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RESEARCH ARTICLE

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Monitoring upstream fish passage through a Mississippi River lock and dam reveals species differences in lock chamber usage and supports a fish passage model which describes velocity-dependent passage through spillway gates

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Abstract

Nearly 200 fish were released below Lock and Dam 2 (LD2) in the Upper Mississippi River and tracked to determine both whether and how they passed through this structure, and if passage could be explained using a computational fish passage model (FPM) which combines hydraulics with fish swimming performance. Fish were either captured and released downstream of LD2 in Pool 3 or captured in Pool 2 (upstream of LD2) and displaced below LD2. Tagged fish were tracked using 13 archival receivers located across LD2. Approximately 90% of all fish approached LD2 many times with the displaced species likely attempting to home. Of 112 common carp, 26% passed through LD2 with 15% (most) going through the lock and 6% through the spillway gates. Similar values were seen for bigmouth buffalo. In contrast, although 42% of 31 channel catfish passed through the lock, only 3% went through the gates. Finally, of 22 walleye, only 14% passed through the lock and none through the gates. Ninety percent of all documented passages through the spillway gates occurred when the gates were out of the water and water velocities through these gates were at their lowest levels, an attribute described and predicted by the FPM at LD2. This study strongly suggests that fish passage through spillway gates of LDs is determined by water velocity and can be predicted with a FPM, whereas passage through locks is determined by species-specific behavioural preferences. Both attributes could be exploited to reduce passage of invasive carp at certain locations.

KEYWORDS

carp, displacement, fish passage model, invasive, lock chamber, open river, spillway gates, swimming performance

1 | INTRODUCTION

Nearly all rivers worldwide are now regulated by dams whose modified flows seem to impede the natural movement of the many species of migratory fishes typically found living in these systems (Dynesius & Nilsson, 1994). Among the many types of barriers to fish movement, locks and dams (LDs), which combine navigational locks with gated spillways to create water depths suitable for navigation, are of special concern because they are commonly used in large shallow rivers such as the Mississippi River. Although it is well established that LDs impede the natural movement of river fishes (Argent & Kimmel, 2011; Liermann, Nilsson, Robertson, & Ng, 2012; Poff, Olden, Merritt, & Pepin, 2007), the causes and the extent to which fish movements are impacted are not well understood. This situation has recently garnered attention in the Mississippi River where LDs appear to be blocking upstream movement of invasive silver carp, *Hypophthalmichthys molitrix*, and bighead carp, *H. nobilis*, which were introduced in the 1970s (Kolar et al., 2005; Lubejko et al., 2017; Tripp, Brooks, Herzog, & Garvey, 2014).

All 29 LDs in the Upper Mississippi River have similar designs that offer two pathways for upstream-moving fishes: navigation locks and spillway gates. Spillway gates comprise the majority of each LD structure and serve to regulate water levels for navigation. Typically, spillway gates rest on the river bottom when closed and are raised to pass water underneath, when/as river flow (depth) increases. Water velocities under gates range from extremely high when nearly closed, to low when raised out of the water, a condition known as "open river," the frequency of which varies with location and presumably affects fish passage. In contrast, water velocities are negligible in navigational locks whose mitre gates open to allow boats to pass, at which time fish could also pass.

The U.S. Army Corps of Engineers (USACE), which manages Mississippi River LDs, operates them by adjusting individual gate openings to create adequate depth for lock operation while balancing flow/velocity to reduce scour. Although commonly hypothesized that water velocities (gate openings) determine overall fish passage rates through LDs, this hypothesis has not yet been tested directly because biologists have to date been unable to pair an understanding of hydraulics with fish swimming performance and behaviour. Complicating this scenario is the fact that velocities vary with depth, whereas fish swimming performance (the relationship between how long/far a fish swim at different speeds) varies by species, length, and environmental conditions. Nevertheless, tracking studies suggest that fishes are routinely blocked by LDs in the Mississippi River. Knights, Vallazza, Zigler, and Dewey (2002) noted that lake sturgeon, *Acipenser fulvescens*, appeared to be blocked by Mississippi River LDs during gate-controlled river conditions (i.e., not in open river). Zigler, Dewey, Knights, Runstrom, and Steingraeber (2004) also noted a similar scenario for paddlefish, *Polyodon spathula*, where most LD passages seemed to occur at times when gates were likely out of the water. In another seminal study of both upstream and downstream passages of 11 species of fish across six LDs, Tripp et al. (2014) noted that nearly 80% of all upstream passages occurred during times of open river. In addition, they found that some species were seemly more efficient at passing than others, suggesting possible differences in fish behaviour or physiological swimming ability. Tripp et al. (2014) also described a relationship between gate opening and fish passage rate although they unfortunately lacked data on water velocity. Finally, in the only study to systematically monitor passages through a lock versus spillway gates, Lubejko et al. (2017) found that only three of several hundred acoustically tagged silver and bighead carps were able to overcome spillway gates in controlled river condition at Starved Rock Lock and Dam in the Illinois River. These authors speculated that the low passage rates for carp at this location were related to high (but unknown) water velocities under partially closed spillway gates.

