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# Historical and contemporary movement and survival rates of walleye (*Sander vitreus*) in Lake Winnipeg, Canada



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# ABSTRACT

Understanding patterns of fish movement in large lake ecosystems is essential for determining appropriate management actions as differences in movement behaviour can influence life history traits such as growth and survival. Lake Winnipeg in Manitoba, Canada supports the 2nd largest walleye (Sander vitreus) commercial fishery in North America. We used mark-recapture models to determine movement and estimate survival of walleye between basins of Lake Winnipeg in historical and contemporary contexts, comparing a tag-recovery study completed historically during 1974–1977 with a contemporary (2017–2019) acoustic telemetry study. Mark-recapture models revealed comparably low but detectable annual transitions between basins from historical (0.3-1.2%) and contemporary datasets (7-8.5%). Historically, fish > 300 mm more frequently moved in a south to north direction. Contemporary estimates suggest similar length-based directionality in that fish > 350 mm were always more likely to move in a south-north direction. Contemporary annual survival derived from mark-recapture models ranged between 27 and 45% and 64.3% when derived from catch curve analysis, while independently derived annual historical survival estimates ranged between 50 and 69% and 45.5% from catch curve analysis. Using the contemporary dataset, we also observed seasonal variation in movement and survival between basins, with the greatest movement across the lake occurring during the fall. Our results demonstrate a persisting pattern of low but measurable movement, suggesting between basin movement is not unusual for Lake Winnipeg. Further, low walleye survival rates reported here for the two time periods studied, support recent management actions to reduce fishing pressure across the lake.

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### Introduction

Understanding behavioural movement patterns of organisms in ecosystems is critical to determining vulnerability and life history strategy in ecological and resource management contexts. Quantifying movement patterns and behaviour can reveal seasonal variation in patterns of habitat use (Van Moorter et al., 2016). A clear understanding of species movement patterns is of even greater relevance when the species of interest provides ecosystem services, such as commercial, recreational, and Indigenous subsistence fisheries. Migration, and movement generally, is inherently energetically costly (Kitchell et al., 1977; Roff, 1988) and is often driven by resource acquisition (Jonsson and Jonsson, 2006; Rennie et al., 2012a, 2012b). As such, movement is intimately linked to life history traits such as growth, survival, and reproduction (Raabe et al., 2020; Rennie et al., 2012a; Roff, 1988). As freshwater systems undergo fluctuations and alterations due to anthropogenic and natural related changes, these influences may affect fish and their subsequent movement and survival patterns (Allan et al., 2005; Nathan et al., 2008; Richter et al., 1997; Sass et al., 2017).

Freshwater fish movement is a relatively common phenomenon and often associated with exploiting different habitats to gain a fitness advantage (Gross et al., 1988). Resident and migratory individuals are regularly observed in the same population, suggesting some energetic threshold may be required to initiate movement (or criteria for individuals to evaluate the benefits of movement vs. staying) may be involved (Bronmark et al., 2014; Chapman et al., 2011; Lucas and Baras, 2000). Habitat heterogeneity is a particular feature of large lake ecosystems (Eadie and Keast, 1984) and

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has been implicated in long-range migrations for several Great Lakes species (Ebener et al., 2010; Wang et al., 2007). Recent walleve (Sander vitreus) movement studies on the Laurentian Great Lakes have revealed significant long distance migration patterns in populations (Hayden et al., 2014; Mckee, 2018) driven by factors including spawning site fidelity (Hayden et al., 2017; Wang et al., 2007) and thermal preference (Peat et al., 2015). Differences in movement strategies within a population have also been shown to be associated with different growth rates (Mckee, 2018) suggesting the decision to migrate can have a significant influence on the life history of fish (growth and survival) in freshwater systems. Thus, a clearer understanding of the factors associated with fish movement can aid in the development of better management strategies and conservation efforts (Brooks et al., 2017; Crossin et al., 2017; Donaldson et al., 2014). This is true both in terms of understanding whether migrating stocks across regions may respond to regional differences in commercial and recreational fishing regulations (Crossin et al., 2017) and exploitations, but also in testing for potential differences among sub-populations in estimating commonly growth-derived estimates of life history traits such as survival, growth rate, and length at maturity (Charnov et al., 1993; Ricker, 1975).

