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Analysing Habitat Connectivity and Home Ranges of Bigmouth Buffalo and Channel Catfish Using a Large-Scale Acoustic Receiver Network

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Abstract: The determination if fish movement of potadromous species is impeded in a river system is often difficult, particularly when timing and extent of movements are unknown. Furthermore, evaluating river connectivity poses additional challenges. Here, we used large-scale, long-term fish movement to study and identify anthropogenic barriers to movements in the Lake Winnipeg basin including the Red, Winnipeg, and Assiniboine rivers. In the frame of the project, 80 Bigmouth Buffalo (*Ictiobus cyprinellus*) and 161 Channel Catfish (*Ictalurus punctatus*) were tagged with acoustic transmitters. Individual fish were detected with an acoustic telemetry network. Movements were subsequently analyzed using a continuous-time Markov model (CTMM). The study demonstrated large home ranges in the Lake Winnipeg basin and evidence of frequent transborder movements between Canada and the United States. The study also highlighted successful downstream fish passage at some barriers, whereas some barriers limited or completely blocked upstream movement. This biological knowledge on fish movements in the Lake Winnipeg basin highlights the need for fish passage solutions at different obstructions.

Keywords: fish passage; fish telemetry; river restoration; ecohydraulics; *Ictiobus cyprinellus*; *Ictalurus punctatus*

1. Introduction

River connectivity may be interrupted by dams, weirs, and culverts, resulting in fragmentation of habitat [1]. Damming of large rivers is likely the most noticeable form of river fragmentation [2] and it is often observed to lead to hydromorphological alteration of the water course and changes in the biota [3]. The fragmentation of riverine ecosystems can result in a decline of fish biodiversity [4,5]. Particularly, the blockage of the migration of anadromous (e.g., salmon) and catadromous (e.g., eel) fishes has led to population declines or even extirpation of populations [6,7]. However, there is a lack of appreciation for the movement needs of potadromous fishes and the various scales that riverine fish species may move. This makes it more challenging to demonstrate the importance of river connectivity and the dispersal of riverine fishes that are crucial for population processes such as reproduction, rearing, and feeding [8]. Several freshwater fish species undertake long distance movements if their riverine habitat corridor is not impeded and competition for feeding and spawning sites can increase as dams disconnect, isolate, and reduce the number and size of habitats [9,10]. Consequently, river restoration efforts have focused on establishing connectivity to enable longitudinal and lateral fish movement to meet the life-history requirements for these species [11]. River restoration efforts that reconnect fragmented habitats are generally successful at improving fish populations [12] and isolated habitats are quickly recolonized after the removal of barriers [13]. If the removal of a barrier is unfeasible, increasing river connectivity through the installation of effective fish passage structures can be an alternate management strategy [14–17].

Riverine fish conservation requires including various spatial scales when considering longitudinal connectivity of rivers to allow access to resource use that may be influenced by food availability, water temperature, and suitable habitats that are found in different river sections [18]. Determining the scale of freshwater fish movements and the size of their home ranges remain a research priority particularly for imperiled species [19,20]. Here, we focus on two freshwater fish species with long distance movement behavior. Bigmouth Buffalo (*Ictiobus cyprinellus*) is a filter-feeder using its very fine gill rakers to strain food items from the water [21]. Bigmouth Buffalo spawn in the spring to early summer and lay adhesive eggs on plants. Currently, little is known about the movement patterns and home ranges of Bigmouth Buffalo. Channel Catfish (*Ictalurus punctatus*) are an omnivorous, benthic fish [21]. Channel Catfish spawn during spring or summer when the water warms to an optimal temperature of 21–28 °C. A mark-recapture study using Floy tags demonstrated that Channel Catfish undergo migratory movements [22], however, the study did not allow for determination of timing or extent of these movements. Both species are of interest from a biodiversity conservation perspective in the Lake Winnipeg basin, Canada. First, the loss of access to spawning and/or the degradation of spawning habitat due to water management practices is thought to have contributed to the decline in Bigmouth Buffalo (in the Saskatchewan – Nelson River watershed; SARA 2016a, www.dfo-mpo.gc.ca/species-especes/profiles-profils/bigmouth-buffalo-grande-bouche-eng.html). Second, Channel Catfish is the only known host fish of the endangered Mapleleaf (*Quadrula quadrula*; SARA 2016b, http://dfo-mpo.gc.ca/species-especes/profiles-profils/mapleleaf-feuillederable-sk-eng.html). The mussel is in decline and appears to be limited to the Red, Assiniboine, and Roseau rivers as well as tributaries on the east side of Lake Winnipeg. Barriers result in habitat loss and fragmentation, altered flow regimes, and may increase mortality by entrainment in turbines. Consequently, knowledge on fish movement is essential to inform conservation and recovery strategies, fishery management actions, and fish passage approaches to avoid migration barriers for these fishes.

The specific objectives of this study were to: (1) describe fish movement and home range of two fish species, Bigmouth Buffalo and Channel Catfish, in the Lake Winnipeg basin, (2) determine the transitions between different regions in the Lake Winnipeg basin using continuous-time Markov models on the telemetry data, and (3) to analyze if and to what extent fish passage may be impeded by the multiple anthropogenic structures in the Lake Winnipeg system including Red, Winnipeg, and Assiniboine rivers using a large-scale acoustic receiver network.

2. Materials and Methods

2.1. Study Site

Lake Winnipeg is the largest lake in the province of Manitoba, Canada (52°7′N 97°15′W) covering 24,514 km^2 (Figure 1). The lake is relatively shallow, elongated, and isothermal, with a mean water depth of 12 m and spanning 416 km from north to south [23]. Lake Winnipeg's watershed measures about 982,900 km^2 and covers much of Alberta, Saskatchewan, Manitoba, northwestern Ontario, Minnesota, and North Dakota. The lake drains to the north into the Nelson River at an average annual rate of 2066 $m^3 \cdot s^{-1}$ and ultimately into Hudson Bay. Lake Winnipeg is eutrophic, receiving excessive amounts of nutrient run-off from agricultural land use. Lake Winnipeg is also one of the largest hydro reservoirs in the world and supports one of the most productive commercial and recreational fisheries for Walleye (*Sander vitreus*). Several aquatic invasive species are established in the lake including

Common Carp (*Cyprinus carpio*), Zebra Mussel (*Dreissena polymorpha*), and Spiny Water Flea (*Bythotrepes longimanus*).