Seeking to quantify the relationship between spillway gate operation, water velocity, and fish upstream swimming abilities at LDs, we (Zielinski, Voller, & Sorensen, 2018) recently developed an agent-based fish passage model (FPM). This FPM pairs high-resolution water velocity data of different operating conditions of spillway gates with fish swimming performance data for different species of different sizes to predict if, when, and where fish could pass. Our approach uses swimming performance data as a physiological basis for upstream passage because these data are more readily available than detailed swimming behaviours around LDs, and they theoretically can provide insights on the upper bounds of passage likelihood at any structure (Zielinski et al., 2018). We developed this FPM because all existing fish passage models presently rely on simplified hydraulics (e.g., FishXing; Furniss et al., 2006), or require extensive telemetry data to develop behaviour rules for the swimming behaviour of each species (e.g., the Eulerian–Lagrangian-agent method; Goodwin, Nestler, Anderson, Weber, & Loucks, 2006; Goodwin et al., 2014). No existing FPM had ever been used to model upstream movement of fish through large complex flow control structures including Mississippi River LDs. Our FPM assumes that (a) fish are only motivated to move upstream; (b) fish swim at their distance-maximizing ground speed (Castro-Santos, 2005); and (c) fish follow the path of least resistance until they physiologically exhaust. The model simulates movement of fish through a stochastic, complex flow field where the maximum distance achieved by each fish is determined through a combination of physiological capacity and local water velocity as determined by three-dimensional computational fluid dynamics (CFD) models. Due to the lack of fish behavioural data below spillway gates, the model uses stringent assumptions and physiological thresholds to estimate swimming distance, which presumably result in an overestimate of the likelihood of passage (Zielinski et al., 2018). Although overestimation is desirable when attempting to identify gate operations that reduce invasive fish passage, a direct test of model predictions has not yet been performed but is needed to be sure that the model is not underestimating. This is important because were its predictions validated, it could be used to propose new spillway gate operations at many LDs to create more uniform and overall faster velocities, thus reducing both overall fish (carp) passage and scour in ways that the USACE might find acceptable (Zielinski et al., 2018).

The present study determined the upstream passage rates of several species of fish through a LD in the Upper Mississippi River to quantify the rates with which these fishes passed a LD, describe the path they use (i.e., lock or spillway gates), and how observed passage compares with our FPM. With one exception (walleye), the passage of the fish we studied had also not been studied before.

2 | METHODS

2.1 | Study location

Our study took place in the Upper Mississippi River at Lock and Dam 2 (LD2), Hastings, Minnesota, USA (44°45′35″N 92°52′09″W). This structure was chosen because it is relatively typical of others although its spillway gates are open less than most, its fish populations are relatively typical of the Upper Mississippi River and it is located close to us making it practical. This LD is 220 m long and has 19, 9-m-long, tainter gates, a hydropower plant (impassable to fish because of its turbines), and an active lock chamber (39 m wide × 184 m long; Figure 1). Its spillway gates are typically out of the water only 2% of the year (Fishpro, 2004). This LD lacks overflow spillways so fish can only pass through the spillway gates or lock (Figure 1).

2.2 | Experimental design

To address our objective, we sought to catch, tag, and track a variety of fish over a 3-year period. We focused on the most common large fish (i.e., fish most likely to pass) found in the area: common carp (*Cyprinus carpio*), walleye (*Sander vitreus*), channel catfish (*Ictalurus punctatus*), and bigmouth buffalo (*Ictiobus cyprinellus*). We focused on the common carp because it was abundant year-round, invasive, and only for it were we able to identify swimming performance data (see below). We sought to track at least 20 individuals of each species using two strategies to increase sample size and focused on upstream movement. First, we captured, tagged, and then released fish in Pool 3 (Pool 3 fish) downstream of LD2 in the spring and late fall to incorporate possible spring movement. Second, we also captured fish in Pool 2 (Pool 2 fish), upstream of LD2, and then displaced them to Pool 3, hoping that they would attempt to return. Homing behaviour has been demonstrated in numerous freshwater fishes (Lucas & Baras, 2003) including common carp (Crook, 2004). We therefore displaced species of interest in an attempt to increase the number of fish approaching the dam, especially outside of natural migration periods.

Experiments commenced in the fall of 2016 and continued until fall 2018, excluding the time when the river was covered with ice and LD2 was closed to boat traffic. All fish were tagged with acoustic transmitters (Section 2.3) and their passage rates assessed using an archival

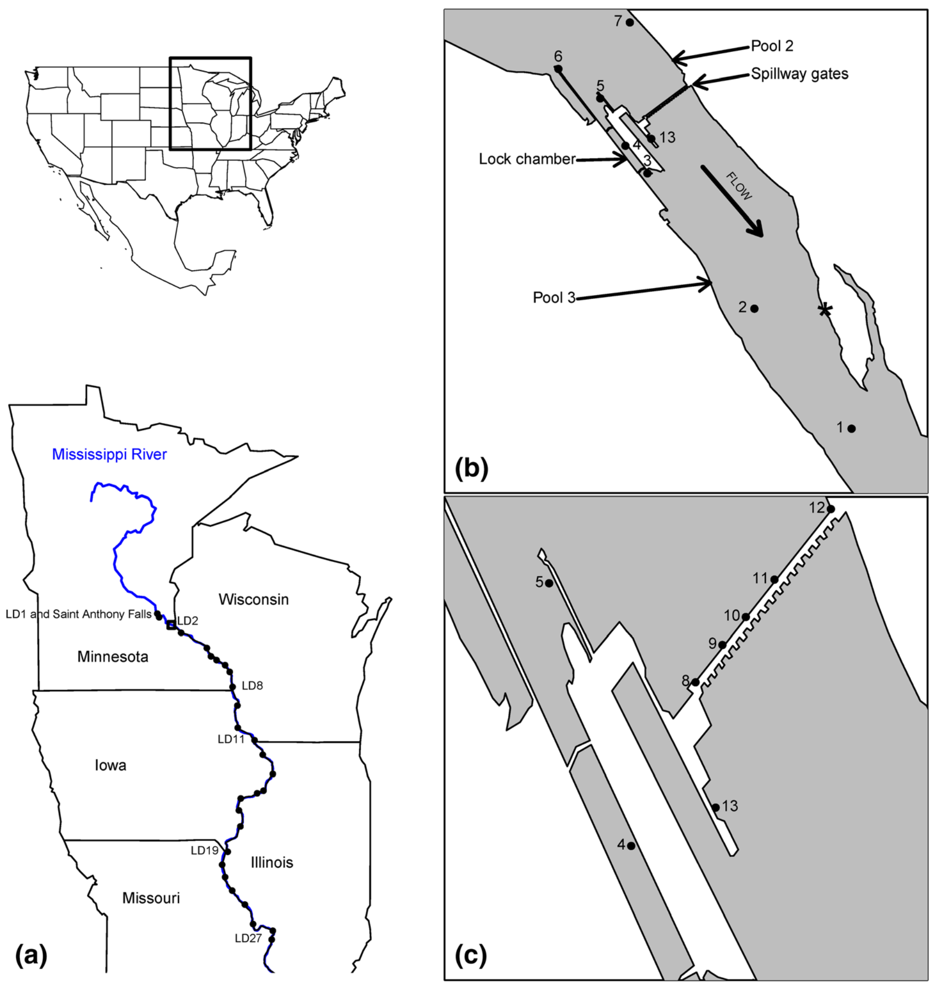

FIGURE 1 (a) Location of Lock and Dam 2 (LD2) on the Mississippi River, Hastings, Minnesota, USA. (b) Position of acoustic receivers on and around LD2 and the location of surgery/release site (*). (c) Enlargement of LD2 showing the position of spillway gate receivers (#8 to #12) [Colour figure can be viewed at wileyonlinelibrary.com]

array (Section 2.5). Fish passage rates were also simulated using our FPM model (Section 2.7).

