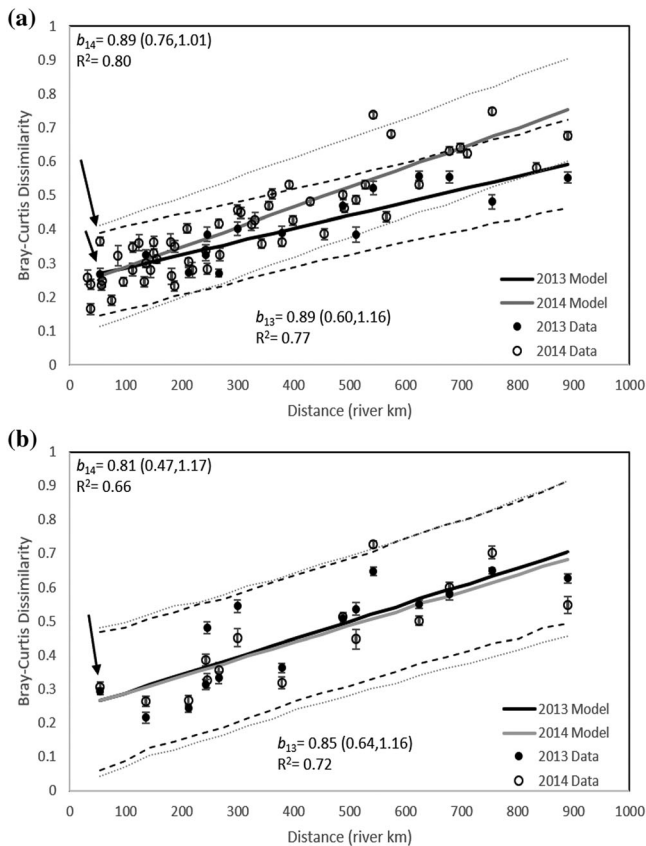
Note. Long Term Electrofishing data were only analysed for year 2014 and are limited to main channel sites.

#### 3.2 | The relationship between distance and similarity among pools on the Mississippi River

The distance-similarity model showed a strong relationship between physical distance among locations and similarity of fish communities throughout the UMR (Pools 4–26). That is, pools separated by a greater distance had less similar fish communities. Because similarity values were not strongly influenced by the choice of species list, we used only the >1% catch list to generate the distance to similarity relationship. In both years and in both habitats, the association between distance and similarity had a standardized slope > 0.8 and  $R^2$  values ranging from .66–.80 depending on year and habitat (Figure 3). The standardized slopes were very similar, with 95% confidence intervals that were credible and always had substantial overlap.

The main focus of this analysis was the similarity between Pool 19 and Pool 20, which have a physical separation of 54.3 river km using our methodology (some areas of Pool 19 are adjacent to Pool 20 and are separated by only a few metres). For 2013, using main channel data, the distance-similarity model predicted two sites separated by ~55 river km would have a similarity falling between 0.59 and 0.8 (95% credible interval, Figure 3a), and the actual similarity between Pool 19 and Pool 20 was 0.74. In 2014, the distance-similarity model predicted a similarity between 0.57 and 0.86 (Figure 3a), and the actual similarity was 0.64. If Lock and Dam 19 were having a major effect on fish community structure, we would have expected these similarities to be lower than the predicted values. These results were also similar when using data from side channel habitats. The distance-similarity model predicted two sites separated by ~55 river km would have a similarity between 0.53 and 0.94 (this interval was very similar for both years, Figure 3b). The actual measured similarities between Pools 19 and 20 were 0.71 and 0.69 for 2013 and 2014, respectively.

Given the LTEF data were available for main channel habitats in 2014, we also estimated the typical similarity value for pools neighbouring Pools 19 and 20 (Pools 16–21 and 25–26). If the similarity between Pools 19 and 20 was lower than the normal similarity, then this could be evidence that Lock and Dam 19 has a greater effect than other dams. The similarity between neighbouring pools were, on average, 0.75 (SD = 0.06; Table 4). The similarity between Pools 19



