

# Bigmouth Buffalo (*Ictiobus cyprinellus*) migratory behaviour and seasonal home range overlap are functions of geographic space in a fragmented riverscape

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## Abstract

In temperate rivers, where environmental conditions vary seasonally, many fishes migrate among summer, spawning, and winter habitats. Dams disrupt these migrations, limiting access to habitat and potentially affecting populations. Bigmouth Buffalo (*Ictiobus cyprinellus*) is a species of fish with at-risk populations in central Canada. The impact of dams on the extent of Bigmouth Buffalo migration and the overlap between summer and winter home ranges is unknown. Here, we assessed the migratory history of 80 Bigmouth Buffalo tagged with acoustic transmitters in the Red River (USA and Canada), a large binational waterway regulated by semi-passable dams. We sought to understand when and why Bigmouth Buffalo migrate, and how river use varies seasonally. Following more than 6 years of data collection, we found that the degree and probability of overlap between winter and summer home ranges varied by river section between barriers. Importantly, overlap was lowest in the longest continuous river section where well-defined migratory behaviours were observed. The results of this study reveal previously unknown details about Bigmouth Buffalo migration, demonstrate the consequences of river fragmentation on geographic space use, and highlight the importance of river connectivity to fish migration.

**Key words:** fish telemetry, connectivity, migration, fish passage, movement ecology, dams

## Introduction

Efforts to conserve migratory animals are routinely challenged by increasing anthropogenic disturbance and limited baseline data on habitat patch use (Bauer et al. 2016; Cohen et al. 2018; Marra et al. 2019). Migration is an essential component of life history strategies in heterogeneous environments, yet access to high-quality habitat may be limited if disturbance impacts structural connectivity. As disturbance often precedes initial data collection, conservation planning must rely on the status quo or establish quasi-baselines (Franklin et al. 2024). Information on habitat patch use is especially salient to conservation efforts directed towards migrants that are impacted by climate change and at risk because of severed connectivity (Nuñez et al. 2013; Keeley et al. 2021).

In aquatic ecosystems, barriers such as dams and weirs disrupt both longitudinal and lateral connectivity within and among networks of flowing waters and adjacent habitats (Grill et al. 2019). This impedes the flow of nutrients and aquatic organisms to fundamentally alter the environmental conditions to which species and populations have adapted. These barriers confine aquatic organisms to fragments of a river network, limiting the accessibility of geographical space

and therefore hampering the ability to move between seasonally changing habitats with different ecological niche conditions (Rahel and McLaughlin 2018; Franklin et al. 2024). Ultimately, the interplay between barrier positioning and habitat heterogeneity influences accessibility to habitat with seasonally-specific suitability.

Bigmouth Buffalo (*I. cyprinellus*) is a potamodromous North American freshwater fish and the largest member of the family Catostomidae. It is the only catostomid to use a filter-feeding strategy and strain plankton from the water (Stewart and Watkinson 2004). The species currently holds the record for oldest teleost, with the most recent maximum age estimate of 127 years (Lackmann et al. 2023). As with other periodic life history strategists (Winemiller and Rose 1992), Bigmouth Buffalo have delayed maturity, broadcast spawn with no parental care, reproduce infrequently, and exhibit high fecundity (Lackmann et al. 2019). At the northern extent of its range in south-central Canada, reproduction occurs from late-May to early-June in shallow marshes, flooded riverbanks, or lake shores (Stewart and Watkinson 2004). Precipitous declines in Canadian populations during the mid-late 20th century have been attributed to commercial fish-

ing, habitat fragmentation, and potential competition with naturalized Common Carp (*Cyprinus carpio*; Goodchild 1989). In response, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) assessed the Saskatchewan-Nelson River populations as “species of concern” (COSEWIC 2009). Shortly thereafter, Bigmouth Buffalo was listed as Special Concern under the federal Species at Risk Act in 2011 (Fisheries and Oceans Canada 2020).

Bigmouth Buffalo occupy several watersheds across North America where dams and barriers are ubiquitous (Barbarossa et al. 2020). In one of the few riverine systems where Bigmouth Buffalo movement has been assessed, the Red River of the Hudson Bay Basin, home ranges can exceed hundreds of kilometers in undisrupted stretches of river (Enders et al. 2019). Where rivers span degrees of latitude and resource availability changes seasonally, habitat fragmentation is likely to disrupt migratory behaviours (Fretwell and Lucas 1970; Fretwell 1972). Examining how and when Bigmouth Buffalo occupy habitats in fragmented systems is a logical step toward uncovering the factors impacting an already imperiled species.

To better understand the effects of river fragmentation on Bigmouth Buffalo migration and seasonal home ranges, we examined 6.5 years of passive telemetry data collected in the Red River watershed. Specifically, we investigated the conditions under which Bigmouth Buffalo moved between summer and winter home ranges, and the overlap between these ranges, across river sections characterized by varying lengths. Due to the potential for seasonally changing habitat suitability and high habitat heterogeneity in the river network (Enders et al. 2019), Bigmouth Buffalo should exhibit distinct summer and winter home ranges (i.e., minimal overlap). Because Bigmouth Buffalo have large home ranges but limited dam passage in this river system (Enders et al. 2019), we hypothesized that the degree of seasonal home range overlap is a function of unrestricted geographic space as delineated by river section. In this context, the probability of home range overlap will be minimized where Bigmouth Buffalo are most at liberty to find the seasonally available resources and conditions that maximize fitness among the heterogenous riverscape. This research is intended to enhance the long-term survival of Bigmouth Buffalo by uncovering consequences of habitat fragmentation, thereby informing effective management strategies for the species.

## Methods

### Study site

The study area is contained within the Lake Winnipeg watershed (~1 000 000 km<sup>2</sup>), which encompasses parts of Alberta, Saskatchewan, Manitoba, Ontario, Minnesota, North Dakota, South Dakota, and Montana (Fig. 1—inset map). Land use in the watershed is dominated by cropland agriculture with considerable nutrient inputs draining north into Lake Winnipeg (ECCC 2020). In the current study, 80 Bigmouth Buffalo were tracked in the Red River sub-watershed, including the eastward flowing Assiniboine River and northward flowing Red River of the North (herein referred to as the Red

River; Fig. 1). Given the low elevation landscape, the Red River sub-watershed is prone to both recurring flooding and periods of low discharge.

The Red River is the largest river in the sub-watershed and forms the boundary between Minnesota and North Dakota, flowing approximately 885 river kilometers (rkm) north from Minnesota/North Dakota (ND), USA to Manitoba (MB), Canada. It is a low-energy, suspended sediment, mud-dominated, meandering river that occupies a shallow valley eroded into a clay plain with an alluvium that is primarily silt (Brooks 2003; Brooks 2017). Within the United States the river is typically one continuous run with some riffles present in the sections between Fargo and Riverside (F-R) and Wahpeton to Fargo (W-F; Fig. 1). Between Wahpeton and Drayton (W-F, F-R, R-D; Fig. 1), the river has high sinuosity (ranges from 1.7 to 2.3) and a low gradient (ranges from 0.04 to 0.25 m·km<sup>-1</sup>; Topp et al. 1994). In Canada (D-S, S-L, LW; Fig. 1), the Red River widens to eventually form a large delta (Netley-Libau Marsh) at the south end of Lake Winnipeg. Most of this reach is influenced by Lake Winnipeg seiche.