2.3 | Fish capture and tagging

Fish were captured using a combination of techniques including boat electrofishing (5–12 A, 80–150 V, 20–60% duty cycle, and 60–120 pulse frequency), standard gillnets (20-min set and 90-m length × 2-m depth), mesh sizes (7.6-, 8.9-, 10.2-, and 12.7-cm square measure mesh), hoop nets (1.2-m-diameter frame and 3.8-cm square measure mesh), and angling in both pools. Techniques varied with river stage, temperature, and species. Only fish larger than 50 cm (TL) were kept. To reduce the stress associated with high water temperatures, gillnets and hoop nets were not used when the water temperature was above 24°C. Instead, only common carp (electrofishing) and channel catfish (angling) were sampled. Captured fish were transported for tag implantation to the surgery site, 200 m downstream of LD2 in Pool 2 (Figure 1) in a 400-L holding tank with recirculating water. Fish were anesthetized in a 1:7000 solution of eugenol (Sigma, St. Louis, MI) following established procedures (Hajek, Klyszejko, & Dziaman, 2006). Briefly, a 5-cm incision was made on the ventral side of the anaesthetized fish just posterior of its pelvic fins and a tag inserted into their body cavity following established protocols (Penne & Pierce, 2008). We used 22.7- and 26.15-g DART tags (model DART10, ATS, Isanti, MN, USA), which have both individually coded acoustic (3-s pulse rate and 416.7 kHz) and radio signals (49 and 50 kHz) with an 8- to 12-month battery life. Once a tag had been inserted, a sterile 14-gauge needle was inserted posterior to the incision, enabling us to thread the radio antenna through the muscle wall of the fish. The incision was closed using 4 to 5 interrupted re-absorbable sutures (2–0, Ethicon PDS II). Tagged fish were then placed in the river in a 1.3 × 1.3-m net pen until they recovered (approximately 20 min) before being released.

2.4 | Fish release

We released the three fish commonly caught in Pool 3 on site (common carp, channel catfish, and walleye; Table 1) and the three most common fishes caught in Pool 2 (common carp, channel catfish, and bigmouth buffalo; Table 2) into Pool 3. There were no known mortalities, and 88% of tagged fish were eventually detected by receivers upstream of the surgery site, suggesting mortality was low. Protocols were approved by the University of Minnesota Institutional Animal Care and Use Committee (#1605-33753A).

2.5 | Acoustic array and monitoring

Fish distribution and movements around LD2 were monitored between August–November 2016, April–November 2017, and April–August 2018 using an array of archival receivers (SR 3001; Advanced Telemetry Systems, Isanti, MN; continuous scan). We used 12 receivers in 2016 and 13 in 2017 and 2018 (Receiver #13 was added to monitor below spillway gates, Figure 1). Five receivers were installed in spillway gates using custom-built mounts in stop-log recesses located upstream of the gates to try and detect fish passing through the gates. Range tests showed these receivers detected fish within 250 m at times of moderate-low turbulence with reduced and highly variable ranges at times of high flow and turbulence (especially in the spillway gates). Three receivers were also positioned in or

TABLE 1 Fish captured and released in Pool 3 (nondisplaced)

Capture periods	Species	Number	Average total length (mm)	Standard deviation (mm)	Capture dates
Spring 2017	Common carp	15	713	34	04/20/2017 to 05/04/2017
	Walleye	13	689	39	04/19/2017 to 05/05/2017
	Channel catfish	2	602	45	04/21/2017 to 05/05/2017
Fall 2017	Common carp	20	721	50	10/10/2017 to 10/19/2017
	Walleye	6	663	35	10/12/2017 to 10/23/2017
	Channel catfish	1	570	—	10/23/2017
Spring 2018	Common carp	21	738	64	04/27/2018 to 05/10/2018
	Walleye	3	688	61	05/16/2018 to 05/23/2018
	Channel catfish	12	755	77	04/27/2018 to 05/17/2018

TABLE 2 Fish captured in Pool 2 and displaced to Pool 3

Year	Species	Number	Average total length (mm)	Standard deviation (mm)	Capture dates
2016	Common carp	17	631	36	08/23/2016 to 09/27/2016
	Channel catfish	5	672	33	09/27/2016 to 10/06/2016
	Bigmouth buffalo	7	610	42	09/15/2016 to 09/27/2016
2017	Common carp	39	684	53	05/08/2017 to 10/09/2017
	Channel catfish	11	639	49	05/09/2017 to 06/29/2017
	Bigmouth buffalo	14	622	48	05/22/2017 to 08/23/2017

around the lock (attached to recessed ladder rungs), two others were fixed to U.S. Coast Guard buoys on custom rebar mounts (design by Alan Katzenmeyer, USACE), and two were mounted to sunken concrete blocks that were attached to the shore of the river via cable. Range tests showed that the full width of the river was typically covered by Receivers #6 and #7 (Figure 1). Receivers #1 and #2 were positioned further downstream to monitor possible mortality or downstream swimming in case fish were not encountered approaching LD2.