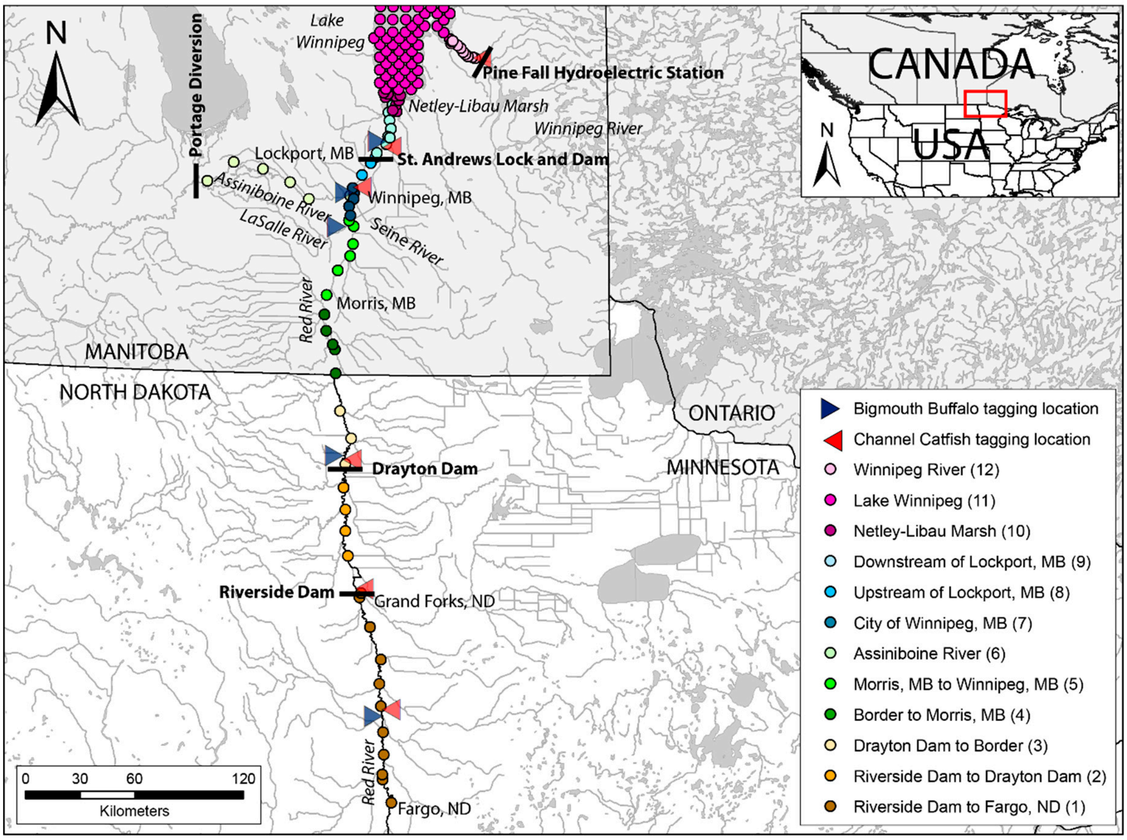

Figure 1. Map of the Lake Winnipeg basin including the Red, Winnipeg, and Assiniboine rivers and Netley-Libau Marsh. Tagging (►) and receiver (●) locations are indicated. Potential barriers to fish movement are the St. Andrews Lock and Dam, Drayton Dam, and Riverside Dam on the Red River, Portage Diversion Dam on the Assiniboine River, and Pine Falls Hydroelectric Generating Station on the Winnipeg River. River sections with the Section ID in parenthesis for the movement analysis using continuous-time Markov models are indicated on the map with different color codes.

The main tributaries of Lake Winnipeg analyzed in this study include the Red River flowing into the lake from the south and the Winnipeg River from the southeast (Figure 1). The Red River originates at the confluence of the Bois de Sioux and Otter Tail rivers between the States of Minnesota and North Dakota. It is approximately 885 km long and flows northward through the Red River Valley, forming most of the border of Minnesota and North Dakota before flowing into Manitoba. It empties into Lake Winnipeg through the Netley-Libau Marsh. There are three water level control structures in the main stem of the Red River: The St. Andrews Lock and Dam, the Drayton Dam, and the Riverside Dam, that potentially pose barriers to habitat connectivity and therefore fish movement. The St. Andrews Lock and Dam is located in Lockport, Manitoba at RKM 43.6 from the mouth of the Red River (Figure 1). It was constructed in the early 20th century to facilitate commercial navigation from Lake Winnipeg to the City of Winnipeg by inundating the Lister Rapids during the navigation season. The facility is operated and maintained by Public Works and Government Services Canada and consists of a dam, a navigation lock, and a fishway. Fish can move upstream through the lock and the fishway and downstream through the lock, fishway, and the spill.

The Drayton Dam, situated at RKM 327.3 on the Red River, was constructed in 1964 to provide water supply for agricultural and municipal use. It is located approximately 3 km north of Drayton, North Dakota (Figure 1). The dam consists of a concrete weir with a spillway length of 68.5 m and a crest elevation of 3.7 m above the natural riverbed. It operates as a run-of-river control structure and has no dedicated fish passage features.

The Riverside Dam at RKM 476.5 in Grand Forks, North Dakota (Figure 1) was originally built in 1922 as a water control structure. In 2001, it was restored to a rock ramp to provide erosion control, eliminate a hydraulic roller, provide fish passage and spawning habitats, as well as whitewater boating opportunities. It consists of a rock arch rapid with a 5% slope (3% near banks). Interestingly, it was the largest full width rock ramp fishway in terms of tonnage and height in the world at time of construction [24].

The Winnipeg River flows from Lake of the Woods to Lake Winnipeg (Figure 1). There are eight hydroelectric dams on the 235 RKM long river with the most downstream facility being the Pine Falls Hydroelectric Station at Powerview, Manitoba (commissioned in 1952). Flows on the Winnipeg River are controlled through the various dams by the Lake of the Woods Control Board. None of the dams on the Winnipeg River including the Pine Falls Hydroelectric Station provide for upstream fish passage. Downstream migrants can pass through the turbines or spillways.

The Assiniboine River originates in eastern Saskatchewan. It flows east into Manitoba (Figure 1). Its junction with the Red River is in the City of Winnipeg, Manitoba. The 1070 km long meandering river is prone to spring flooding. In 1970, the Portage Diversion Dam, located at RKM 163, was completed to divert flood flows into Lake Manitoba at Portage la Prairie, Manitoba. Fish can move downstream over the spillway but there is no upstream fish passage installation at the Portage Diversion Dam.

2.2. Fish Collection

Depending on the fish species, different collection methods were used. Bigmouth Buffalo (n = 80) were caught by boat electrofishing at five tagging locations in the Red River (Figure 1, Table 1). Channel Catfish (n = 161) were caught by angling with barbless hook and landed with rubber nets or with hoop nets (1 m diameter, 2.5 cm bar mesh). Collection efforts for Channel Catfish were conducted at six tagging locations (Figure 1, Table 1), including the Lower Red River and Winnipeg River where high recreational fishing efforts occur for trophy Channel Catfish.

Table 1. Tagging location with section ID, mean length, and body mass of Bigmouth Buffalo and Channel Catfish tagged with acoustic transmitters in the frame of the Lake Winnipeg Fish Movement Study. Bigmouth Buffalo were caught by boat electrofishing and Channel Catfish by angling.