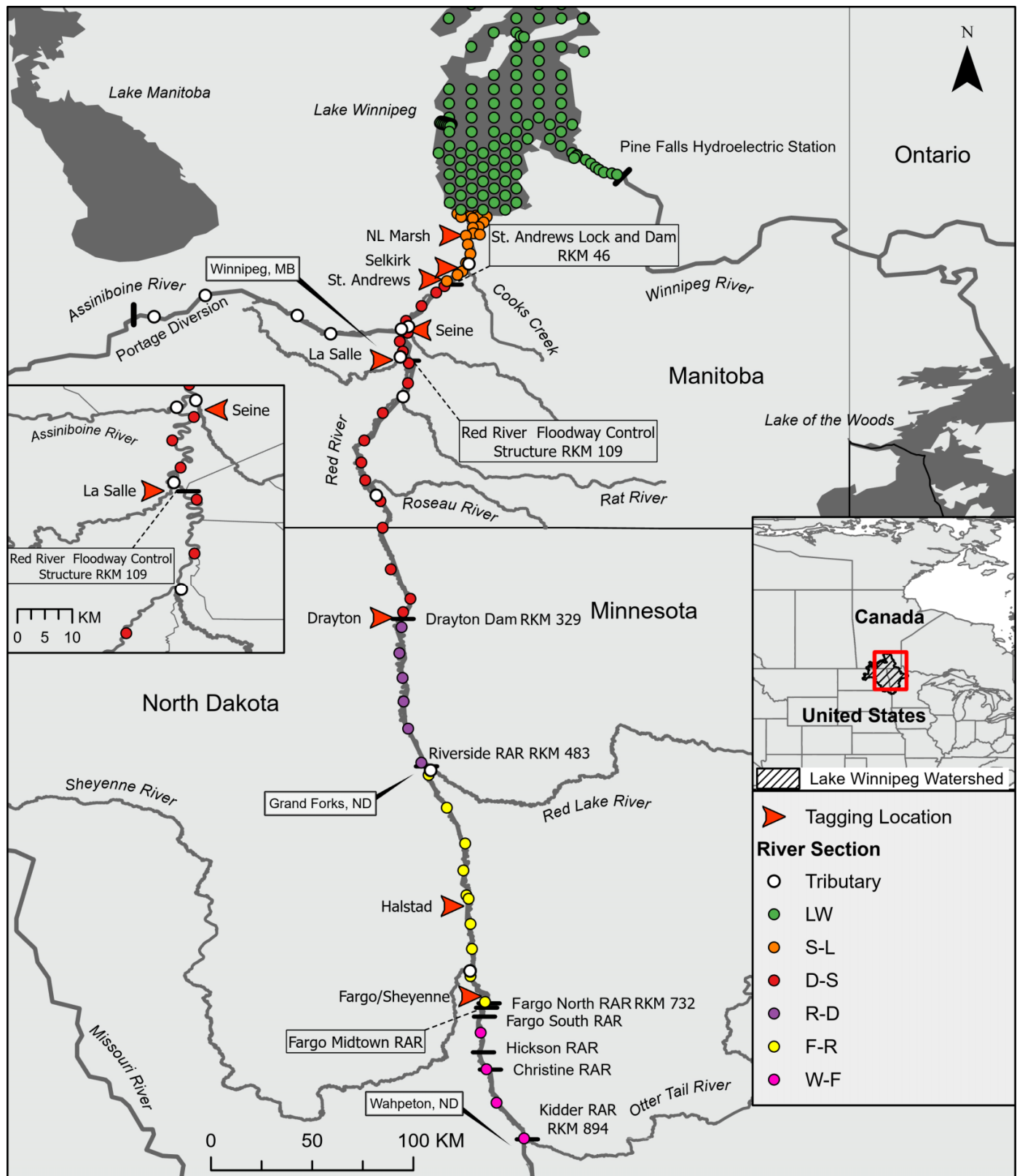
There are four types of barriers (lock and dam, low-head dam, radial arm floodgates, rock arch rapid (RAR)) that may cause fragmentation along the river, including: Kidder RAR (ND), Hickson RAR (ND), Christine RAR (ND), Fargo South RAR (ND), Midtown RAR (ND), Fargo North RAR (ND), Riverside RAR (ND), Drayton Dam (ND), Red River Floodway Control Structure (MB), and St. Andrews Lock and Dam (SALD; MB) (Fig. 1). We evaluated migration as well as summer and winter home ranges within and across sections of the Red River that were divided by partial movement barriers (Fargo North RAR, Riverside RAR, Drayton Dam, SALD; Fig. 1). These structures were previously shown to restrict movement resulting in low transition probabilities (Enders et al. 2019). Further details of these sections and partial movement barriers are described below.

The cities of Fargo-Moorhead along the Red River were the locations of the Fargo North (built in ca. 1933), Fargo Midtown (built in ca. 1961) and Fargo South (built in ca. 1933) dams, originally constructed for flood control. From 1999 to 2003, these three dams were converted to RAR to eliminate a hydraulic roller drowning hazard, mimic the microhabitat of natural rapids, and improve fish passage (Aadland et al. 2005). The resulting structures provide a step-pool channel with a centerline slope of 5% to allow passage of weaker swimming species (Aadland 2010).

The Riverside Dam (built ca. 1922) was located in the City of Grand Forks, North Dakota, approximately 476 rkm from the mouth of Lake Winnipeg. Originally designed for municipal water supply, the structure was modified in 2001 into one of the world’s largest full river width RAR to manage erosion, eliminate a dangerous hydraulic roller, and provide fish passage and spawning habitat (Aadland 2010). The conversion from low-head dam to rapids was achieved by constructing a wedge of fieldstone and cobble into a 5% slope (3% near shore) over the existing dam, above which ten boulder weirs now provide grade control, pool habitat, and fish-passable velocities (Aadland 2010).

The Drayton Dam at rkm 327 was constructed in 1964 to supply water for agricultural and municipal uses. The dam

**Fig. 1.** Map of the Lake Winnipeg watershed (inset map) and focal area with tagging locations and receiver arrays. Barriers (lock and dam, floodway control structure, low-head dam, and rock arch rapid (RAR) are defined by black rectangles. Receiver arrays are colored based on river section from home range overlap analysis (Wahpeton, ND to Fargo, ND (W-F); Fargo North RAR to Riverside RAR (F-R); Riverside RAR to Drayton Dam (R-D); Drayton Dam to St. Andrews Lock and Dam, MB (D-S); St. Andrews Lock and Dam to Lake Winnipeg, MB (S-L); and Lake Winnipeg, MB (LW)). Map source: State of North Dakota, Esri, TomTom, Garmin, FAO, NOAA, USGS, EPA, NPS, USFWS.



was originally designed as a concrete weir with a spillway length of 68.5 m and a crest elevation of 3.7 m above the natural riverbed. Operated as a run-of-the-river water control structure, the Drayton Dam was never intended to readily facilitate fish passage. The most recent evaluation of fish movement indicates that upstream passage is indeed limited for Bigmouth Buffalo (Enders et al. 2019).

The Red River Floodway, a trapezoidal-shaped diversion canal about 48 km long and 160–370 m wide, was constructed in response to a devastating flood in 1950 (Brooks 2017). The floodway begins just upstream (south) of Winnipeg, bypassing the city on the east side, before rejoining the river just downstream of the St. Andrews Lock and Dam. The Floodway Control Structure is just downstream of the Floodway entrance in the mainstem of the Red River. It regulates the Red River through Winnipeg when discharge exceeds 900–1000 m<sup>3</sup>·s<sup>-1</sup> by raising submerged radial arm gates to divert a portion of flow into the Floodway channel (Brooks 2017). During operation, the control structure is a barrier to upstream fish movement.

The St. Andrews Lock and Dam (SALD) at rkm 44 is located in Lockport, Manitoba. The lock and dam was operational in 1910 and designed for flood control and navigation over Lister Rapids. In 1913, the structure was retrofitted with a concrete alternate orifice and slot fishway with two sloping chutes running north and south. Fish can move upstream through the fishway or lock, when operated, and downstream through the fishway, lock, or over the dam (Enders et al. 2019). Species found in the fishway include Walleye (*Sander vitreum*), Sauger (*Sander canadense*), Saugeye (*S. vitreum* × *S. canadense*), White Sucker (*Catostomus commersonii*), Shorthead Redhorse (*Moxostoma macrolepidotum*), Channel Catfish (*Ictalurus punctatus*), Common Carp (*Cyprinus carpio*), Silver Chub (*Macrhybopsis storeriana*), River Shiner (*Notropis blennioides*), Moon-eye (*Hiodon tergisus*), Goldeye (*Hiodon alosoides*), White Bass (*Morone chrysops*), and Freshwater Drum (*Aplodinotus grunniens*) (Willis 1994). Although Bigmouth Buffalo have not been documented in the fishway, they are known to pass the St. Andrews Lock and Dam, both upstream and downstream (Enders et al. 2019).

## Receiver deployment

Acoustic telemetry receiver stations (Innovasea, VR2W and VR2Tx, Nova Scotia, Canada,  $n = 235$ ) were established in the Red River, Assiniboine River, and Lake Winnipeg beginning in 2016. Because the current study is part of a larger, multi-species ( $n = 9$ ) fish movement research and monitoring program in the basin, receiver distribution and spacing was decided by two main factors: (1) equipment availability through time and (2) location and number tagged. Receivers were gradually added to the study system as they became available (Table S1). Most fish in the overall program have been tagged in S-L, LW, and near the city of Winnipeg, with relatively less tagging outside of Canada. Based on these factors, receiver spacing in the Red River was 30 km in the USA portion of the river, 20 km from the USA border to the south end of Winnipeg, 10 km from Winnipeg to the St. Andrews Lock and Dam, and 5 km from St. Andrews Lock and Dam to Lake

Winnipeg (Fig. 1). Five receivers were deployed with a 30 km spacing in the Assiniboine River up to the Portage Diversion (rkm 151; Fig. 1). In 2016, receivers deployed at Drayton, ND, Halstad, MN, and Grand Forks, ND were replaced with the 30 km spacing design. Receivers were further deployed in distributary channels and wetlands associated with Netley-Libau Marsh ( $n = 8$ ) and into several smaller Red River tributaries, including: Devil's Creek, Cook's Creek, Seine River, La Salle River, Rat River, Roseau River, Red Lake River, and Sheyenne River. Receivers in Lake Winnipeg were arranged in a 5 km grid from the mouth of the Red River to just north of Gimli, a 7 km grid from Gimli to the Narrows, and a 14 km grid into the North Basin. By 2022, the total distance covered by the receiver network in rivers was approximately 860 rkm (Fig. 1). All river deployments were switched to VR2Tx receivers in 2017, with the exception of section LW where ~30% of receivers were still VR2W models in the final study year (Fig. 1, Table S1). Range testing was conducted at a receiver station in the Red River (rkm 24) in 2016, 2017, and 2018 (Table S2).

Receivers were connected to a 12.7 mm threaded rod (~50 cm long) with four cable ties. The threaded rod was fixed to the center of a ~45 cm × 45 cm × 10 cm granite block that weight ~50 kg. A rope ~12 m long was attached to an eye bolt fastened to the top of the threaded rod. The rope was further attached to a ~11–14 kg cross net anchor. The anchor was deployed upstream at which time the boat drifted until the rope was nearly tight. The granite block was then lowered in an upright orientation to the bottom, near the thalweg.