2.6 | Analysis of tagged fish data

Data were downloaded and then filtered to remove uncertain detections (i.e., single detections that were not followed by another within 3 s or multiples thereof within 18 s). We then determined the number of times that fish approached (challenged) LD2 by calculating the total days that individual fish were detected immediately below it at either Receiver #3 and/or #13. An individual detection on a single day was defined as an "approach." Approach rates between nondisplaced (Pool 3) and displaced Pool 2 fish were compared by a Mann–Whitney *U* test. Passage rates and paths of individuals through the spillway gates or lock chamber were also examined. First, we confirmed passage through the structure to get a passage rate. A fish was considered to have "passed" when it was detected at either upstream Receiver #6 and/or #7. Passage rate was the number of fish determined to have passed divided by the number of that species that had been released below LD2. Second, we determined path of passage. Successful passage through the lock required that a fish be detected at Receivers #3, #4, and/or #5 followed by #6 or #7 in that order (Figure 2). Alternatively, to be considered as having passed through the spillway gates, passage had to include #6 and/or #7 (and possibly Receiver #13) but not Lock Receivers #3 and #4. For a 3-week period in 2018 (May 1 to May 24) Receivers #4 and #5 failed; when a fish was detected at #3 before being detected upstream at #6 of #7 during this period, its passage was labelled as "unknown." Receiver #7 failed for 97 days; to confirm that we did not miss possible spillway passages during this time, we compared passage rates when it was working (the vast majority of the study) with when it was not and found there was no indication of missed passages (see Section 4). Because the vast majority of fish moved upstream and approached LD2 for weeks (see Section 3), we did not specifically evaluate downstream passage although a few incidents were coincidentally noted. To test if passage distribution (i.e., passage rates through the lock vs. spillway gates) differed between Pool 2 and Pool 3 fish, we performed a 2 × 2 chi-square analysis (unknown passages were not included in this analyses), and when no difference was found (see Section 3), we combined these fish to take advantage of the larger sample sizes. Total passage rates of common carp and channel catfish were also compared with a 2 × 2 chi-square test.

2.7 | Computational agent-based FPM

Hypothetical passage rates of common carp through LD2 was modelled using our FPM model (Zielinski et al., 2018). This took place in two steps. First, we determined the hydraulic conditions of the river throughout the study (eight river flows between 7,000 cubic feet per second [cfs] and 61,000 cfs [open river]). We simulated flow distribution and water velocities below LD2 using ANSYS Fluent (version 19.2) CFD (see Supporting Information S1). The CFD model was developed using detailed river bathymetry, LD structure engineering plans, and records of gate operations provided by the USACE. The CFD model calculated velocities in three dimensions and was validated using field collected velocity data (see Supporting Information S1). Second, we modelled common carp passage through the spillway gates of LD2 using the hydraulic data calculated for all eight river flow conditions (see Supporting Information S2). We only examined common carp because we had the most telemetry data for this species, and they were the only species with swimming performance data for

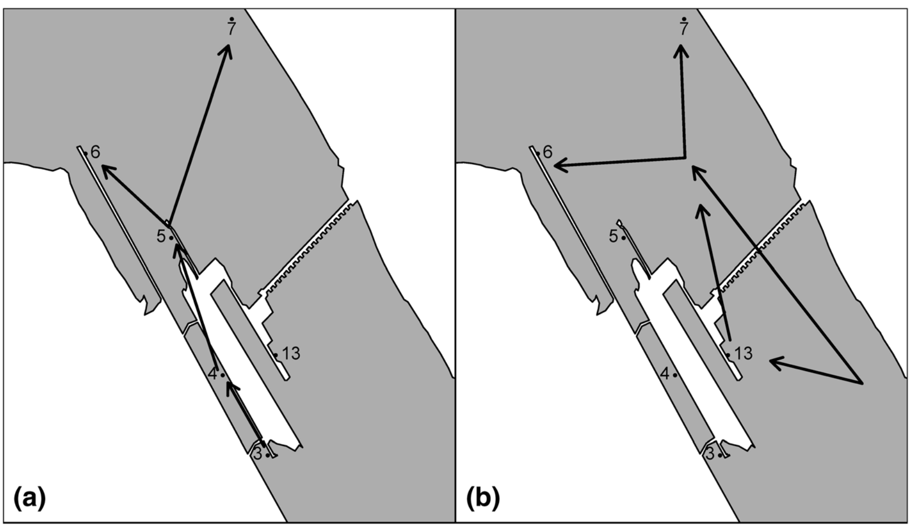

FIGURE 2 Sequence of fish detection at different locations used to determine whether fish passed through the lock chamber (a), or spillway gates (b), at Lock and Dam 2. Each number represents the location of a receiver. Arrows indicate the sequence of detections

large individuals (>50-cm TL) like we were tracking. Because data for common carp were sparse and had not been fit to a swim speed to endurance time curve before, we derived a relationship for its swimming performance using available data (see Supporting Information S3). We then used established protocols for the FPM (Zielinski et al., 2018) to generate 5,000 "agents" (simulated common carp), which were assigned sizes (e.g., total length 60, 65, 70, 75, and 80 cm) and swimming abilities that matched the range of the fish we had captured. Agents were randomly seeded 200 m downstream of the LD at depth of 1 m (studies using common carp implanted with depth acoustic tags showed them to swim at a medium depth of 1.1 m ± 1 m; Finger et al., 2019) and their upstream swimming and passage simulated (Zielinski et al., 2018). Simulations were conducted in three dimensions and repeated for all eight flow conditions and fish sizes with the option of lock passage removed. The fish passage index (FPI) was calculated by dividing the total number of successful passages by the total number of individuals simulated in each size class, and these values were binned into 10 groups (500 agents in each group) to obtain a sample variance. Mean ± *SD* passage index values were then calculated and plotted for each flow and compared to that seen for tagged common carp.

3 | RESULTS

3.1 | River conditions

During the course of this study, the Mississippi River fluctuated between 7,100 and 67,000 cfs and had a median river discharge of 32,160 cfs (1st quartile: 22,480 cfs, 3rd quartile: 42,880 cfs). LD2 was in open-river condition a total of 5 days (April 30 to May 4, 2018, Figures 3 and 4a).