Species	Year	Section ID	Section of Tagging Site	n	Mean (± S.D.)	Mean (± S.D.)
					Length (mm)	Body Mass (kg)
Bigmouth Buffalo	2017	1	Fargo, ND to Riverside Dam	12	593.25 (65.0)	3.11 (1.0)
	2017	3	Drayton Dam to Border	8	564.9 (48.6)	2.72 (0.5)
	2016	5	Morris, MB to Winnipeg, MB	20	561.2 (58.6)	2.85 (0.9)
	2016	7	City of Winnipeg, MB	20	621.1 (57.8)	4.01 (1.2)
	2017	9	Downstream of Lockport, MB	20	683.7 (83.3)	6.23 (2.6)
Channel Catfish	2017	1	Fargo, ND to Riverside Dam	9	671.8 (117.0)	3.46 (2.1)
	2017	2	Riverside Dam to Drayton Dam	16	751.4 (106.6)	5.53 (2.5)
	2017	3	Drayton Dam to Border	15	690.1 (93.6)	3.65 (1.6)
	2016	7	City of Winnipeg, MB	24	660.8 (73.7)	3.33 (1.2)
	2016	9	Downstream of Lockport, MB	67	751.2 (113.9)	5.66 (2.8)
	2016	12	Winnipeg River	30	640.0 (52.3)	2.98 (1.1)

2.3. Fish Tagging

Upon capture, fish were placed in holding tanks filled with ambient river water. Captured fish were measured and weighed immediately, only individuals with a body mass >1.2 kg were tagged, and undersized individuals (>2% tag: body weight) were released (Table 1). Acoustic telemetry transmitters (VEMCO, V16-4H, 16 mm diameter, 24 g, $6\frac{1}{2}$ years battery life, with an average transmission delay of 120 s with a pseudo random uniform interval between 80–160 s) were implanted in fish. As Channel Catfish are part of the recreational and commercial fisheries, individuals were also tagged with an external Floy tag (Floy Tag Inc., Floy T-bar anchor). Fish were placed into the Portable Electroanesthesia System (PES™, Smith-Root, Vancouver, WA, USA) to immobilize them during surgery, without use of chemical anesthetics. The PES™ was set to 100 Hz, 25% duty cycle, and 40 V. Pulsed direct current is an appropriate sedation for adult fish because it provides a surgery window of 250–350 s and fish recover quickly with minimal impact to vertebral integrity [25]. Upon sedation, fish were placed in a padded v-shaped trough. Ambient river water was continuously pumped over the gills using a recirculating flow-through pump system to maintain normal respiration during the surgical period (<5 min). A small incision was made posterior to the pectoral girdle just dorsal of the ventral midline. The acoustic transmitter was inserted posteriorly into the peritoneal cavity. Transmitter expulsion is common in Channel Catfish [26]. Consequently, for Channel Catfish a specific surgical procedure was used that tethers the transmitter around the cleithrum and/or supracleithrum near the scapula by looping a monofilament suture through the transmitter and around the bone [27]. Subsequently, the incision was closed with three to four interrupted sutures (standard surgical knots; 3-0 polydioxanone-II violet monofilament; Ethicon, Cincinnati, OH, USA). Fish were put in the recovery tank and released 10–15 min post-surgery at the tagging location. Surgical procedures were carried out in accordance with approved animal use protocols of Fisheries and Oceans Canada (FWI-ACC-2016-018, FWI-ACC-2017-001) and the University of Nebraska-Lincoln (Project ID: 1208).

2.4. Receiver Array

Acoustic receivers (VEMCO, VR2W and VR2Tx receivers, $n = 247$) were placed in Lake Winnipeg and the Red, Winnipeg, and Assiniboine rivers (Figure 1). Receiver spacing in the rivers varied between 5 to 30 km covering an accumulated distance of 860 RKM (Figure 1). As upstream passage at the Portage Diversion Dam and the Pine Falls Hydroelectric Station is impossible, no receivers were placed upstream of these two barriers. In Lake Winnipeg, receivers were installed on a 7×7 km grid [10]. Data from the receivers were downloaded annually (2016–2018) in the open water season, usually from June–September.

2.5. Data Manipulation and Analysis

All data manipulations and analyses were conducted in R [28]. The telemetry dataset for Bigmouth Buffalo and Channel Catfish consisted of >1.3 million individual detections. Subsequently, the 'dplyr' library for data manipulations was used to augment the computational efficiency of the subsequent data analyses [29]. Fish movements, home ranges, and river system connectivity between habitats were analyzed using the R package 'riverdist' [30] and the data analysis was separated by year. The R package 'riverdist' allows to read river network shape files, compute network distances as well as to as to display and calculate fish home ranges on a linear framework using telemetry data. To create the river network in R, we imported spatial coordinates (lat/long) and used the 'convUL()' function in the 'PBSmapping' package [31] to convert the lat/long coordinates into UTM and then applied the 'line2network()' function in 'riverdist' to create a river network, which was used to calculate the home range estimates. Fish movement data were used to calculate the home ranges in the Lake Winnipeg basin by species and year to describe and compare movements of Bigmouth Buffalo and Channel Catfish in the basin.

2.6. Continuous-Time Markov Model

Fish movement in the Lake Winnipeg basin was simulated by a continuous-time Markov model (CTMM) to recognize the continuous movement patterns that fish exhibit. Receivers were grouped using a combination of geographical proximity, geopolitical boundaries, tributaries, and/or physical barriers (see Figure 1, Table 2). A multi-state model was used to describe and quantify how fish transitioned between k unique states ($S = \{1, 2, \ldots, k\}$), and transitions were only allowed between adjacent states (i.e., river sections in the Lake Winnipeg basin; Table 2). Assuming that an individual fish is able to freely change back and forth between k states in continuous time, a $k \times k$ transitional intensity matrix (Q matrix), was defined as follows:

$$q_{rs}(t) = \frac{\lim_{\delta t \to 0} P[S(t+\delta t) = s \middle| S(t) = r]}{\delta t}, r \neq s$$

where t is time and q_{rs} is the instantaneous rate of change from the current state r to the next state s. The rows of the Q matrix sum to zero, while the diagonal entries are defined by $q_{rr} = -\sum_{s \neq r} q_{rs}$ and the off-diagonal entries can be any non-negative number [32]. Transition probabilities on both extents of the receiver network could not be predicted by the CTMM (Table 4). Subsequently, given that the Fargo, North Dakota to Riverside Dam river section was the southernmost extent of our receiver network, there is only a one way transition to an adjacent state possible. As a result, we can only predict transition from state 1 to state 2 but not transitions upstream from Fargo. Due to imperfect detections of the receivers, some fish movements in and out of a given state may have been undetected, leading to a potential of underestimating movements in the system.

Table 2. Transition matrix representing allowable transitions between states/sections represented in the continuous-time Markov model (CTMM). Dashes (-) represent no permissible transition while q_{rs} entries represent allowable transitions between different sections. In **bold** are the transition over the barriers (i.e., St. Andrews Lock and Dam, Drayton Dam, and Riverside Dam).