## Fish capture and tagging

Bigmouth Buffalo ( $n = 80$ ) were captured by boat electrofishing at eight tagging locations in the Red River drainage (Fig. 1). Tagging efforts spanned 2 years with 40 fish tagged in the La Salle ( $n = 20$ ) and Seine Rivers ( $n = 20$ ) in 2016. The additional 40 fish were tagged in 2017 between the Fargo/Sheyenne ( $n = 8$ ), Halstad ( $n = 4$ ), Drayton ( $n = 8$ ), St. Andrews ( $n = 9$ ), Selkirk ( $n = 9$ ), and Netley-Libau Marsh ( $n = 2$ ) tagging locations. Tagging efforts targeted Bigmouth Buffalo near the confluence of major tributaries, downstream of dams, and floodplain habitats. All Bigmouth Buffalo were tagged within 4 rkm of the Red River proper (Fig. 1). Fish were indiscriminately captured and held in tanks filled with ambient river water before being measured for weight (nearest gram), fork length (mm), and total length (mm). Tag burden was minimized by only retaining animals with a body mass > 1.2 kg (<2% tag:body mass; Crossin et al. 2017). To avoid the use of chemical anesthesia, retained fish were placed into the Portable Electroanesthesia System (PES., Smith-Root, Vancouver, WA, USA) for immobilization during surgery. 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 (Vandergoot et al. 2011). 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 inci-

sion was made posterior to the pectoral girdle just dorsal of the ventral midline. Sex was determined by attempting to examine gonads through the incision; however, the sex assignment was uncertain for >50% of tagged fish. An acoustic transmitter (Innovasea, V16-4 H, 16 mm diameter, 24 g, 6.5-year battery life, average transmission delay of 120 s with a pseudo-random uniform interval between 80 and 160 s) was inserted posteriorly into the peritoneal cavity. The incision was closed with three to four interrupted stitches (standard surgical knots; 3-0 polydioxanone-II violet monofilament suture; Ethicon, Cincinnati, OH, USA). The tag and all other surgical equipment were soaked in a disinfectant (Betadine; Avrio Health L.P., New York, New York) and rinsed in filtered water prior to use. Surgical gloves were worn to reduce the risk of infection. Post-surgery, fish were placed in a recovery tank for 10–15 min. All fish achieved full recovery as evidenced by their ability to maintain equilibrium and strong reflex reaction to grabbing the caudal peduncle. Upon recovery, fish were released at the tagging location. Fish capture and surgical procedures were approved by Fisheries and Oceans Canada's Ontario, Prairie and Arctic Animal Care Committee (OPA-ACC; FWI-ACC-2016-018, FWI-ACC-2017-001), following the Canadian Council on Animal Care (CCAC) guidelines; and the University of Nebraska-Lincoln's Institutional Animal Care and Use Committee (IACUC; Project ID: 1208), accredited by the Association for Assessment and Accreditation of Laboratory Animal Care (AAALAC).

We used a one-way ANOVA to test for differences in body size (fork length) among tagging locations. Length was log-transformed to achieve homogeneity of variance as indicated by a Levene Test. Pairwise comparisons were evaluated with a Tukey HSD test ( $\alpha = 0.05$ ). Residuals were visually inspected to further validate the model (Zuur et al. 2010).

## Environmental variables

Environmental variables for the Red River were downloaded from online gauging datasets using R packages tidyhydro (Water Survey of Canada, Albers 2017) and dataRetrieval (USGS, De Cicco et al. 2022). Starting in 2017, most receiver models in the river network were VR2Tx that also recorded temperature. Water quality data, collected bi-weekly during the open water season by the City of Winnipeg for each year (e.g., <https://legacy.winnipeg.ca/waterandwaste/sewage/monitoring/2017RiversReports.stm>), were included to increase the spatial resolution of turbidity and water temperature data. Temperature, discharge, and turbidity data (Fig. 2) were interpolated for any given location and date using distance-based interpolation from the gstat package in R (Pebesma 2004; Gräler et al. 2016).

## Telemetry analysis

Erroneous detections (e.g., due to noise or code collisions) and impossible movements were removed prior to the analysis (Pincock et al. 2010). Initial data processing was completed using the R package *actel*, which provides a reproducible method for identifying erroneous detections, generating outputs for future analysis, and visualizing fish movements (Flávio and Baktoft 2020). Actel computes movement

events based on thresholds of time between detections and minimum number of detections. The initial data filtering procedure identified movements for individual fish when at least two detections were recorded on a receiver. A new movement event was logged when the fish was detected again outside of the one-hour time interval at any given receiver (Flávio and Baktoft 2020).

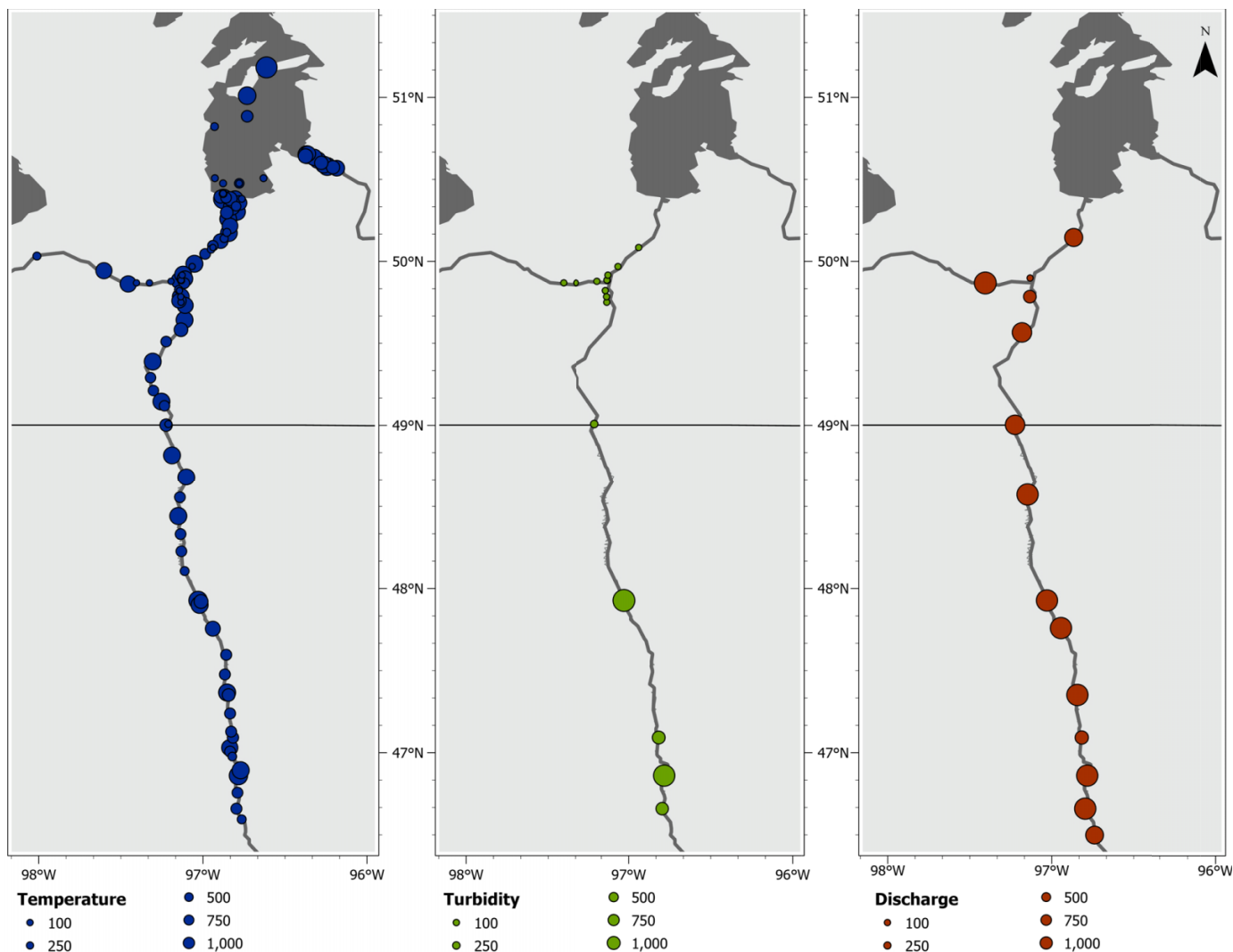
## Fish excluded from analysis

Of 3 689 629 detections, 430 were identified as erroneous based on speed and jump checks in the *actel* data filtering system. These erroneous detections arose due to overlapping detection ranges and impossible movement speeds among receivers in the Netley-Libau Marsh and the Winnipeg River. Of the 80 tagged Bigmouth Buffalo, one fish was never detected, and nine others were not detected for longer than 1-year post-release, with many failing to transmit in the final year of monitoring (2022) due to battery depletion. Only fish that were considered active for the entire year (detected before the first day of the year of interest and detected after the year of interest) were used for migratory analysis (see below). This criterion subsequently removed the movements from the year when a fish was tagged. The number of individuals included in the analysis ranged between 36 and 69 each study year from 2017 to 2022 (Table S3).

## Migration assignment

We defined migration as the directed movement of an individual over a distance greater than that associated with regular daily activities, resulting in redistribution across the landscape for some fitness benefit (Dingle and Drake 2007; Semlitsch 2010). Under this definition, we classified the movements of Bigmouth Buffalo through visual inspection of latitudinal positions over time, changepoint analysis, and metrics that are associated with migratory behaviour (successive unidirectional movements at increased speed). Changepoint analysis allows for the identification of points in a time series where a statistical property changes rapidly (Killick et al. 2012). Due to the orientation of the Red River and the direction of migratory movements, latitude was a sufficient proxy for a fishes broad-scale position in the riverscape (Fig. 1). Detections in the Assiniboine River were excluded from migration assignment because of the small number of fish ( $n = 4$ ) that occupied the river for extended periods of time. We converted the detected locations of each Bigmouth Buffalo into a time series of daily latitude using the last observation carried forward (LOCF) to fill in days where the fish was not detected (Colborne et al. 2019). The daily latitude of each individual was subset by year before changepoints were identified based on the mean using the *changepoint* package in R (Killick and Eckley 2014; Killick et al. 2022) and the binary segmentation method, specifying a maximum number of two changepoints (one fall and one spring migration in a year). Outside of the previously documented periods for migrations (April–May, September–October), Bigmouth Buffalo home ranges are typically less than 90 rkm (Enders et al. 2019). Therefore, if an individual made successive unidirectional movements—at speeds > 0.5 m·s<sup>-1</sup>—to a site > 90

**Fig. 2.** The locations of the collected water temperature, turbidity, and discharge time series data, with the relative size of the circle indicating the number of observations at that location. Map source: State of North Dakota, Esri, HERE, Garmin, FAO, NOAA, USGS, EPA, and NPS.



rkm away this increased our confidence that the movement was associated with a migration. Movement speed was calculated automatically by the residency analysis in *actel*.