3.2 | Approach (challenge) behaviour

We detected a grand total of 164 (88%) of our tagged fish below LD2 (i.e., 93% of tagged common carp, 86% of walleye, 87% of channel catfish, and 67% of bigmouth buffalo) on at least one occasion with channel catfish approaching less frequently than common carp. Pool 3 fish approached the downstream side of LD2 numerous times; individual common carp approached a median of 28 times (16.3, 43.5 first and third quartiles), channel catfish 5 times (3.0, 11.5), and walleye 29 times (12.5, 47.0). Similar values were noted for displaced Pool 2 fish: Common carp approached a median of 14 times (5.0, 48.0), channel catfish 5 times (3.0, 14.3), and bigmouth buffalo 6 times (3.0, 7.8). No differences were noted in the approach behaviour of Pool 3 and displaced Pool 2 common carp or channel catfish (Mann–Whitney *U* test: $W = 1084.5$, $p = .084$; Mann–Whitney *U* test: $W = 85.5$, $p > .1$).

3.3 | Passage rates and paths

A grand total of 186 fish was captured, tagged, and released below LD2. Of these fish, half (93) were displaced Pool 2 fish and the other half, Pool 3 fish. Overall, we monitored 54 (29%) upstream passages into Pool 2 (Table 3), with most fish passing through the lock chamber but some passing though the spillway gates and then during open-river condition. Only 8 out of the 54 passages (15%) could not have their route assigned. Known passages through the lock ($n = 36$) occurred at all river stages (Figure 4c), whereas all 10 known spillway gate passages (with the exception of one) occurred during open river (see below). Known passages through the spillways gates were only rarely confirmed by receivers located in the spillways but these events (as monitored by the two most upstream receivers) coincided with open river when turbulence was extremely high in the spillways, and we knew their range was very limited.

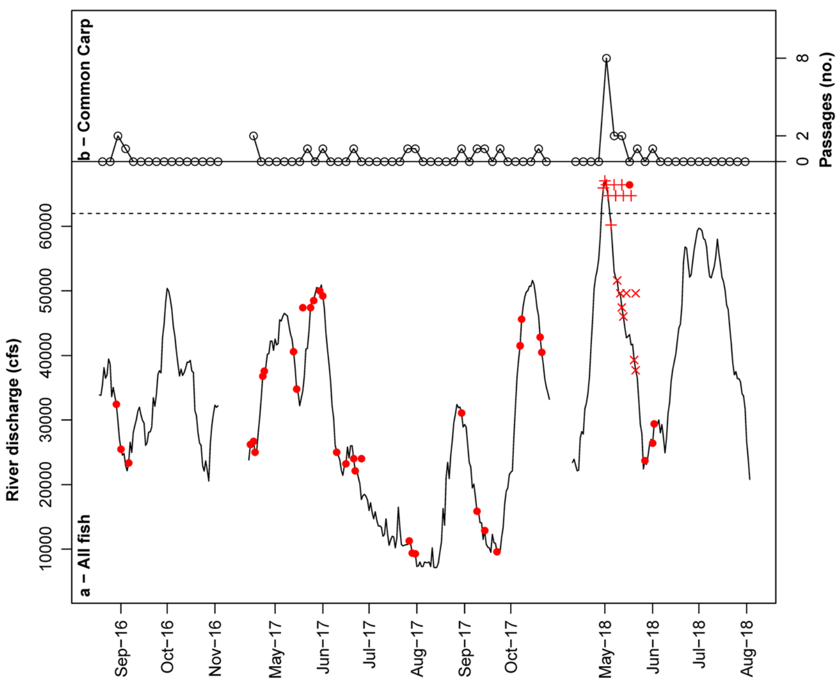

FIGURE 3 Plot showing fish passages monitored throughout this study. The top graph (a) shows the number of spillway gate passages for common carp only. The bottom graph (b) shows all passages for all fish versus river flow. Each symbol represents an upstream passage (circle: lock chamber, +: spillway gates, and x: unknown). The dashed line denotes when the river went into "open river," and the gates came out of the water [Colour figure can be viewed at wileyonlinelibrary.com]

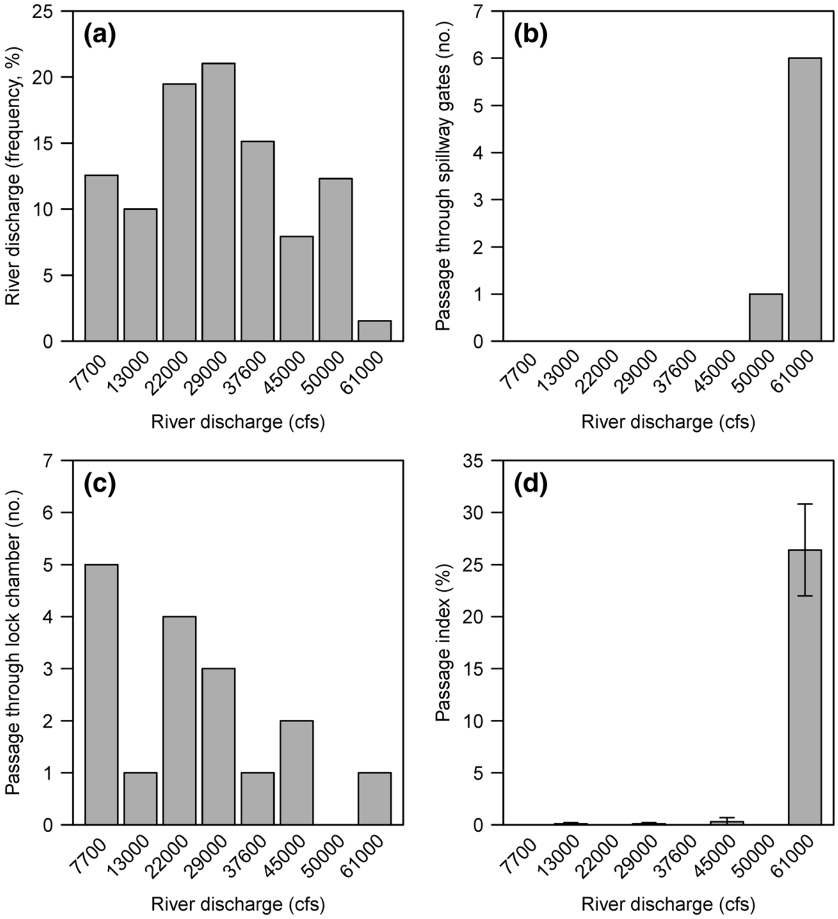

FIGURE 4 Overall common carp passage rates and river conditions. (a) Relative frequency of river flows experienced during the course of this study. (b) The number of common carp passages measured through the spillway gates during different river flows. (c) The number of common carp passages measured through the lock chamber during different river flows. (d) Passage index through the spillway gates for common carp as calculated by the fish passage model. Open-river conditions occur at a flow of 61,000 cfs