**FIGURE 3** Association between Bray–Curtis similarity index and the distance between pool midpoints in river kilometres (km) using data from Long Term Resource Monitoring (LTRM; Pools: 4, 8, 13, 19, 20, and 26) and Long Term Electrofishing (LTEF; Pools: 16, 17, 18, 21, and 25) programs. Long Term Electrofishing data were only analysed for year 2014 and are limited to main channel sites. The arrow points to the similarity between Pools 19 and 20 (where the dam sits). (a) is for main channel samples and (b) is for side channel samples. Filled circles represent 2013 data and open circles represent 2014 data. The black line is the regression mean for 2013 and the grey line is the regression mean for 2014. Error bars around the points are standard deviation from the resampling procedure. Dashed lines are 95% credible intervals around the model estimate

and 20 in 2014 is 1.7 standard deviations lower than the neighbouring pool average (0.64), but in 2013 the similarity between Pools 19 and 20 is very close to the average (0.74, Table 4). As a result, there is not clear evidence that Lock and Dam 19 is associated with a substantially larger similarity than occurs in other neighbouring pools.

## 4 | DISCUSSION

Our results showed a strong relationship between physical distance among locations and similarity of fish communities, consistent with previous research in this and other ecosystems (Araújo et al., 2013; Chick et al., 2006; Soininen et al., 2007). Previous researchers have focused on environmental conditions and dispersal barriers as potential drivers of distance-decay in community similarity (Morlon et al., 2008). In the UMR, pools separated by the largest physical distances

are characterized by very different geomorphic features (i.e., environmental conditions) that likely contribute to differences in fish community structure. Upper reaches (Pools 4–13) are characterized by large backwater areas with lacustrine habitat and abundant vegetation. These semi-lentic habitats promote populations of centrarchids (Aday, Parkos, & Wahl, 2009; Savino & Stein, 1982; Smith, 2002; Warren, 2009). In contrast, lower reaches (Pools 16–26) are often leveed or channelized for agricultural and navigation purposes (Grubaugh & Anderson, 1988), yielding riverine habitat features (i.e., straight and narrow channels, high current velocities, and limited habitat diversity). *Ictiobus* spp., channel catfish (*Ictalurus punctatus*), white bass (*Morone chrysops*), freshwater drum (*Aplodinotus grunniens*), gizzard shad (*Dorosoma cepedianum*), common carp (*Cyprinus carpio*), and silver carp (*Hypophthalmichthys molitrix*) are dominant species in lower reaches preferring these conditions (Pflieger, 1997; Upper Mississippi River Conservation Committee, 2004). In addition, some species appear to be restricted to either the northern or southern reaches due to the species' thermal limitations. For example, yellow perch (*Perca flavescens*) prefer impounded backwater habitats with vegetation and slow water velocities consistent with conditions found in upper reaches and Pool 19 (Pflieger, 1997; Upper Mississippi River Conservation Committee, 2004). For these reasons, it seems likely that changes in environmental conditions are a major contributor to the distance-decay relationship.

By contrast, little evidence supported a strong role of dispersal barriers in driving differences in the overall fish community structure. Soininen et al. (2007) proposed using the similarity halving distance (the distance at which community similarity is reduced to half the initial similarity) as a metric of comparing distance-decay relationships among different ecosystems and taxa. Araújo et al. (2013) found that the halving distance for fish communities over 2 years in the undammed Tocantins River was 702 and 1,387 km, compared with 682 and 972 km in the 2 years of our study. The halving distance in the Tocantins River appeared to be much shorter after a large, impassable dam was installed (51% and 83% decrease). In Soininen et al. (2007), the halving distance of highly mobile taxa with few dispersal barriers (i.e., flying taxa) was about the same as those we observed in the UMR. Chick et al. (2006) considered the strong distance-decay relationship itself to be strong evidence against fragmentation as a major cause of variation in fish community structure in the UMR, instead reasoning environmental and geomorphic settings were more important. In addition, the most likely dispersal barrier (LD19) did not appear to be driving unexpectedly low similarity between Pools 19 and 20.