Migration assignment was based on a set of rules (see Box S1 for detailed definitions) and conducted by two researchers independently. Discrepancies in the assignments were resolved by joint consensus. Upstream migration was assigned to southward movements from a summer to a winter site, and downstream migrations were assigned to northward movements from a winter to a summer site. We deemed the end of a migration as the first time of arrival on the last day of directed movement (i.e., subsequent movement event was at the same receiver) or the time before a movement in the opposite direction. If an individual appeared to stop or change direction, but then continued its initial path within a two-week period, the movement was still considered to be a migration.

Once each migratory event (upstream departure, upstream destination, downstream departure, downstream destination)

was classified, we summarized the characteristics of these events by determining Julian day, water temperature (°C), and latitude of each event. We also determined the total migration distance (rkm) for the upstream and downstream migrations. The cumulative number of fish migrating each week was overlaid on a heatmap of interpolated temperature, flow, and turbidity. To define the migration periods, yearly logistic curves were fit using nonlinear least squares to the cumulative number of fish that migrated each week. A logistic curve has three parameters, the asymptote ( $aymp = 1$ ), a midpoint when rate is steepest ( $mid$ ), and a scale parameter which sets the slope of the curve ( $scale$ ). The logistic curves were fit with nonlinear least squares using a self-starting logistic model (SSLogis) from the R package *stats* (R Core Team 2023). To determine the statistical significance of the coefficient estimates, we calculated the  $p$ -value associated with the Wald statistic. The fitted curve was then used to determine the spring and fall migration periods as all values  $>0$  and  $<1$  for the model fit to the cu-

mulative number of migrators per week in the respective period.

## Repeatability

Observations of migratory events for individuals on multiple occasions allowed us to calculate repeatability or the amount of behavioural variation arising from individual differences (Bell et al. 2009). Here, repeatability can be considered as the proportion of total variation in migration that can be attributed to differences between (compared to within) individuals (Nakagawa and Schielzeth 2010). We determined the repeatability and adjusted repeatability of characteristics (i.e., Julian day, water temperature, and latitude of departure and destination; and distance moved) associated with each Bigmouth Buffalo migration (herein referred to as migratory event characteristic) using linear mixed effects models for each migratory event characteristic as the response variables, and transmitter as a random effect (Nakagawa and Schielzeth 2010). Repeatability and adjusted repeatability were calculated using the *rptR* package in R calculating 95% confidence intervals from 10 000 bootstrap iterations and p-values were estimated using likelihood ratio tests, with a significance level of  $\alpha = 0.05$  (Stoffel et al. 2017). Year was tested as a fixed effect to account for: (1) annual changes in confounding factors that might influence phenology of the trait in question (Biro and Stamps 2015); and (2) estimate relative repeatability across years (i.e., adjusted repeatability), which is typically greater than the estimate of repeatability that ignores time related change (Kürten et al. 2022). Statistical assumptions were visually assessed and validated for each model.

## Summer and winter habitat overlap

Daily LOCF datasets of fish locations were split into winter and summer seasons for all fish—regardless of meeting the conditions for migration—by removing the period defined as spring or fall migration using the fitted values from the logistic regression. Overlap between summer and winter ranges was determined using the R package *riverdist* (Tyers 2022), where values ranged from 0 to 1. A value of 0 represented no overlap whereas all values  $> 0$  were converted to 1 and represented overlap between summer and winter ranges. River sections were defined by potential impediments to movement (Fig. 1). These structures were previously shown to restrict movement resulting in low transition probabilities (Enders et al. 2019). Fish were assigned to the river section in which they cumulatively spent the most time per season. This assignment was then compared to where they spent the most time overall to determine site fidelity (i.e., a binary indicator of whether the fish were in the area most used). Movements into tributaries were also included in seasonal linear home range, with tributaries included in the section where their confluence occurred. Fish that spent most of their time in the Wahpeton to Fargo (W-F) or Lake Winnipeg (LW) sections for a given season were not included in the analysis due to low sample size upstream of the Fargo North RAR and the change from linear (upstream or downstream) to multidirectional movement paths associated with the lake. The proportion of the section used was calculated by dividing home range size

by total length of the most used section; values greater than one (i.e., indicating passage across at least one of the obstacles dividing sections) were set to one. Linear mixed models (lme4, Bates et al. 2015) were used to determine: (1) the effect of river section, section use, year, and season, grouped by individual (random intercept), on log-transformed seasonal home range size (distribution = Gaussian); and (2) the effect of river section, section use, grouped by individual (random intercept), on the probability of overlap (distribution = binomial, link = logit). The model was validated by visual inspection of the residuals. While home range and body size are typically related (McCloughlin and Ferguson 2000), Bigmouth Buffalo lengths were considerably skewed among river sections, thus preventing us from including this term in the analysis of home range size and overlap.

## Results

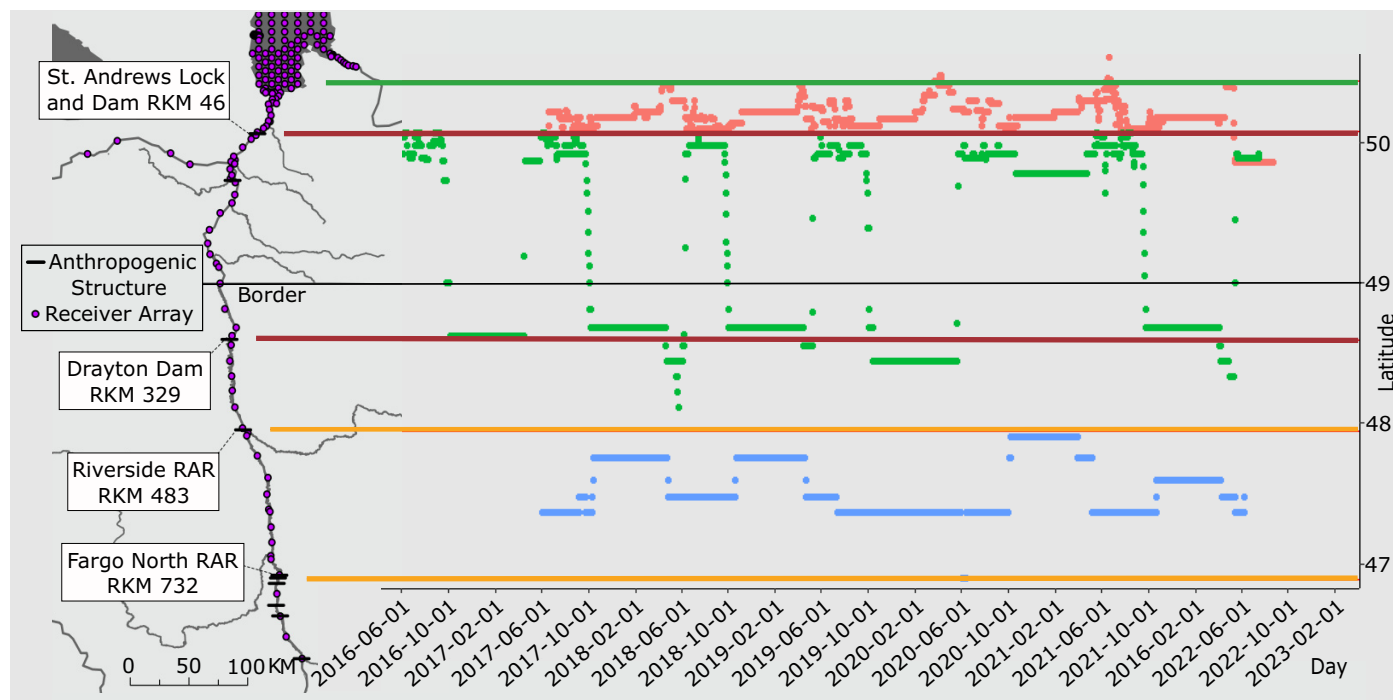
Total length of Bigmouth Buffalo differed significantly by tagging area ( $F_{2,77} = 12.75$ ,  $p < 0.01$ ), with those in the Red River downstream of SALD being significantly larger ( $0.684 \text{ m} \pm 0.015 \text{ SD}$ ) than all other areas (Tukey HSD,  $p < 0.05$  in all cases). Fish tagged between Drayton Dam and SALD ( $0.587 \text{ m} \pm 0.010 \text{ SD}$ ) were not significantly different than those tagged between Fargo North RAR and Riverside RAR ( $0.593 \text{ m} \pm 0.020 \text{ SD}$ ). There were no fish tagged between Riverside RAR and Drayton Dam or between Wahpeton to Fargo North RAR (Fig. 1).