TABLE 3 Upstream passage rates through Lock and Dam 2 through the lock and spillway gates

Species	Experiment	Fish captured	Lock	Spillway	Unknown	Total
Common carp	Pool 3[a]	56	4	3	5	12 (21%)
	Pool 2[b]	56	13	4	0	17 (30%)
	Total	112	17	7	5	29 (26%)
Channel catfish	Pool 3[a]	15	3	1	3	7 (47%)
	Pool 2[b]	16	10	0	0	10 (63%)
	Total	31	13	1	3	17 (55%)
Walleye	Pool 3[a]	22	3	0	0	3 (14%)
Bigmouth buffalo	Pool 2[b]	21	3	2	0	5 (24%)
Grand total		186	36	10	8	54 (29%)

[a]Pool 3 = Nondisplaced fish.

[b]Pool 2 = Displaced fish.

Of a total of 93 Pool 3 fish, 22 (24%) passed through LD2 (Table 3). Of 56 common carp, a total of 12 (21%) passed through LD2, of which 4 of the 12 (33%) passed through the lock, and 3 (25%) passed through the gates, with 5 (42%) being undetermined (Figures 3 and 4c,d and Table 3). All three common carp known to pass through the gates did so in 2018 during open river conditions when river flow exceeded 61,000 cfs (Figure 3). Of the 22 Pool 3 walleye, 3 (14%) passed, and all 3 went through the lock (Table 3). Of the 15 Pool 3 channel catfish, a total of 7 (47%) passed through LD2 of which 3 of 7 (43%) passed through the lock, and 1 (14%) through the gates in 2018 and then during open river (3 were unknown; Table 3).

Of the 93 Pool 2 fish, 32 (34%) passed through LD2 (Table 3). Of 56 common carp, 17 (30%) passed through LD2, of which 13 of 17 (76%) passed through the lock, and 4 (24%) through the gates (Figure 4b,c). All spillway gate passages occurred in 2018 when the river was in open-river condition, except for one that occurred the following day when the river was still at 60,200 cfs (Figure 3). There were no unknown passages. Of the 16 Pool 2 channel catfish, 10 (63%) passed through LD2, and all of these (100%) through the lock (Table 3). There were no unknown passages. Of the 21 Pool 2 bigmouth buffalo, 5 (24%) passed through LD2, of which 3 (60%) passed through the lock, and 2 (40%) through the spillway gates. Both spillway gate passages happened in 2018 during open river. There were no unknown passages.

Displaced Pool 2 common carp seemingly used the lock more frequently than did Pool 3 common carp (23% vs. 7% of all fish, respectively) as did channel catfish (63% vs. 20% of all fish; Table 3). However, the passage routes of Pool 2 and Pool 3 fish did not differ significantly (common carp: $\chi^2 = 0.21$, $df = 1$, $p = .65$; channel catfish: $\chi^2 = 0.24$, $df = 1$, $p = .60$). Accordingly, we combined these datasets for common carp to plot overall passage rates for this species through the lock and spillways gates at different flows that matched those used for the FPM to evaluate for possible relationships (Figure 4b,c). When Pool 2 and Pool 3 fish were combined we detected a species difference in the proportion of upstream passage rates for common carp and channel catfish (26% and 55%, respectively; $\chi^2 = 8.04$, $df = 1$, $p < .01$). Further, we found that overall more channel catfish passed through the lock (15 of 33; 39%) than common carp (17 of 112; 15%).

3.4 | Fish passage model

Hydraulic modelling showed that although velocities at a depth of 1 m below LD2 did not vary greatly with river flow for flows below 61,000 cfs (open river), notable differences were seen when the gates were opened (Figure 5). In addition, when we examined water velocity with depth, we found velocities greater than 3 m/s occurred directly below the gate openings except during open river when velocities dropped below 2 m/s throughout the water column (Figures 6 and S1.1). Similarly, the FPM for common carp predicted that no common carp could pass for all flow conditions less than 45,000 cfs (FPI of 0%), only a few might pass at 45,000 cfs (FPI of 1%), none at 50,000 cfs, and a relatively large number during open river (>61,000 cfs; FPI of almost 30%; Figure 4d). Simulated fish tracks suggested common carp might pass at many locations across LD2 during open-river conditions, but are blocked across most of the structure at lower flows (Figures 5a,b and 6).

4 | DISCUSSION

This study investigated upstream passage of common carp, channel catfish, walleye, and bigmouth buffalo through a Mississippi River LD whose spillway gates rarely opened fully. We found that outside of a short 5-day period coinciding with open-river conditions and low water velocities under the spillway gates, these species passed through the lock chamber at a modest and species-specific rate and did not pass through the spillway gates. It appeared that the lack of passage through the spillway gates was likely caused by high water velocities that exceeded fish swimming abilities. A strong dependence of passage on high flows seen around open-river condition, was also described by our FPM (Zielinski et al., 2018). The high passage rate through the spillway gates during open river at LD2 is also consistent with that suggested by other studies (Lubejko et al., 2017; Tripp et al., 2014). Together, our results combined with our other simulations of the FPM (unpublished) suggest that many LDs likely impede upstream migration of both native and invasive fishes because of high water velocities during gate-controlled flow conditions but which change at the time of open river. Comparisons between FPM results (e.g., FPI ~2% at <61,000 cfs, but ~30% at open river) and the observed passage rates of common carp (e.g., 0% at <61,000 cfs, but ~6% at open river) provide evidence that our FPM provides reasonable, albeit conservative overestimates of fish passage for this type of structure.