		To State/Section											
		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
From State/Section	**1**	q_{11}	$\boldsymbol{q_{12}}$	-	-	-	-	-	-	-	-	-	-
	2	$\boldsymbol{q_{21}}$	q_{22}	$\boldsymbol{q_{23}}$	-	-	-	-	-	-	-	-	-
	3	-	$\boldsymbol{q_{32}}$	q_{33}	q_{34}	-	-	-	-	-	-	-	-
	4	-	-	q_{43}	q_{44}	q_{45}	-	-	-	-	-	-	-
	5	-	-	-	q_{54}	q_{55}	-	q_{57}	-	-	-	-	-
	6	-	-	-	-	-	q_{66}	q_{67}	-	-	-	-	-
	7	-	-	-	-	q_{75}	q_{76}	q_{77}	q_{78}	-	-	-	-
	8	-	-	-	-	-	-	q_{87}	q_{88}	$\boldsymbol{q_{89}}$	-	-	-
	9	-	-	-	-	-	-	-	$\boldsymbol{q_{98}}$	q_{99}	q_{910}	-	-
	10	-	-	-	-	-	-	-	-	q_{109}	q_{1010}	q_{1011}	-
	11	-	-	-	-	-	-	-	-	-	q_{1110}	q_{1111}	q_{1112}
	12	-	-	-	-	-	-	-	-	-	-	q_{1211}	q_{1212}

Note: (1) Fargo, ND to Riverside Dam, (2) Riverside Dam to Drayton Dam, (3) Drayton Dam to Border, (4) Border to Morris, MB, (5) Morris, MB to Winnipeg, MB, (6) Assiniboine, (7) City of Winnipeg, MB, (8) Upstream of Lockport, MB, (9) Downstream of Lockport, MB, (10) Netley-Libau Marsh, (11) Lake Winnipeg, (12) Winnipeg River.

Additionally, the 'msm' library can calculate retention times (i.e., sojourn times or times spent in different sections) in the CTMM, where the retention times are exponentially distributed with mean $-1/q_{rr}$. Finally, a P_{next} matrix was constructed that defines the probability of changing from state r to state s in the next transition, regardless of the time elapsed. The diagonal entries of the P_{next} matrix are equal to zero.

3. Results

3.1. Home Ranges

Over the three study years, tagged Bigmouth Buffalo were consistently detected in high numbers (90–100% of tagged population) whereas Channel Catfish detection decreased by up to 40–78% of a given tagged population (Table A1). Bigmouth Buffalo consistently showed large individual home ranges varying from 4.2 to 621.9 km per year whereas individual Channel Catfish movement ranged from 3.4 to 101.3 km (Figure 2, Table 3). In all years, Bigmouth Buffalo had significantly larger home ranges than Channel Catfish (2016: mean 177.5 km vs. 32.7 km; $p < 0.001$; 2017: mean 132.6 km vs. 91.0 km; $p = 0.03$; 2018: mean 150.9 km vs. 60.0 km; $p < 0.01$, Figure 3). Fish were predominately moving in the open water season between April to October and were relatively inactive during the ice-on season from November to March (Figure 4).

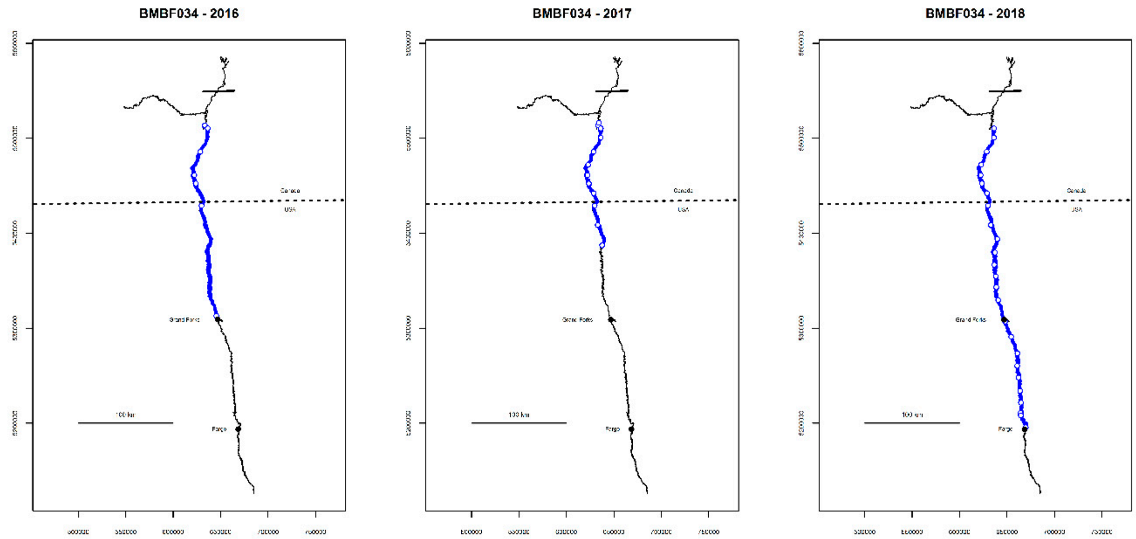

Figure 2. Example of the annual home range (km) of an individual Bigmouth Buffalo (BMBF034) from 2016 to 2018.

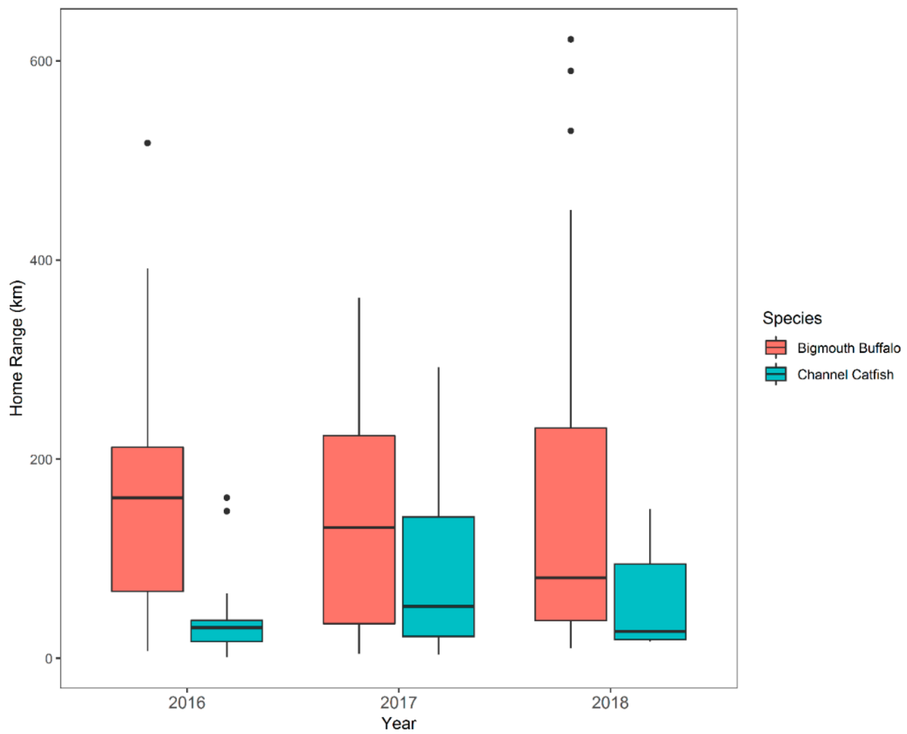

Figure 3. Home range (km) for Bigmouth Buffalo and Channel Catfish tagged with acoustic transmitters in various locations in the Lake Winnipeg basin.