## Characteristics of migration

Bigmouth Buffalo only met the criteria for migration in the longest unimpeded section of river (Fig. 3). Generally, these movements were directed downstream in the spring, departing from areas near Drayton Dam to locations around the La Salle and Seine rivers in Canada where a large proportion of fish were tagged (mean distance =  $210 \text{ rkm} \pm 107 \text{ SD}$ ). Subsequent upstream movements in the fall were from Canada to locations in the United States, generally downstream of Drayton Dam (rkm 280–310; 82% of destinations). In smaller sections of the river and the Assiniboine, movement patterns tended to be less directed (Fig. 3). Individuals in the section downstream of SALD moved regularly between the dam and into Netley-Libau Marsh, occasionally spending time in Lake Winnipeg. One individual moved approximately 60 km from the mouth of the Red River to Traverse Bay in the southeast portion of Lake Winnipeg. Individuals in the upper portions of the array (sections R-D, F-R, W-F; Fig. 1) often remained in their tagging section, but some individuals made longer distance movements outside of the reach in which they were tagged. Bigmouth Buffalo movement patterns were typically within the Red River proper for the majority of this study. Only two individuals spent greater than 50% of their time in tributaries, but over 88% were detected moving into a tributary at some point. The average proportion of time spent in tributaries was estimated at 13.2% (SD = 16.3%).

Migratory individuals generally moved from the United States to Manitoba in the river section between SALD and Drayton Dam. Spring movements from overwinter to spawning/summer ranges often began between rkm 252 and rkm

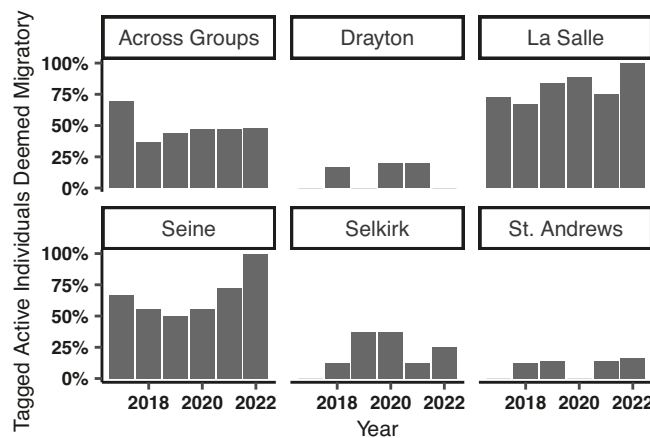
**Fig. 3.** Daily movements of three individual fish (IDs 19234, red dots, 20035, green dots, and 14985, blue dots) that represent typical movements in different sections of the river, with barriers indicated by the red horizontal lines, along with an orange horizontal line indicating the rehabilitated Riverside Dam (ND) and Fargo North Dam locations, and a green horizontal line indicating the confluence of the Red River with Lake Winnipeg. Map source: State of North Dakota, Esri, HERE, Garmin, FAO, NOAA, USGS, EPA, and NPS.



370 (near Drayton Dam; 70% of departures). Directed movements typically ceased between rkm 102 and rkm 112 (near the La Salle River; 63% of destinations). Most downstream migratory movements occurred after ice out when temperatures were rising. Downstream departure water temperatures averaged 10.6 °C (SD = 5.92), opposed to destination temperatures on the day of arrival of 12.6 °C (SD = 5.48). Upstream migration movements in the fall usually started between rkm 72 and rkm 132 (near the city of Winnipeg; 81% of departures) and ended below the Drayton Dam (rkm 280–310; 82% of destinations). The notable exception to this pattern occurred in 2019 and 2022, the only years that directed movements concluded upstream of Drayton Dam. Upstream migrations coincided with decreasing temperatures where departures (16.5 °C ± 0.7 SD) had higher temperatures than the destination areas (12.9 °C ± 1.0 SD) on the day of arrival. Temperature on the day of arrival to downstream destinations was on average 3.6 °C lower than the temperature on the day of departure (paired one way *t* test, *p* < 0.05).

The average speed of fish migrating upstream was 0.273 m·s<sup>-1</sup> (*n* = 1093, SD = 0.141) with a range of 0.003–0.883 m·s<sup>-1</sup> compared to fish migrating downstream with an average of 0.715 m·s<sup>-1</sup> (*n* = 988, SD = 0.464) and range of 0.002–1.960 m·s<sup>-1</sup>. Speeds during non-migratory behaviours averaged 0.374 m·s<sup>-1</sup> (SD = 0.323) with observed maximum speed of 2.46 m·s<sup>-1</sup>. Movement speeds exceeding 1.75 m·s<sup>-1</sup> (*n* = 20) were only observed between receiver arrays with spacing of

**Fig. 4.** Percentage of Bigmouth Buffalo migrating each year by tagging group and across all groups. The Netley-Libau Marsh, Halstad, and Fargo/Sheyenne tagging groups were excluded from the depiction as no observed migrations were recorded for fish in these locations.



less than 10 rkm. Movement speed had a weak positive correlation with temperature (*r* = 0.21, *p* < 0.01) and day length (*r* = 0.30, *p* < 0.01).

There were differences in the proportion of migratory individuals between years and between tagging locations (Fig. 4).

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Fish tagged in the La Salle and Seine rivers consistently had higher proportions of migratory individuals than the other tagging locations. There was additional variation in the proportion of migratory individuals across years within tagging groups; however, the proportion of migratory individuals in the entire tagged population remained relatively stable (Fig. 4). Of Bigmouth Buffalo that migrated at some point ( $n = 39$ ), most individuals ( $n = 31$ ) skipped migratory movements during at least two years of observation. Of individuals that were consistent in migratory behaviour (skipped one or fewer migrations,  $n = 8$ ), all except one of those individuals were tagged in the La Salle or Seine rivers.

Most (75%) of the 20 fish tagged downstream of SALD were able to pass upstream of the structure at some point and three individuals passed three or more times. Upstream passages only occurred between April and September, with the highest number recorded in August ( $n = 11$ ). Seven fish that successfully passed SALD also made migratory movements. Only one of these individuals showed consistent annual migratory behaviour after passing the dam. While eight of the fish did not migrate after passing SALD, most remained in upstream sections for several years. For example, after passing SALD in the fall of 2019, one individual swam to areas near the Halstad tagging location where it remained for the entire study (Fig. 1). Bigmouth Buffalo were not observed traveling upstream through the Red River floodway control structure while it was in operation (Fig. 1).

The majority of tagged individuals were able to pass upstream over Drayton Dam during the study ( $n = 43$ ), with a total of 120 upstream passage events. Nine fish were detected at the closest downstream receiver but never passed the dam. Due to receiver spacing, we cannot determine if those fish made passage attempts. Upstream passages over Drayton Dam did not occur outside of March–October. April ( $n = 48$ ) and May ( $n = 29$ ) had the highest number of passes followed by September ( $n = 12$ ), October ( $n = 11$ ), June ( $n = 11$ ), July ( $n = 5$ ), March ( $n = 2$ ), and August ( $n = 2$ ). Many of the spring passes were associated with migratory individuals that overwintered downstream of the dam and moved upstream before making a return trip downstream. Upstream passage over the other dams was less common, with 27 of these events recorded at the Riverside RAR and only four over the Fargo RAR.

### Repeatability of migratory characteristics

Repeatability analyses for Bigmouth Buffalo phenology of migratory events showed that individual repeatability was  $<0.4$ , such that fish reached their winter destinations with some annual consistency (Julian day; upstream destination:  $R = 0.192$ ,  $p = 0.023$ ; Table 1). Further, individuals tended to depart from the same winter location (latitude of upstream departure:  $R = 0.215$ ,  $p < 0.015$ ; Table 1) and returned to similar spawning/summer locations (latitude of downstream destination;  $R = 0.548$ ,  $p < 0.001$ ; Table 1; and downstream departure:  $R = 0.222$ ,  $p < 0.008$ ; Table 1) annually. Stream temperatures at the onset of downstream migration were consistent across years (temperature of downstream departure:  $R = 0.328$ ,  $p = 0.002$ ; Table 1). The timing

of spring migration (Julian day of downstream departure), the distance of fall migration (distance upstream), the temperature when spring migrations ended (downstream destination temperature), and the latitude of winter locations (latitude of the upstream destination) were inconsistent across years ( $p > 0.05$  in all instances; Table 1). Adding year as a fixed effect to the linear mixed effect models prior to calculating repeatability accounted for some of the model variance and increased estimates (Table 1).

### Migratory periods

The start, end, and length of the migration periods were variable across years and seasons (Fig. 5). Spring migration was initiated alongside distinct changes in several measured environmental variables including an increase of water temperature, higher flows, and a spike in turbidity (Fig. 5). No clear change was observed in the measured environmental variables to indicate the end of spring migration or start of fall migration (Fig. 5). The midpoint of the spring migration ranged from early April (week 14 in 2021) to early May (week 19 in 2020), depending on year (Table 2). The widest spring migration start date range was in 2022 (scale parameter = 0.67) and the narrowest in 2021 (scale parameter = 2.70, Table 2). Fall migration midpoint ranged from late September to late October (Table 2). The widest fall migration start date range was in 2018 (scale parameter = 0.61) and the narrowest in 2021 (scale parameter = 1.68, Table 2).

### Summer and winter range size and overlap

On average, winter mean home ranges were smaller (23.5 km) than summer mean home ranges (48.9 km, Fig. 6a). On average, seasonal home ranges encompassed a greater percentage of the total river section in summer (35.4%) than winter (13.3%, Fig. 6b) and was highest in summer in the section of river between SALD and Lake Winnipeg where measured geographic space was most limited (90%, Fig. 6b). The top two models for summer and winter home range size included season, and one of the top two models further contained site fidelity (top model is presented in Table 3), all other models  $\Delta AIC > 2$  (Table S4). Home range size was significantly larger in the summer and when fish were outside their most used section. The proportion of variance explained by the random effect of individual ID was low ( $ICC = 0.06$ ) and including ID as a random effect was a small improvement to the explained variance (marginal  $R^2 = 0.128$ , conditional  $R^2 = 0.184$ ). There remained a sizable portion of the variance in home range size not explained by the model. Importantly, the absence of river section from the top model indicated that it provided little explanatory power (Table 3).