The most important finding of our study was likely that the water velocities created by spillway gates, and calculated by our FPM, exerted quantifiable effects on fish passage through LD2. This model accurately predicted that even large common carp (80 cm) could not pass through LD2 gates except when the gates were completely (or very nearly) open. Although we experienced receiver failure on several occasions and may have missed some passages when Receivers #4 and #5 failed (19 days of 379 days in the study), it seems very unlikely that we missed any through the spillway gates even when Receiver #7 failed (97 days all during closed river). In particular, we did not detect any spillway passages during the entire 282-day period that the array was fully functional and this included the entire spectrum of river flow conditions including 5 days of open river. The fact that fish did not pass during gate-controlled flow, but did during open river, was consistent with FPM predictions. Nevertheless, our study represents but a single test of the FPM at a location which is very impermeable to passage (LD2 gates are very rarely out of the water). Additional tests of the FPM are warranted at more permeable locations. Although this study highlights the need to collect more data on fish swimming behaviour and performance to update the model, it seems reasonable that our FPM (given its conservative nature) might be used to guide efforts to adjust gate openings to impede bigheaded carps in the Upper Mississippi River. Study of LD8 suggests that this could be accomplished by precisely balancing flows across gates to create uniformly medium-to-high velocities that simultaneously reduce both scour and fish passage (Zielinski et al., 2018). Although a weakness of using the FPM to block invasive carp is that gates cannot be adjusted in open river conditions, at least in some locations, open river is relatively rare (LDs 2, 4, 5, and 8; Fishpro, 2004). Further, by simply adjusting gate to balance flows, up to 50% reductions in carp passage seem possible for most of the year (Zielinski et al., 2018; unpublished results). This could reduce the risk of spawning and improve the efficiency of carp removal programs (Lubejko et al., 2017). Eventually, possible effects of gate adjustments on the likelihood of native fish passage might also be considered but this would require both location-specific behavioural and swimming performance data to the FPM and these data presently do not exist.

We believe our second most important finding is that different species of fish use lock chambers to different extents that are seemingly not velocity dependent and can be substantial. Nearly twice as many channel catfish passed through LD2 than common carp, and those that did, passed exclusively through the lock chamber. Walleye also seemed to prefer the lock. Lock passage rates for all four species we studied also exceeded values previously reported for bigheaded carps (Lubejko et al., 2017; Tripp et al., 2014), suggesting that bigheaded carp might

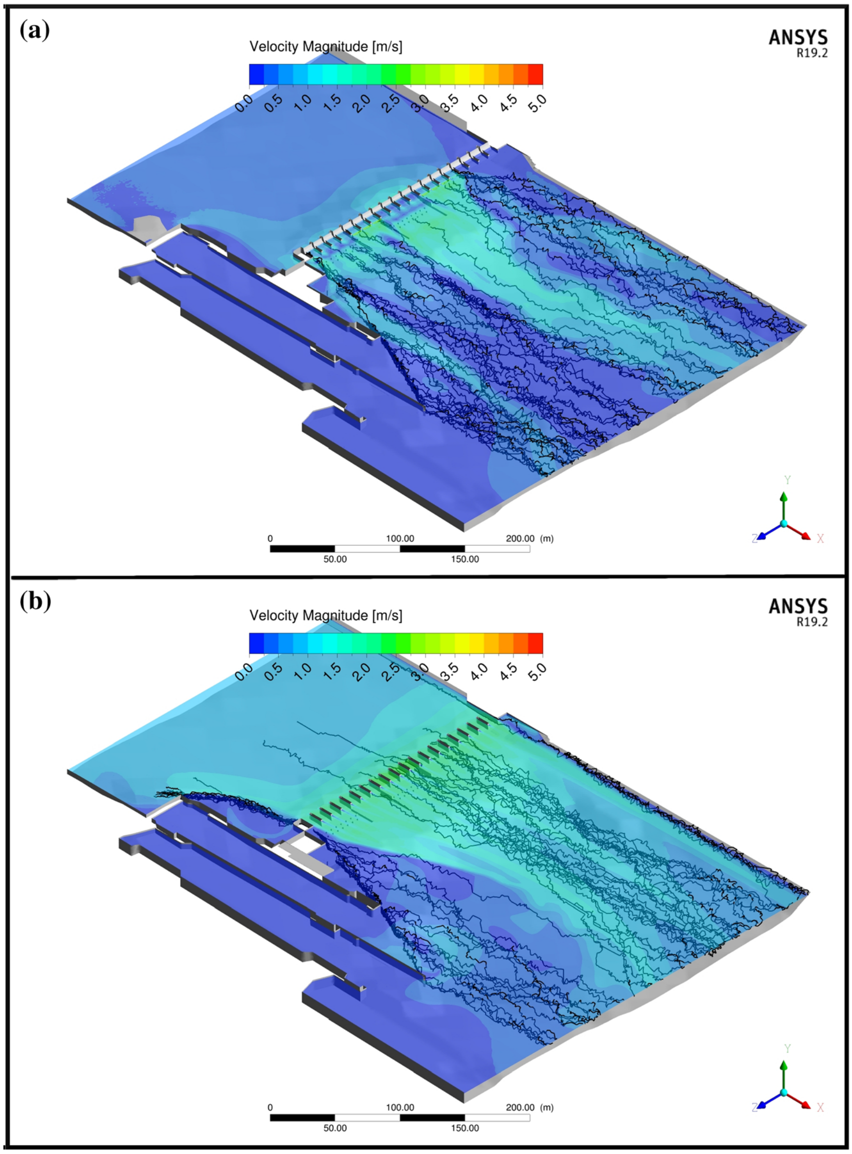

FIGURE 5 Plots showing simulated common carp (black tracks) superimposed on calculated surface water velocities downstream of Lock and Dam 2 in two dimensions (calculations were 3-D) at (a) 29,000 cfs and (b) 61,000 cfs (open river) [Colour figure can be viewed at wileyonlinelibrary.com]

be less likely than many fish to use locks and could perhaps be blocked at these locations using taxon-specific acoustic deterrents (Taylor, Pegg, & Chick, 2005; Vetter et al., 2017; Zielinski & Sorensen, 2016) with minimal impact on many native fish (Moser, Darazsdi, & Hall, 2000; Smith & Hightower, 2012). Finally, the overall passage rates we noted generally exceeded those noted by Tripp et al. (2014) and Lubejko et al. (2017), supporting the suggestion (Tripp et al., 2014) that there are location and species differences in passage rates.