Table 3. Inter-annual variations in species-specific river movements.

Species	Year	Distance (km)		
		Minimum	Mean (± S.D.)	Maximum
Bigmouth Buffalo	2016	7	177.5 (119.7)	517.5
	2017	4.2	132.6 (105.2)	361.9
	2018	10	150.9 (148.0)	621.6
Channel Catfish	2016	0.8	32.7 (28.0)	161.5
	2017	3.5	91.0 (93.8)	292.1
	2018	16.8	60.0 (56.6)	149.6

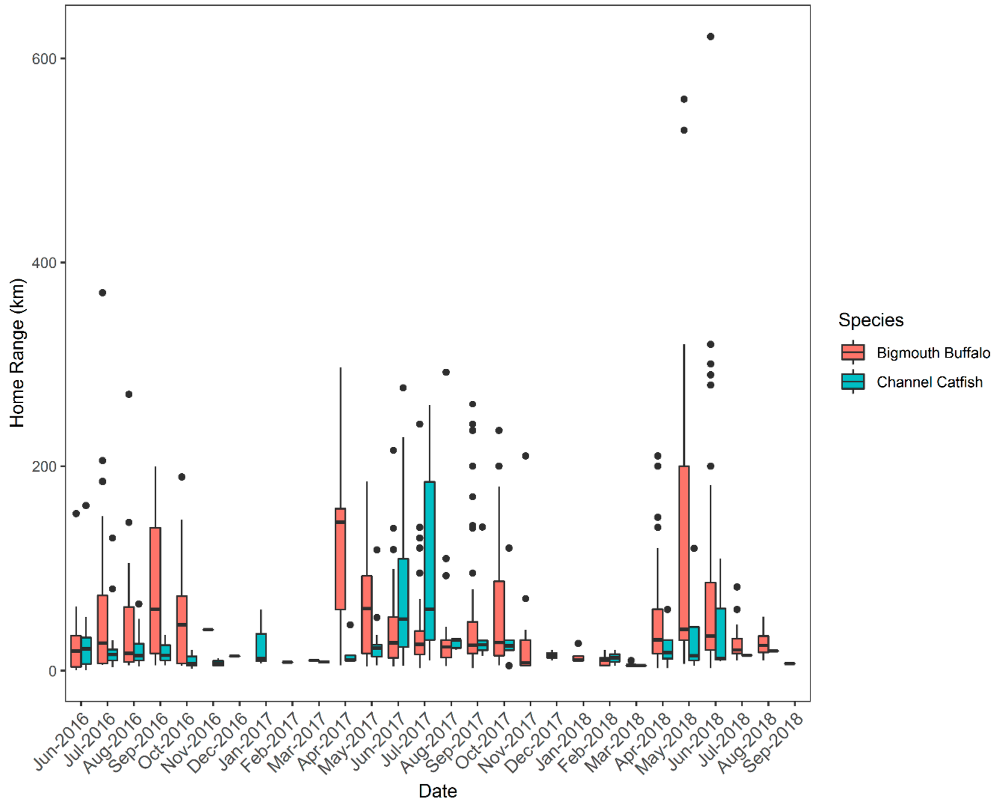

Figure 4. Monthly home range (km) of Bigmouth Buffalo and Channel Catfish tagged with acoustic transmitters in the Lake Winnipeg basin.

3.2. Transitions Over Barriers in the Basin and Between River Sections

Using the continuous-time Markov model (CTMM), we were able to predict the probability of fish transitioning to the adjacent river/lake sections (Figure 1) given the current section in which they were observed (P_{next}; Tables 4 and 5). For Bigmouth Buffalo in Section 2 (Riverside Dam to Drayton Dam), there was a low probability (4%) to move upstream over the rock ramp at the Riverside Dam but a 96% probability to migrate downstream over the Drayton Dam (Table 4). The probability for upstream transitions over the Drayton Dam was 46%. In regards to the St. Andrews Lock and Dam, the downstream transition probability of Bigmouth Buffalo was 3%, in comparison to an even lower upstream transition probability of 0.5%. The predicted transition probabilities between unimpeded rivers sections were relative high ranging between 39–100% (Table 2a). The CTMM did not predict an upstream transition probability for Channel Catfish at any of the three barriers on the Red River (i.e., Riverside, Drayton, and St. Andrews dams) but there was a very high probability for Channel Catfish to migrate downstream over the Drayton Dam (100%, Table 5). The predicted transition probability for Channel Catfish to migrate downstream over the St. Andrews Lock and Dam was also higher with

44% in comparison to Bigmouth Buffalo (3%). The transition probabilities for Channel Catfish did not appear to be limited during unimpeded river sections as up-and downstream transition probabilities were equal in unimpeded reaches (Table 2b).

Table 4. P_{next} matrix to estimate the probability of Bigmouth Buffalo moving to the next upstream or downstream section in the Lake Winnipeg basin. In **bold** are the transition over the barriers (i.e., St. Andrews Lock and Dam, Drayton Dam, and Riverside Dam). *Transition probabilities on both extents of the receiver network cannot be predicted.

		To Section											
		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
From Section	**1**	-	**1.000***	-	-	-	-	-	-	-	-	-	-
	2	**0.039**	-	**0.961**	-	-	-	-	-	-	-	-	-
	3	-	**0.455**	-	0.545	-	-	-	-	-	-	-	-
	4	-	-	0.53	-	0.47	-	-	-	-	-	-	-
	5	-	-	-	0.352	-	-	0.648	-	-	-	-	-
	6	-	-	-	-	-	-	1	-	-	-	-	-
	7	-	-	-	-	0.543	0.066	-	0.391	-	-	-	-
	8	-	-	-	-	-	-	0.966	-	**0.034**	-	-	-
	9	-	-	-	-	-	-	-	**0.005**	-	0.995	-	-
	10	-	-	-	-	-	-	-	-	0.974	-	0.026	-
	11	-	-	-	-	-	-	-	-	-	1.000*	-	-
	12	-	-	-	-	-	-	-	-	-	-	-	-

Table 5. P_{next} matrix to estimate the probability of Channel Catfish moving to the next upstream or downstream section in the Lake Winnipeg basin. In **bold** are the transition over the barriers (i.e., St. Andrews Lock and Dam, Drayton Dam, and Riverside Dam). *Transition probabilities on both extents of the receiver network cannot be predicted.