In most instances, there was no overlap between the winter and summer ranges (198/321 observations). The average winter and summer range overlap was 26.8% when overlap occurred (overlap  $> 0$ ; Fig. 6c). The top two models for summer and winter overlap included river section, and one of the top two models further contained site fidelity, although site fidelity was not significant (top model is presented in Table 3), all other models  $\Delta AIC > 2$  (Table S4). The probability of overlap was highest downstream of SALD (Table 3, Fig. 6d).

**Table 1.** Repeatability estimates (R) for migration events across years for Bigmouth Buffalo with two or more years of observations.

Metric	Event	Agreement repeatability			Adjusted repeatability (year as fixed effect)				
		R	SE	CI (95%)	p	R	SE	CI (95%)	p
Julian Day	Upstream departure <sup>a</sup>	0.011	0.056	0.000–0.187	0.498	0.170	0.100	0.000–0.373	0.040
	Upstream destination <sup>a</sup>	0.136	0.097	0.000–0.342	0.072	0.281	0.108	0.053–0.481	0.002
	Downstream departure <sup>b</sup>	0.060	0.075	0.000–0.254	0.295	0.428	0.109	0.190–0.617	<0.001
	Downstream destination <sup>b</sup>	0.000	0.052	0.000–0.176	1.000	0.000	0.000	0.000–0.000	0.500
Distance	Upstream <sup>a</sup>	0.000	0.050	0.000–0.173	1.000	0.047	0.069	0.000–0.234	0.271
	Downstream <sup>b</sup>	0.149	0.096	0.000–0.350	0.057	0.353	0.112	0.114–0.554	<0.001
Temperature	Upstream departure <sup>a</sup>	0.000	0.050	0.000–0.171	1.000	0.015	0.059	0.000–0.196	0.431
	Upstream destination <sup>a</sup>	0.129	0.091	0.000–0.327	0.078	0.308	0.109	0.078–0.499	0.001
	Downstream departure <sup>b</sup>	0.328	0.109	0.099–0.524	0.002	0.496	0.104	0.262–0.669	<0.001
	Downstream destination <sup>b</sup>	0.000	0.050	0.000–0.171	1.000	0.075	0.080	0.000–0.273	0.245
Latitude	Upstream departure <sup>a</sup>	0.215	0.103	0.003–0.411	0.015	0.184	0.101	0.000–0.385	0.027
	Upstream destination <sup>a</sup>	0.085	0.081	0.000–0.273	0.184	0.116	0.090	0.000–0.315	0.083
	Downstream departure <sup>b</sup>	0.222	0.104	0.010–0.421	0.008	0.419	0.109	0.183–0.605	<0.001
	Downstream destination <sup>b</sup>	0.548	0.099	0.317–0.703	<0.001	0.567	0.098	0.341–0.723	<0.001

**Note:** Confidence intervals were estimated through parametric bootstrapping and *p*-values are estimated through likelihood ratio tests (Stoffel et al. 2017). Sample sizes are denoted by superscripts (<sup>a</sup> = 30 individuals, 108 observations; <sup>b</sup> = 29 individuals, 105 observations). Statistical significance is defined by asterisks (*p* < 0.001\*\*\*, *p* < 0.01\*\*, *p* < 0.05\*). Upstream departure = leaving summer range; Upstream destination = arriving at winter range; Downstream departure = leaving winter range; Downstream destination = arriving at summer range.

Although higher than the home range model, variance explained by including individual ID as random effect was low (ICC = 0.21). Including ID as a random effect more than doubled the variance explained (marginal  $R^2 = 0.134$ , conditional  $R^2 = 0.315$ ).

## Discussion

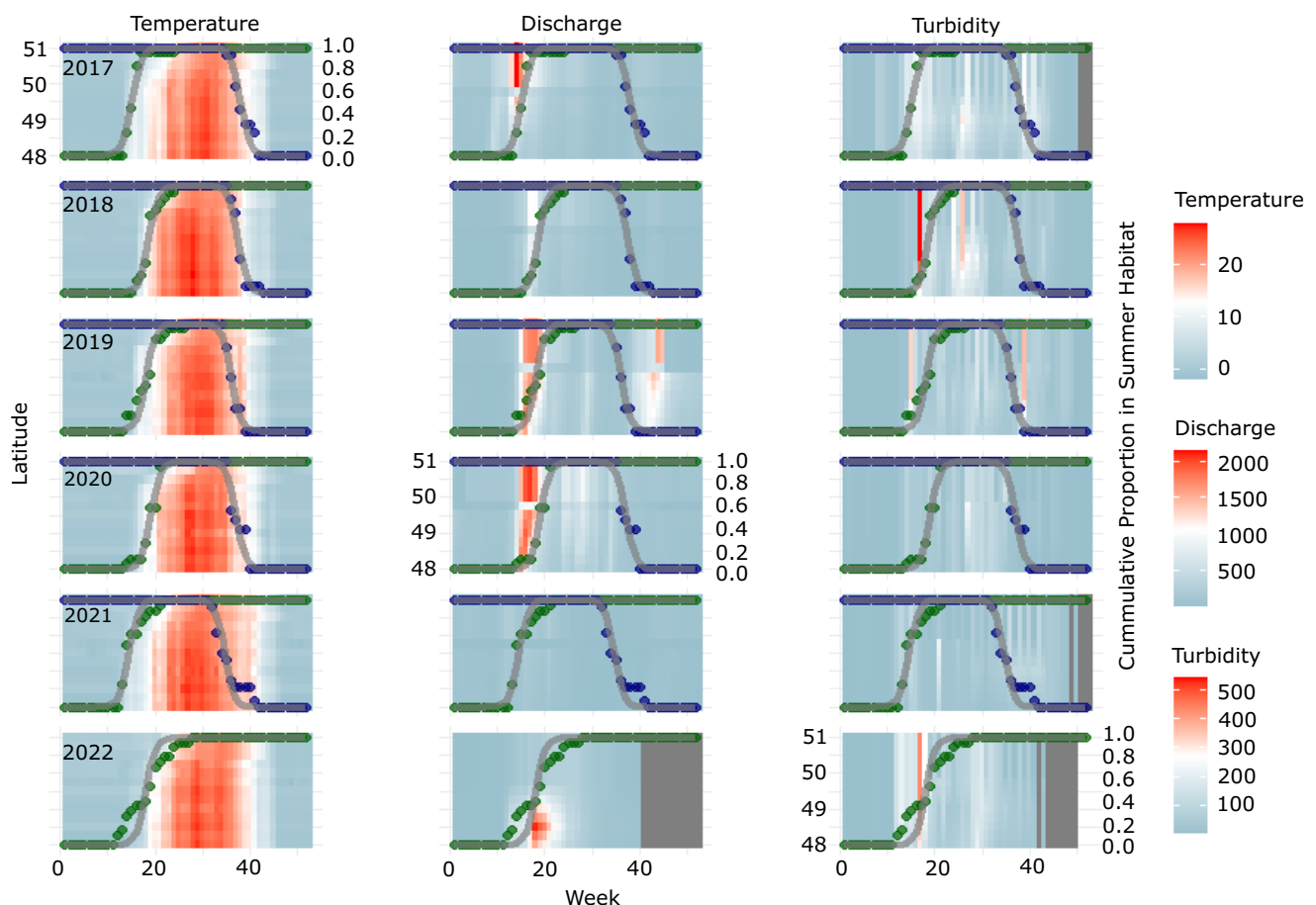
Long-term monitoring of individual Bigmouth Buffalo movements in the Red River revealed notable differences in migratory behaviour and the use of distinct seasonal home ranges across river sections in a fragmented river network. The comparison of seasonal home range overlap and size between river sections of different lengths indicated an upper and lower bound to summer home range sizes for Bigmouth Buffalo. These findings add to the limited body of information available to resource managers tasked with conserving or restoring Bigmouth Buffalo and its habitat.

Many spring migrations, likely coinciding with reproduction (COSEWIC 2009), started with a rapid increase in water temperatures and higher river discharges (Fig. 5). The downstream destination was the most repeatable behaviour estimated (Table 1), and observations of spawning activity and sexually mature fish in the La Salle River support the assertion that Bigmouth Buffalo use this tributary for spawning (Watkinson DA, personal observation). There was high individual variation in the start and end dates of spring migration (Table 1), with many fish departing several weeks later in the season. By this time, summer water temperatures had nearly peaked and spring flows were considerably decreased (Fig. 5). Low variability in the timing of spring spawning migration is generally considered necessary to derive fitness benefits from enhanced breeding success (Hulthén et al. 2022 and references therein); however, a number of species, partic-

ularly those considered long-lived or burdened by high reproductive costs (e.g., long migrations), will skip spawning as a survival tactic to offset mortality (Jørgensen et al. 2006; Lowerre-Barbieri et al. 2011; Rideout and Tomkiewicz 2011; Gallagher et al. 2018). Among the longest-lived teleosts, Bigmouth Buffalo are known to skip spawning (Lackmann et al. 2021; Lackmann et al. 2023). If this occurs, migration can still provide lifetime fitness benefits if the broader destination serves as the summer feeding grounds. Moreover, individuals that failed to migrate at all (Fig. 4) show that partial migration also occurs in the system (Chapman et al. 2012). Documenting this phenomenon here is important, as partial migration can stabilize and bolster population resilience in heterogenous environments (Kerr et al. 2010; Chizinski et al. 2016; van Leeuwen et al. 2016).