Finally, our results also suggest that displacing common carp and channel catfish is a valid and interesting method to pursue to study passage. The fact that after displacement, fish moved upstream might indicate a tendency to return to former habitat and maybe use a home range. Indeed, homing has been observed for both fish species (Crook, 2004; Dauphinais, Miller, Swanson, & Sorensen, 2018; Pellett, Van Dyck, & Adams, 1998). The robustness of this apparent homing behaviour was supported by the lack of statistical difference between Pool 3 and Pool 2 fish passage rates. Nevertheless, dedicated studies of homing are needed.

In conclusion, our study, is the first to provide fine-scale detail on fish upstream passage through a LD structure in the Upper Mississippi River. Ours is also the first comparison between field observations and models of upstream fish passage through LDs based on water velocity. The concordance between field and modelling shows in a quantifiable manner that water velocity likely determines passage through spillway gates. It also strongly supports the long-suspected significance of spillway gate openings and open river to fish passage and the supposition that LDs, which rarely experience open-river conditions are especially important to riverine fish population dynamics and blocking invasive fish. Notably, we also demonstrate how species-specific behavioural tendencies of several previously unstudied species pass through lock chambers that could be used in managing invasive carp, perhaps with the help of our FPM. Although our validation of FPM predictions shows this tool could be useful, additional work could improve it by adding a behavioural component to make it more accurate, perhaps reducing the extent to which it overestimates. In particular, the utility and accuracy of the FPM would be improved by obtaining information

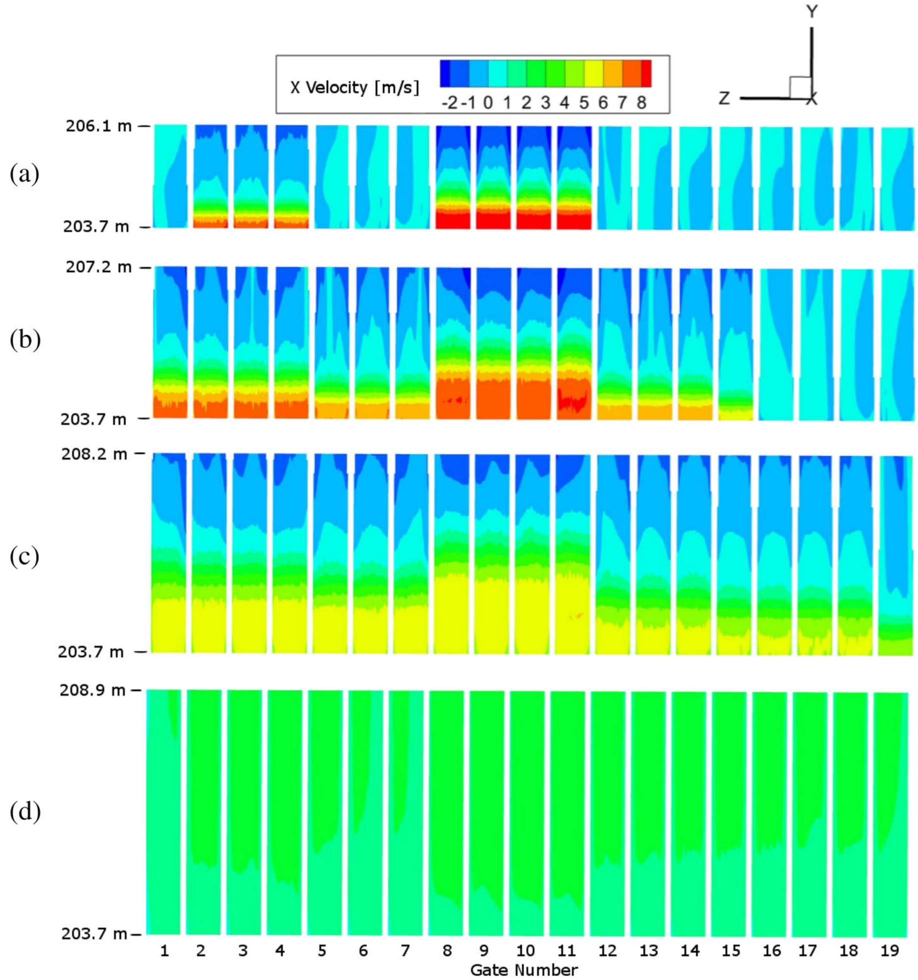

FIGURE 6 Plot showing calculated water velocities (meters/second) immediately downstream of the spillway gates running across the width of Lock and Dam 2 from the west to the east side of the spillway gates with depth at (a) 13,000 cfs, (b) 29,000 cfs, (c) 45,000 cfs, and (d) 61,000 cfs. Dark blue colours at the surface are areas of reversed flow (water flowing in upstream direction) caused by partially open gates. The gaps between velocity contours are concrete piers separating spillway gate bays. The *x* axis denotes bay number and *y* axis denotes the elevation (depth) [Colour figure can be viewed at wileyonlinelibrary.com]

on the frequencies with which fish challenge LDs and how they do so as the FPM presently assumes individuals only challenge once, and do so by finding an optimal path from a randomly determined starting place. Deviations from this seemingly conservative assumption could alter the absolute number of passages across time. An updated model with a behavioural component(s), combined with information on the number of fish actually present, would permit calculation of the actual number of fish passaging. By developing and testing this model here, we believe that we have highlighted how a better understanding of fish ecology, swimming performance, and fish behaviour below LDs could be used both manage native fishes and control invasive species.

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DATA AVAILABILITY STATEMENT

The data that support this study are available online (https://conservancy.umn.edu/handle/11299/201400?show=full).

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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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