		To Section											
		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
From Section	**1**	-	**1.000***	-	-	-	-	-	-	-	-	-	-
	2	**0.000**	-	**1.000**	-	-	-	-	-	-	-	-	-
	3	-	**0.000**	-	1.000	-	-	-	-	-	-	-	-
	4	-	**-**	0.000	-	1.000	-	-	-	-	-	-	-
	5	-	-	-	0.407	-	-	0.593	-	-	-	-	-
	6	-	-	-	-	-	-	1.000	-	-	-	-	-
	7	-	-	-	-	0.598	0.038	-	0.363	-	-	-	-
	8	-	-	-	-	-	-	0.564	-	**0.436**	-	-	-
	9	-	-	-	-	-	-	-	**0.000**	-	1.000	-	-
	10	-	-	-	-	-	-	-	-	0.224	-	0.776	-
	11	-	-	-	-	-	-	-	-	-	0.074	-	0.926
	12	-	-	-	-	-	-	-	-	-	-	1.000*	-

Note: (1) Fargo, ND to Riverside Dam, (2) Riverside Dam to Drayton Dam, (3) Drayton Dam to Border, (4) Border to Morris, MB, (5) Morris, MB to Winnipeg, MB, (6) Assiniboine, (7) City of Winnipeg, (8) Upstream of Lockport, MB, (9) Downstream of Lockport, MB, (10) Netley-Libau Marsh, (11) Lake Winnipeg, (12) Winnipeg River.

Generally, Channel Catfish had a higher retention times in each of the sections compared to Bigmouth Buffalo (Table 6). Section 1 (Fargo, North Dakota to Riverside Dam) had the highest retention time estimates for both species. However, fish were able to freely move upstream from Fargo, ND into the Bois de Sioux and Otter Tail rivers and subsequently out of the range of our receivers, so any potential movements further upstream were not captured by our receiver network. Retention times for Bigmouth Buffalo were likely lower compared to Channel Catfish due to their increased mobility (Table 3) resulting in Bigmouth Buffalo likely spending less time in distinct sections. Fish residency in the Assiniboine River was very similar between the two species with 27.3 and 28.1 d for Bigmouth Buffalo and Channel Catfish, respectively. However, even though the retention times were similar, Bigmouth Buffalo appear to have swum further distance upstream with three individuals detected near the Portage Diversion Dam (near RKM 151) whereas Channel Catfish were not detected at the

Portage Diversion Dam. Movements from fish tagged in the Red River into the Winnipeg River (via Lake Winnipeg) were generally limited, as Channel Catfish were estimated to spend only 1.0 day in the Winnipeg River and no Bigmouth Buffalo moved into the Winnipeg River.

Table 6. Predicted mean retention times (in days) in a given river or lake section (see Figure 1) by the CTMM.

Section	River/Lake Section	Reach Length/Area	Bigmouth Buffalo	Channel Catfish
1	Fargo, ND to Riverside Dam	255 km	137.3	134.9
2	Riverside Dam to Drayton Dam	120 km	11.1	104.6
3	Drayton Dam to Border	89 km	12.8	7.7
4	Border to Morris, MB	84 km	7.1	13.4
5	Morris, MB to Winnipeg, MB	75 km	12.8	10.7
6	Assiniboine River	150 km	27.3	28.1
7	City of Winnipeg, MB	40 km	12.1	15.7
8	Upstream of Lockport, MB	21.5 km	15.1	24.6
9	Downstream of Lockport, MB	45 km	7.6	21.1
10	Netley-Libau Marsh	115 km^2	4.4	22.4
11	Lake Winnipeg	2862 km^2	5.7	2.0
12	Winnipeg River	15.5 km	-	1.0

3.3. Limitations to Habitat Connectivity in the RED, Winnipeg, and Assiniboine Rivers

In 2016, nine of the tagged Bigmouth Buffalo moved upstream over the Drayton Dam, while no Channel Catfish were detected undergoing an upstream movement over the weir (Table 7). In the following year, a total of twelve Bigmouth Buffalo and 17 Channel Catfish were observed to pass upstream over the Drayton Dam. In 2018, Bigmouth Buffalo completed 13 upstream movements and no Channel Catfish were observed. Downstream passage over the Drayton Dam was observed in 2017 (n = 4 Bigmouth Buffalo and n = 2 Channel Catfish) and 2018 (n = 13 Bigmouth Buffalo). Interestingly, both up and downstream movements over the weir at the Drayton Dam for both species appeared to occur during peak flows or descending hydrographs (Figure 5a,b).

Table 7. Number per fish species and year of up and downstream passage over the St. Andrews Lock and Dam, Drayton Dam, and Riverside Dam. In parenthesis the number of fish present in river section downstream for upstream passage and in the river section upstream for downstream passage. Number of fish detected on the receiver downstream (Downstream Presence) of the Portage Diversion Dam and of the Pine Falls Hydroelectric Station that are both impassable for upstream migrating fish.

Barrier	Passage/Presence	Bigmouth Buffalo			Channel Catfish		
		2016	2017	2018	2016	2017	2018
St. Andrews Locks and Dam	Upstream passage	0 (1)	3 (22)	1 (12)	0 (20)	0 (10)	0 (4)
	Downstream passage	1 (13)	4 (21)	1 (9)	5 (15)	3 (7)	0 (1)
Drayton Dam	Upstream passage	9 (27)	12 (25)	13 (26)	0 (0)	17 (23)	0 (0)
	Downstream passage	0 (5)	4 (20)	13 (19)	0 (0)	2 (11)	0 (0)
Riverside Dam	Upstream passage	1 (5)	0 (20)	3 (0)	0 (0)	0 (11)	0 (0)
	Downstream passage	0 (1)	0 (12)	4 (11)	0 (0)	1 (9)	0 (0)
Portage Diversion	Downstream presence	2 (10) *	1 (16) *	0 (4) *	0 (1) *	0 (0) *	0 (0) *
Pine Falls Station	Downstream presence	-	-	-	27 (30) **	6 (26) **	1 (18) **

* In parenthesis the number of fish observed in the Assiniboine River section. ** In parenthesis the number of fish observed in the Winnipeg River section.

Fewer fish passages were observed at the St. Andrews Lock and Dam; three Bigmouth Buffalo passed upstream over the dam in 2017 and one in 2018. Upstream passage of Channel Catfish was not observed. One single downstream passage of Bigmouth Buffalo was detected in 2016 over the dam, four in 2017 and one in 2018 whereas five Channel Catfish passed downstream in 2016 and three in 2017. Similar to the movement patterns observed in Drayton, up and downstream passage at the St. Andrew Lock and Dam appears also to be associated with peak and descending hydrographs in the open water season (Figure 5c,d).