For spawning Bigmouth Buffalo, flood duration and timing may be among the primary drivers of the observed migration to downstream reaches where flooded riparian vegetation provides ideal habitat in the Red River. These spring conditions are both reflected by the environmental data (Fig. 5) and relatively lower detection frequency observed during downstream migration (Fig. 3). On average, the lower slope and higher discharge of the Red River near Winnipeg results in lower water level fluctuations relative to upstream reaches (ECCC 2023). The peak of the spring flood begins in the US portion of the watershed and moves downstream, thus peaking in Canada later in the year. Flood duration is longer in Canada than in upstream reaches, despite less change in water surface elevation (ECCC 2023). Water surface elevation of the Red River upstream of the La Salle and Seine rivers throughout the City of Winnipeg is influenced by SALD, which annually floods portions of the ephemeral river channels. Downstream of SALD, water surface elevation of the Red River may be further influenced by the se-

**Fig. 5.** Cumulative weekly proportion of migratory Bigmouth Buffalo in their summer habitat for each year in the spring (green points) and fall (blue points) with the predicted values from the logistic regressions (grey lines) used to determine seasons (1 = summer, 0 = winter), overlaid on a heatmap of the interpolated temperature, discharge, and turbidity across latitudes between Drayton Dam, ND (lower most latitude, upstream) and the St. Andrews Lock and Dam, MB (uppermost latitude, downstream).



iche effect of Lake Winnipeg, resulting in capricious floodplain inundation (ECCC 2023). This could result in Bigmouth Buffalo releasing eggs onto habitat that in hours or days becomes dry with changing water surface elevation. Common Carp have been observed spawning in flooded cattail (*Typha glauca*) in Netley-Libau Marsh, where water depth was ~70 cm but completely dry the following day. Larval stranding has been documented for Bigmouth Buffalo in Pound Lake, Saskatchewan (Lackmann et al. 2023). In the Red River, Bigmouth Buffalo spawning downstream of SALD may still have reduced success in years when seiche effects on water surface elevation are high. Such changes to the duration and timing of flooding, in addition to surface temperatures, likely further explain some of the observed variability in migratory behaviour. Additional data are needed to understand flood impacts on behaviour and spawning success.

While reproduction is the most parsimonious explanation for spring migration in mature individuals, and appears to be driven by environmental cues, the fall upstream migration to overwintering habitat is more puzzling. Individuals typically departed from similar latitudes and concluded uni-

directional movements around the same time each year (Julian day of upstream destination; Table 1). Unlike the spring migrations, fall movements did not appear to be initiated by a clear environmental cue, besides decreasing temperatures (Fig. 5) that were significantly lower at time of arrival compared to the onset of migration. The energetic benefits provided by overwintering habitat must outweigh the costs of moving. In the absence of a clear environmental cue or reproductive requirement, we hypothesize that the fall upstream migration is an adaptive strategy to align with a downstream progression, or “green wave,” of resources during the ensuing spring (van der Graaf et al. 2006; Bischof et al. 2012). Although suggested for migrating Arctic Char (*Salvelinus alpinus*) that “jump” ahead of system productivity (Hammer et al. 2022), this hypothesis is rarely applied to aquatic systems. Given the synchronization between plankton blooms and ice-off (Hrycik et al. 2012), the earlier onset of ice-off upstream likely triggers a series of cascading downstream plankton blooms facilitated by increasing light availability and nutrients delivered by snowmelt (Corriveau et al. 2011). During the fall, Bigmouth Buffalo seek the furthest upstream sites

**Table 2.** Parameter values (mid, scale), estimate (E), standard error (SE), Wald Statistic (WS), and *p*-value (*p*) for logistic curves fit using non-linear least squares to weekly cumulative number of fish that started their migration per year and season.

Parameter	Year	Season	E	SE	WS	<i>p</i>
mid	2017	Fall	38.1	0.0902	422	<0.001***
		Spring	15.1	0.0386	390	<0.001***
	2018	Fall	37.6	0.0324	1160	<0.001***
		Spring	18.6	0.0730	255	<0.001***
	2019	Fall	36.1	0.0491	735	<0.001***
		Spring	18.1	0.0914	198	<0.001***
	2020	Fall	37.1	0.1270	292	<0.001***
		Spring	19.0	0.0783	243	<0.001***
	2021	Fall	34.7	0.1300	267	<0.001***
		Spring	14.5	0.1280	113	<0.001***
	2022	Spring	18.0	0.1180	152	<0.001***
	scale	2017	Fall	1.34	0.0794	16.8
Spring			0.67	0.0342	19.5	<0.001***
2018		Fall	0.61	0.0282	22	<0.001***
		Spring	1.09	0.0643	17	<0.001***
2019		Fall	0.84	0.0432	19	<0.001***
		Spring	1.76	0.0805	22	<0.001***
2020		Fall	1.25	0.1120	11	<0.001***
		Spring	1.04	0.0689	15	<0.001***
2021		Fall	1.68	0.1140	15	<0.001***
		Spring	1.42	0.1130	13	<0.001***
2022		Spring	2.70	0.1040	26	<0.001***

Note: Statistical significance is defined by asterisks ( $p < 0.001^{***}$ ).

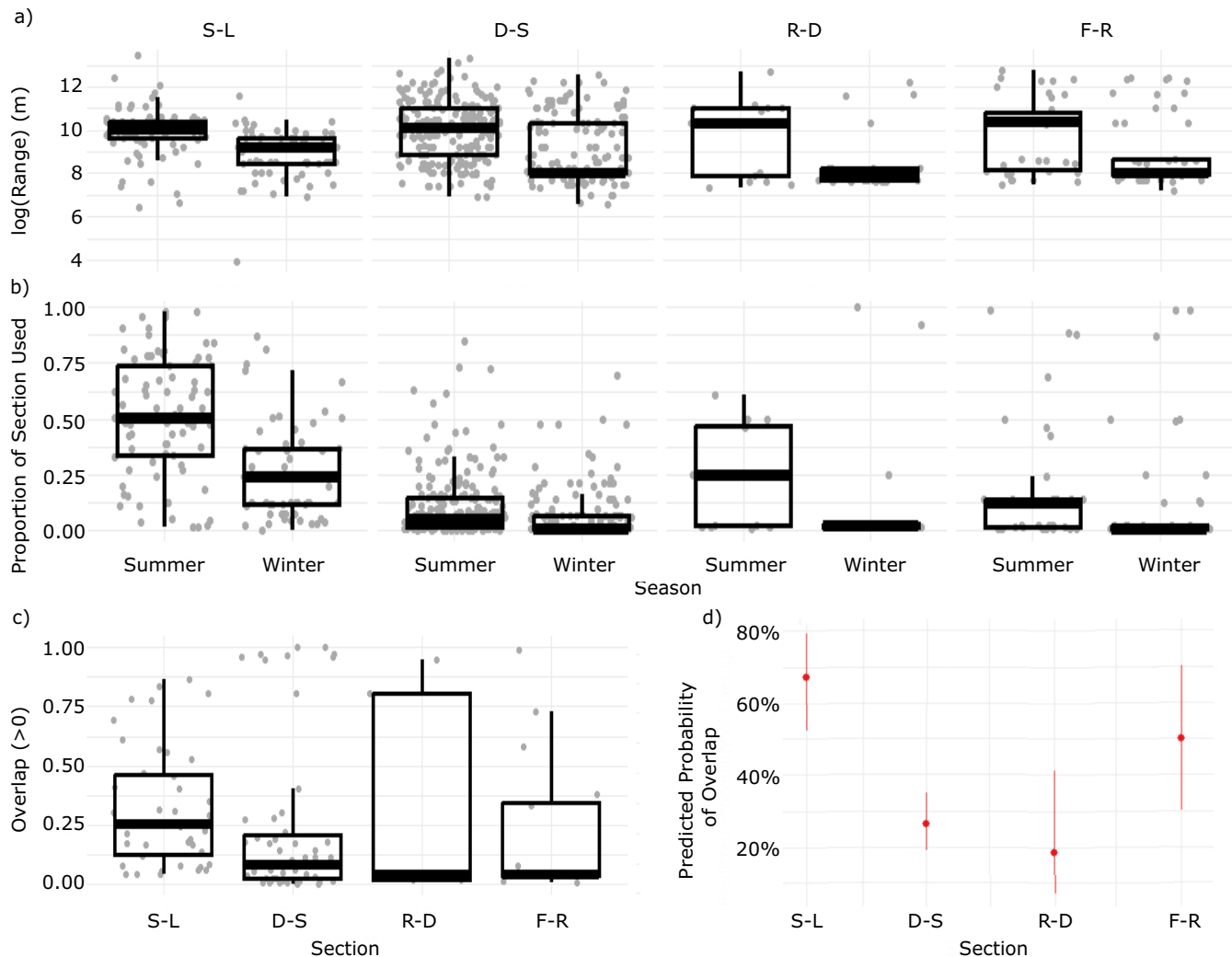
possible, partially blocked only by Drayton Dam, to capitalize on the most profitable spring plankton bloom. Annual discharge offers some support for this hypothesis, as Bigmouth Buffalo ended fall migrations downstream of the Drayton Dam every year except for 2019 and 2022, which coincided with unusually high fall flow events that made the dam passable upstream during the migration window (Enders et al. 2019). Improved passage potential over Drayton Dam resulted in longer and more variable fall migration distances in 2019 than the other years. For example, in 2019 the mean upstream migration distance was 325 rkm (SD = 157) compared to the next highest and less variable distance of 206 rkm (SD = 40) in 2021. Construction was completed in 2023 to replace the Drayton Dam with a full river width rock-rapids style fishway. Assuming the new structure improves passage over a range of flows, it follows that annual fall migrations by Bigmouth Buffalo will continue farther upstream to exploit the fitness benefits of this now fully accessible habitat.