Several possibilities exist to explain why LD19 and other dams on the UMR appear to have little effect on variation of fish community structure. One possibility is simply that we lack the appropriate data to detect this effect. Abundant evidence suggests dams, even semi-permeable navigation dams, can reduce or eliminate movement of certain fish species (Tripp, Brooks, Herzog, & Garvey, 2014; Wilcox et al., 2004; Ziegler, Dewey, Knights, Runstrom, & Steingraeber, 2004). For this to influence community structure, these species must be significant contributors to the community. Many species that may have once

**TABLE 4** Mean (standard deviation) of the Bray–Curtis similarity index values between consecutive pools (Pools 16–21 and 25–26) in the Upper Mississippi River for 2014 (main channel habitats only)

Species list	Pool 1	Pool 2	Physical distance (river km)	Year	Bray–Curtis Similarity (SD)
>1% catch	17	16	37.0	2014	0.84 (0.02)
	18	17	37.4	2014	0.76 (0.02)
	19	18	58.3	2014	0.75 (0.02)
	20	19	54.3	2013	0.74 (0.02)
	20	19	54.3	2014	0.64 (0.01)
	21	20	31.8	2014	0.74 (0.02)
	26	25	56.3	2014	0.76 (0.02)
Mean					0.75 (0.06)
Highly catchable species	17	16	37.0	2014	0.85 (0.02)
	18	17	37.4	2014	0.77 (0.02)
	19	18	58.3	2014	0.81 (0.01)
	20	19	54.3	2013	0.79 (0.02)
	20	19	54.3	2014	0.70 (0.02)
	21	20	31.8	2014	0.83 (0.02)
	26	25	56.3	2014	0.79 (0.02)
Mean					0.79 (0.05)

Note. Mean and standard deviation were calculated after 10% resampling. All pools are separated by navigation dams, but the dam separating Pools 19 and 20 is a high-head dam that is suspected to restrict fish passage. The ">1% catch" species list refers to all species that occupy greater than 1% of the total catch in at least one pool. The "highly catchable" species list refers to species that have been found to be particularly vulnerable to the daytime electrofishing used in this study.

been common in the UMR do not make up a large portion of the 2013/2014 fish community (e.g., paddlefish, lake sturgeon, and skipjack herring). Even if these species were once common and the navigation dams caused them to decline to their current low abundance, we would not be able to detect this with the available data. Unlike the Tocantins River example discussed above, we lack before–after data for this comparison. Most of the species that currently make up >1% of the catch can complete their life cycles in habitats above or below the dam.

Although LD 19 does not appear to be a clear transition point in the river's fish community, it may function as a meaningful barrier for invasive species. Although the upstream spread of the invasive species silver carp and bighead carp (*Hypophthalmichthys nobilis*) from areas downstream of LD19 is evidence fish do use the lock chamber (Larson, Knights, & McCalla, 2017; Tripp et al., 2014), management actions within the lock chamber could presumably reduce the likelihood of upstream spread of invasive fish species as well as prevent the re-establishment of migratory species. Despite species having upstream access through the lock chamber, a greater abundance of invasive carps and migratory native species (i.e., skipjack herring and ebony shell mussel) occupy lower reaches (19 and below), presumably because LD19 has slowed the upstream migration of these species (Coker, Shira, Clark, & Howard, 1921; Kelner & Sietman, 2000; Nielsen, Sheehan, & Orth, 1986).

Regardless of LD19's current minimal impact on fish community structure, long-term monitoring in this ecologically important reach of the UMR could be useful to detect changes in fish community structure in future decades. The high-head structure of LD19 has caused deposition of more than 10 m of sediment behind the dam since its completion in 1913 (Bhowmik & Adams, 1989). Deposition of sediment has reduced water depth in the lower half of Pool 19,

creating an impounded habitat from immediately above the dam to 24 river km upstream. The shallow depths and still waters in this impounded area provide ideal habitat for macrophyte colonization. Aerial surveys have shown increased macrophyte expansion since 1966 (Tazik, Anderson, & Day, 1993; Thompson, 1973). Bhowmik and Adams (1986, 1989) predicted Pool 19 will reach dynamic equilibrium by the year 2050 when the pool volume will be 20% of its initial post-impounded volume. In addition, this study focused only on catch in main channel and side channel habitats, but obviously the pool-wide population of fish species may change as the proportional contribution of habitat changes.

Our study provides important insight on the impacts of dispersal barriers, specifically high-head dams, to fish communities in large river systems. Although dispersal barriers can limit the range of certain species and create abrupt transitions in community structure, our findings describe a strong relationship between physical distance influenced by habitat structure/availability and environmental conditions and fish community similarities.

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## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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