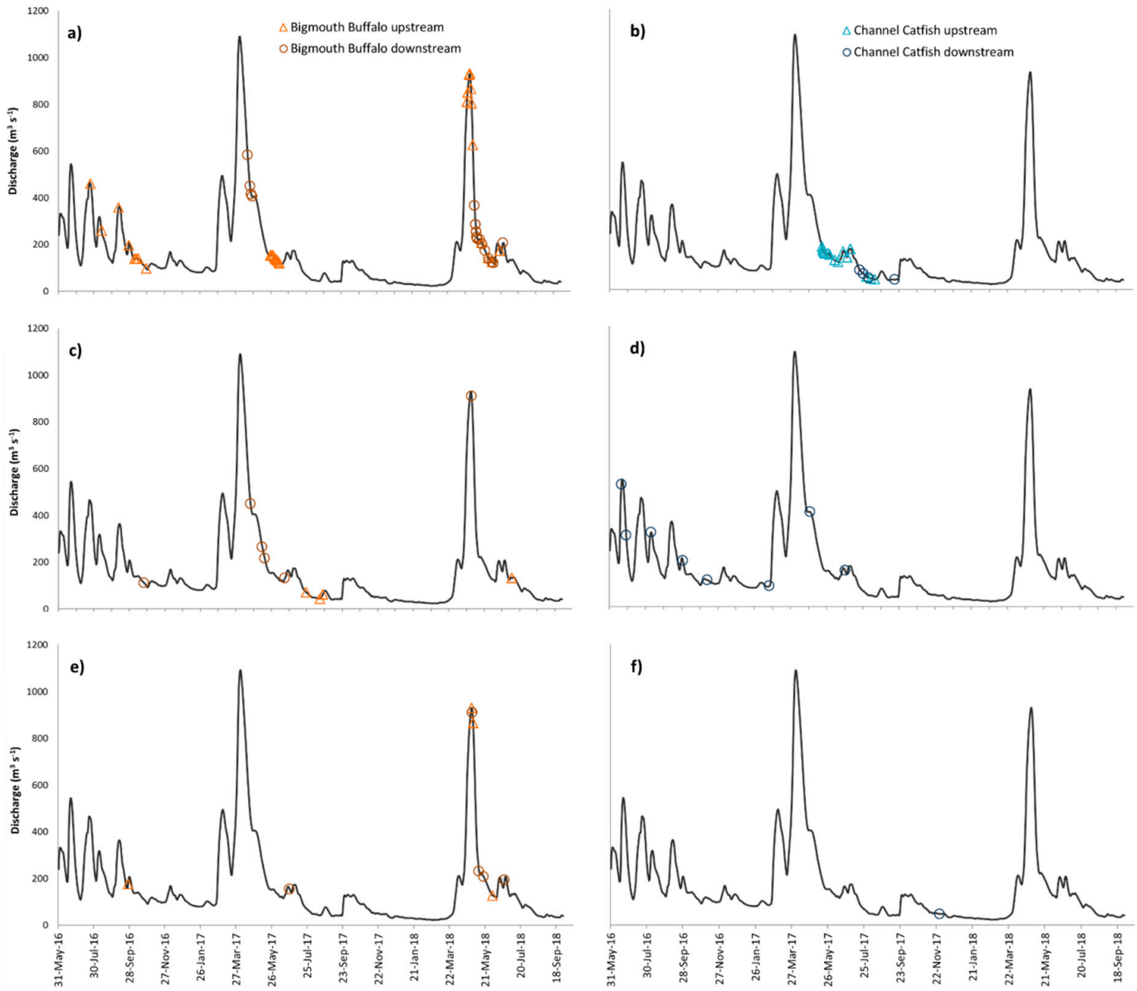

Figure 5. Timing of upstream and downstream movements of (**a**) Bigmouth Buffalo and (**b**) Channel Catfish over the St. Andrews Lock and Dam; (**c**) Bigmouth Buffalo and (**d**) Channel Catfish over Drayton Dam, and (**e**) Bigmouth Buffalo and (**f**) Channel Catfish over the Riverside Dam; in relationship to the discharge (daily mean, m^3 s^{-1}) in the Red River at Emerson, Manitoba (Water Survey of Canada, Hydrometric Station 05OC001).

The Portage Diversion Dam is impassable for upstream fish migration. Tag detections from the receiver closest to the Portage Diversion Dam suggest that the dam blocked the upstream movement of three tagged Bigmouth Buffalo in 2016 (n = 2) and 2017 (n = 1). The individuals remained below the diversion structure for up to four months in the summer, before returning into the Red River.

The Pine Falls Hydroelectric Station does not provide upstream passage. Tag detections revealed that Channel Catfish tagged in the Lower Winnipeg River moved upstream towards the Pine Falls Hydroelectric Station in each study year. In 2016, 2017, and 2018, 27, six, and one, respectively, of the 30 tagged Channel Catfish that were tagged in the Lower Winnipeg River moved up to the Pine Falls Hydroelectric Station where further upstream movement was impeded by the dam.

4. Discussion

The large-scale telemetry study allowed us to gain valuable insights into movement patterns and retention times of fish in the Lake Winnipeg basin and determine bottlenecks for habitat connectivity. Habitat connectivity describes how the environment allows or limits movement between different functional habitats such as feeding, spawning and rearing habitats [33]. Knowledge of species-specific functional connectivity for particular rivers is key given its importance for the persistence of populations. It provides useful perspectives on specific management strategies and is especially valuable in the context of fish passage and barrier removal projects because it can guide decision making to assign restoration priorities [34]. Functional habitat connectivity can be established through fish dispersal and migration patterns using telemetry [35]. By studying fish repeatedly over all seasons and a large geographical area, we observed large scale movement patterns for both, Bigmouth Buffalo and Channel Catfish, in the Lake Winnipeg basin. In particular, Bigmouth Buffalo demonstrated mean annual home ranges of 132.6 to 177.5 km. Our study confirmed the limited information available from other river systems on regular, large-scale movements in Bigmouth Buffalo [36]. In comparison to Bigmouth Buffalo, Channel Catfish had smaller home ranges with mean annual movements ranging from 32.7 to 60.0 km but still completed frequent movements over the geopolitical border. Our findings confirm observations by Siddons et al. [22] that Channel Catfish displayed frequent basin-wide, transboundary movements in the Red River, which is important information for fishery managers from different jurisdictions for the regulation and management of Channel Catfish fisheries.

The inter-specific differences in home range estimates may be influenced by the fact that the majority of Channel Catfish (107 out of 161) were tagged below the St. Andrews Lock and Dam, which may act as a partial barrier to movements [22]. Whereas only 20 of 80 tagged Bigmouth Buffalo were released below the St. Andrews Lock and Dam; thus, their potential for movement may have been less restricted than Channel Catfish. Additionally, Channel Catfish detections decreased each year, either because fish did not move, were not detected on a receiver, lost their tags, suffered natural mortality, were caught in commercial/recreational fisheries and removed from the study system or migrated out of the system. However, evidence in our dataset demonstrated that Bigmouth Buffalo displayed longer and more frequent movements through the available riverine habitats including tributaries (e.g., Seine, La Salle, and Assiniboine rivers) in comparison to Channel Catfish that were mainly observed in the main stems of the Red and Winnipeg rivers.