Home range size did not vary significantly between river sections; however, the proportion of river section covered by an individual's median home range decreased with section length (Fig. 6). Despite the high degree of heterogeneity in available habitats between SALD and Lake Winnipeg (Enders et al. 2019), summer-winter home range overlap was rela-

tively high in this section. For Bigmouth Buffalo, there appears to be an upper bound, similar to migratory Blue Sucker (*Cycleptus elongatus*) in the middle Missouri River (Neely et al. 2009), and a lower bound for home range size. These limits can be mediated by resource availability and concurrent factors such as individual body size (Woolnough et al. 2009), social interactions (e.g., dominance; Bachman 1984) or predation risk (Lima 1998) and harvest (Marantz et al. 2016). In the Red River system, the upper and lower bounds were season specific, with winter home ranges notably smaller than observed in summer. In fact, several of the individuals were only detected at a single receiver in winter. This reduction of home range size is expected, as fish reduce metabolic rate and activity with decreasing water temperature (McMeans et al. 2020). With additional environmental and fish detection data, such observations will be crucial for understanding the impact of climate change on migratory behaviour (Robinson et al. 2009; Kubelka et al. 2022; Howard et al. 2023). For example, genomics, recruitment surveys, or fish community dynamics could help reveal the indicators and consequences of climate change and river fragmentation on Bigmouth Buffalo (Newson et al. 2009; Bloomfield et al. 2022; Lackmann et al. 2023).

It is important to note that our interpretations of home range size, migration date, and rate of movement were lim-

**Fig. 6.** Home range size (a) and proportional use (b) across seasons (winter, summer) and river sections (Fargo North Dam, ND to Riverside Dam (F-R), Riverside Dam to Drayton Dam (R-D), ND, Drayton Dam to St. Andrews Lock and Dam, MB (D-S), and St. Andrews Lock and Dam to Lake Winnipeg, MB (S-L)); overlap (when > 0) between winter and summer home range (c); and predicted probability of overlap across river sections (d).



ited by the study design. For example, error in these estimated metrics will vary from the southern to northern extent of the study system because receiver stations are separated by increasing distances (Fig. 1). Additionally, the use of minimum linear extent as a measure of home range includes extraneous movements that can result in larger estimates of home range compared to other analytical approaches (Vokoun 2003). Receiver detection efficiency at rkm 24 was > 80% up to 400 m in summer and winter, covering the full river width in most sections (Table S2). Nevertheless, large receiver spacing coupled with missed detections does impact how migration is observed. Other explanations for the drivers of migratory movements might emerge with the collection of additional data, such as bathymetry or through tagging more large individuals to detect and statistically control for body size effects among river sections.

Enders et al. (2019) found low transition probabilities from sections downstream to upstream of both SALD (0.005) and

Drayton Dam (0.455). In the current study, we found that the reduced connectivity imposed by these dams influences seasonal home range overlap. Notably, the longest unimpeded section of river, between Drayton Dam and SALD, had the lowest probability of overlap (Table 3) and a pronounced separation of seasonal habitats. This supports the hypothesis that adequate geographic space can lead to seasonally distinct habitat use in a heterogeneous environment. On the contrary, the highest probability of overlap occurred in the section of river between SALD and Lake Winnipeg where space was relatively limited (Table 3). Although differential space use occurs in other riverine species (e.g., Blue Sucker, Lake Sturgeon (*Acipenser fulvescens*), and Flathead Catfish (*Pylodictis olivaris*), Vokoun and Rabeni 2005; Neely et al. 2009; Colborne et al. 2019), the competing influence of river fragmentation is less well understood. Fish that managed to pass upstream of the structure exhibited mixed behaviours including migration, apparent straying or section residency. Variation in

**Table 3.** Results of linear mixed models for seasonal (winter and summer) log transformed home range size ( $n = 683$ ) and overlap (0, 1) between consecutive winter and summer home ranges ( $n = 321$ ), for different river sections (Fargo North Dam, ND to Riverside Dam, ND (F-R), Riverside Dam, ND and Drayton Dam, ND (R-D), and St. Andrews Lock and Dam to Lake Winnipeg, MB (S-L)), with individual fish as random effects ( $N = 75, 69$ ).

Predictors	log(range)		
	Estimates	CI	p
(Intercept)	10.20	9.90–10.51	<0.001***
Season (winter)	–1.06	–1.26 to –0.86	<0.001***
InAreaMostUsed (fidelity)	–0.29	–0.58 to –0.00	0.047*
<b>Random effects</b>			
$\sigma^2$	1.78		
$\tau_{00}$	0.12		
ICC	0.06		
N	75		
Observations	683		
Marginal $R^2$ /conditional $R^2$	0.128/0.184		
Predictors	Overlap		
	Odds Ratios	CI	p
(Intercept)	0.36	0.23–0.55	<0.001***
Section (F-R)	2.78	1.03–7.49	0.043*
Section (R-D)	0.62	0.19–2.09	0.445
Section (S-L)	6.37	2.94–13.82	<0.001***
<b>Random effects</b>			
$\sigma^2$	3.29		
$\tau_{00}$	0.87		
ICC	0.21		
N	69		
Observations	321		
Marginal $R^2$ /conditional $R^2$	0.134/0.315		

**Note:** InAreaMostUsed represents whether fish showed fidelity to the river section in which they used for the greatest number of days. For the home range size model, the intercept estimate can be used to calculate the effects for Summer and where fish passed in-stream structures, i.e., Section Passage. For the overlap model, the intercept estimate can be used to calculate the effect the section of river between Drayton Dam, ND and Andrews Lock and Dam, MB (D-S), on the probability of overlap. Statistical significance is defined by asterisks ( $p < 0.001^{***}$ ,  $p < 0.01^{**}$ ,  $p < 0.05^*$ ). The Random Effects section includes the distribution specific variance ( $\sigma^2$ ), the random intercept variance ( $\tau_{00}$ ), the interclass correlation coefficient (ICC), and the number of unique fish (N). Also included is the marginal and conditional coefficient of determination ( $R^2$ ) and total number of observations used in the model.

behaviour should be expected (Kerr et al. 2010; Chizinski et al. 2016; van Leeuwen et al. 2016), particularly given that large Bigmouth Buffalo could achieve extraordinary ages and spawn periodically in the Red River (Lackmann et al. 2023). With nearly half of those crossing SALD undergoing migration, we believe there is strong evidence to suggest much of the Bigmouth Buffalo population downstream of SALD are unable to maximize fitness similar to conspecifics upstream. In small, fragmented river sections, such as downstream of SALD and upstream of the former Drayton Dam, fish have restricted access to habitats, including those which are most seasonally profitable (Enders et al. 2019). Rehabilitation of the Drayton and similar in-stream barriers should have positive consequences for potamodromous Bigmouth Buffalo.

Over half a decade of telemetry data has provided an unparalleled look into the migratory behaviour of Bigmouth

Buffalo in a fragmented riverscape, emphasizing the critical role of river connectivity for accessing distinct summer and winter habitats. The study system was marked by notable migratory behaviours and distinct seasonal home ranges across different river sections, underscoring how anthropogenic developments such as dams can impact the distribution of migratory fish by limiting access to preferred habitats. Disruptions to habitat connectivity can restrict access to profitable habitat and impose individual fitness and population-level consequences that may take decades to manifest in long-lived species. Bigmouth Buffalo met our migration criteria only in the longest unimpeded river section, with movements generally directed downstream in spring and upstream in fall. Variability in migratory behaviour was linked to factors including flood duration and timing. The study also documented partial migration, a phenomenon critical for population stabil-

ity and resilience under heterogeneous environmental conditions. These findings should be valuable to resource managers and policymakers concerned with habitat deficiencies and who plan strategic remediation in recovery actions for Bigmouth Buffalo and other migratory species.

## Acknowledgements

We would like to thank the various field crews from Fisheries and Oceans Canada, the University of Manitoba, and the University of Nebraska for their efforts to construct the receiver network, download data, and tag Bigmouth Buffalo. Support for this project was provided by Fisheries and Oceans Canada's Species at Risk and Fish Habitat Protection programs, the International Joint Commission International Watersheds Initiative, the Manitoba Fish and Wildlife Enhancement Fund, Manitoba Fish Futures Inc., Manitoba Sustainable Development, the University of Nebraska-Lincoln via the Nebraska Agricultural Experiment Station and the Hatch Act (Project NC 1189) through the USDA National Institute of Food and Agriculture, and the Minnesota Department of Natural Resources.

## Article information

### Editor

Marco Rodriguez

### History dates

Received: 9 January 2024

Accepted: 27 May 2024

Version of record online: 9 October 2024

### Notes

This paper is part of a collection entitled Progress and Priorities for the Recovery of Aquatic Species at Risk in Canada.

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### Data availability

Data analyzed during this study are considered sensitive due to the species' conservation status. At present, raw data will not be released without written consent from the Species at Risk Program of Fisheries and Oceans Canada.

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Eva C. Enders served as Subject Editor at the time of manuscript review and acceptance and did not handle peer review and editorial decisions regarding this manuscript.

## Author contributions

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## Competing interests

The authors declare there are no competing interests.

## Supplementary material

Supplementary data are available with the article at <https://doi.org/10.1139/facets-2024-0003>.

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