Understanding the spatial ecology of fishes is of crucial importance to fishery managers as it offers information on how fishes are distributed in both space and time [9]. For example, although Channel Catfish displayed transboundary movements in the Red River, different recreational fishery harvest regulations currently exist for the Manitoban portion of the of the Red River in comparison to the southern reach managed by Minnesota and North Dakota. Subsequently, our results underline the importance of maintaining habitat connectivity throughout the Red River basin and suggest considering a conjoint transboundary fisheries management plan. Similarly, the decline of Bigmouth Buffalo is attributed to the degradation and/or loss of spawning habitat related to water management practices, principally due to the regulation of water levels and channelization [37]. Furthermore, periods of drought, agricultural water demands, the introduction of Common Carp (*Cyprinus carpio*), and commercial fisheries may have also reduced the population size. In addition, the Portage Diversion Dam constructed in 1970, represents a barrier to upstream movement for fish in the Lower Assiniboine River, and coincides with the decline of Bigmouth Buffalo in the Upper Assiniboine and Qu'Appelle rivers that resulted in a commercial fishery closure for Bigmouth Buffalo in Qu'Appelle River in 1983.

In Canada, the Channel Catfish is the only known host species of the endangered Mapleleaf mussel, and the presence of the fish host is one of the key features determining if a given river system supports a healthy mussel population [38]. Among the threats for Mapleleaf populations are aquatic invasive species (e.g., Zebra Mussel (*Dreissena polymorpha*)), habitat loss and degradation, water quality, and siltation, which can negatively impact filter-feeding mussels. Mapleleaf populations can potentially be recovered by their host, the Channel Catfish, as one of the adaptive functions of mussel parasitism of migrant hosts is they can transport glochidia up and downstream. If passage of Channel Catfish is restricted by barriers, it likely poses a constraint on Mapleleaf populations. Being able to observe Channel Catfish movement over multiple years and large distances, the telemetry study allowed monitoring individual movement patterns of Channel Catfish. We observed Channel Catfish move large distances in the system but also pinpointed impediments in the free movement of Chanel Catfish in the Lake Winnipeg basin due to existing barriers that may inhibit the recolonization and recovery potential of Mapleleaf. Consequently, the telemetry study allowed us to gain valuable information for the Recovery Strategy of Mapleleaf and future risk management strategies [39].

The Portage Diversion Dam on the Assiniboine River and the Pine Falls Hydroelectric Station on the Winnipeg River are obvious barriers to upstream fish passage as no fishways are installed, while the St. Andrews Lock and Dam allows for some upstream fish passage through the locks, and a fishway and weir at Drayton is passable at higher water levels. However, the continuous-time Markov model (CTMM) highlighted a low transition probability at the St. Andrews Lock and Dam, suggesting even with the presence of the locks and the fishway, the structures only provide limited passage opportunities for upstream fish movement. It seems that the downstream movement of both, Bigmouth Buffalo and Channel Catfish, considerably supplement the Lower Red River population downstream of the St. Andrews Lock and Dam, given considerably fewer individuals are returning to the Upper Red River. Upstream movement over the St. Andrew's Lock and Dam occurred exclusively in the months of July and August. Our results highlight that the efficiencies to attract and/or pass fish in the St. Andrews Lock and Dam fishway may be limited. Consequently, a more detailed study at St. Andrew's Lock and Dam will be required to analyze attraction and passage efficiencies, as these are the key components to the success of fishways using adequate high resolution telemetry and time to event data analysis.

Due to the small number of fish tagged, the short observation period, and some unforeseen mortality, only a few fish were observed to navigate upstream passage over the rock ramp on the Riverside Dam site. Furthermore, due to the limitations of the receiver network extent, we were not able to accurately quantify downstream movement over the Riverside Dam. Subsequently, we could not fully assess the success and effectiveness of this river restoration project to provide fish passage by converting an existing low head dam to a rapids using a nature-like fish passage design at this time [24]. However, rock ramps are intended to provide a passable slope for fish by building up material on the existing riverbed directly downstream of the dam crest. The approach is particularly applicable for low head dams but has limitations for high head dams. More specifically, a rock arch rapids design was chosen at the Riverside Dam site [40,41]. The configuration has several advantages: It facilitates energy to be dissipated in the center of the rapids whereas the near bank velocities are reduced; boulders within the arch support each other adding stability; and it allows fish passage by providing low velocity eddies and passage is resilient to changing discharges. Further research should be conducted on the ramp to establish its efficiency [14].

The importance of the natural flow regime with its flow variability (i.e., timing, duration, frequency, and rate of change of flows) is well recognized as a driver of ecosystem processes [3,42]. Our telemetry study enabled us to reveal an interesting timing of fish movement in relation to the hydrograph. Movements of Bigmouth Buffalo and Channel Catfish in the Red River seem to be triggered by peak flows and movements were detected close to the peak or during the descending hydrograph limb. This information is useful for approaches such as by Yarnell et al. [43] that focus on retaining specific process-based components of the hydrograph also referred to as functional flows instead of trying to mimic the full natural flow regime. To optimize the functionality of flows, knowledge about which flows trigger fish movement and other life processes are key elements [44].

Anthropogenic instream barriers, such as weirs and dams serve human needs such as hydroelectric generation or flood control, but they may restrict fish movements. Consequently, when barriers are constructed there is concern in regards to changes in fish community assemblages and for potadromous species that are using diverse habitat types at different times of the year and life stages [45]. Truncated distributions, degraded fish assemblages, and changes in age class composition are frequently observed below dams and weirs in Midwestern and Prairie rivers [46–49]. Continued research will be required to study how the two study species are impacted by barriers and how the barriers impact their reproductive success, and what adjustments are needed to increase the fishway attraction and passage efficiencies.

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Appendix A

Table A1. Number of tagged fish per species and tagging site that were detected in each year of the study.

Species	Section ID	Section of Tagging Site	Year	n
Bigmouth Buffalo	1	Fargo, ND to Riverside Dam	2017	12
			2018	12
	3	Drayton Dam to Border	2017	8
			2018	7
	5	Morris, MB to Winnipeg, MB	2016	20
			2017	20
			2018	17
	7	City of Winnipeg, MB	2016	20
			2017	18
			2018	18
	9	Downstream of Lockport, MB	2017	19
			2018	19
Channel Catfish	1	Fargo, ND to Riverside Dam	2017	9
			2018	1
	2	Riverside Dam to Drayton Dam	2017	12
			2018	3
	3	Drayton Dam to Border	2017	10
			2018	3
	7	City of Winnipeg, MB	2016	22
			2017	8
			2018	2
	9	Downstream of Lockport, MB	2016	64
			2017	31
			2018	14
	12	Winnipeg River	2016	30
			2017	26
			2018	18

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