Lake Winnipeg is the 11th largest lake in the world by surface area and supports one of the largest walleye fisheries in North America, second only to Lake Erie (Franzin et al., 2003). Walleye play a significant role in the Lake Winnipeg ecosystem as a native top predator species, while also contributing millions of dollars in revenue to the Province of Manitoba annually through commercial and recreational fishing activity. Lake Winnipeg has supported an active gill net fishery since the early 1890 s which employs larger gillnet sizes across the north basin versus that of the south basin (Heuring, 1993). The commercial fishery has annually harvested an average of 4.3 million kg of walleye from the lake between 2005 and 2015 (ECCC and MARD, 2020). Additionally, the lake provides subsistence fishing to several Indigenous communities around the lake (ECCC and MARD, 2020). Recent management actions by the Province of Manitoba, including increasing the minimum mesh size of gillnets in the fishery and a guota buy-back program, have been implemented due to concerns regarding management flexibility and stock sustainability based on declines in catch rates (Lumb et al., 2020).

Despite their relative importance to both the ecosystem and the regional economy, very little is understood regarding the movement and survival of walleye across the lake. Past evidence regarding differentiation between north and south basin walleye as distinct stocks is conflicting. A genetic analysis concluded there is no evidence to support separate walleye population structures between the basins (Backhouse-James and Docker, 2012). However, a recent RNA study reported weak population structure across north and south basins presenting evidence of a low rate of mixing between basins (Thorstensen et al., 2020). By contrast, significant differences between walleye from the north and south basins have been reported in growth rate, body condition, diet, and scale morphology (Johnston et al., 2012; Moles et al., 2010; Sheppard et al., 2015, 2018; Watkinson and Gillis, 2005) suggesting the potential for ecological specialization between basins. Uncertainty remains as to the degree walleye use the entire lake over the course of a given year versus remaining within each of the respective basins.

To evaluate and compare historical and contemporary movement and survival rates between the north and south basins of Lake Winnipeg, we applied a multi-state live-dead markrecapture model (Brownie et al., 1993; Kendall et al., 2006; Lebreton et al., 2009; Schwarz et al., 1993; White et al., 2006) to historic fish tagging data and to a subset of contemporary acoustic telemetry detections from gates assigned across the lake (Fig. 1).

We used a coarser gate-based approach to contemporary movement data using the existing acoustic array in an attempt to make historical and contemporary estimates of movement more comparable to one another. Where possible, we investigated movement and survival on a seasonal basis, as walleye movement has been documented to vary seasonally elsewhere (Hayden et al., 2017, 2014). In addition, we examined the role of fish length on movement rates. Based on findings from studies (Backhouse-James and Docker, 2012; Thorstensen et al., 2020) which have concluded mixing does occur between north and south basins, we hypothesised that movement between the two basins does occur but is limited. We expected differences in movement and survival between the time periods given the greater exploitation effort in harvest and different limnological conditions over the past 50 years (i.e., increased total phosphorus and nitrogen loading along with increases in algae blooms during the summer and fall across the lake: Nicholson, 2007: Schindler et al., 2012). We further hypothesized that large, mature fish would demonstrate greater rates of between-basin movement, as they are better suited to manage the increased bioenergetic costs associated with moving larger distances (Roff, 1988).

#### Methods

#### Study area

Lake Winnipeg is located within the Province of Manitoba, Canada and is the 3rd largest freshwater lake entirely within Canadian borders (Johnston et al., 2012). It has an area of 25,750 km and a mean depth of 13 m (Brunskill et al., 1980). The lake can be divided into two relatively separate basins, one to the north and one to the south (Fig. 1). The north and south basins are connected by a narrow channel area that for the purposes of this study is combined into the north and south basins. The south and north basin differ from one another in both their biotic and abiotic features. The south basin is about 2,900 km<sup>2</sup> with a mean depth of 9.7 m and Secchi depth of 10–100 cm. By contrast, the north basin is larger, deeper, and clearer than the south basin (~19,000 km<sup>2</sup>, mean depth of 13.3 m, and Secchi depth between 50 and 260 cm (Brunskill et al., 1980; Wassenaar and Rao, 2012). Doghead Point (51.745428, -96.826436), located relatively central to the channel area of the lake was used as the dividing feature between the south and north basins due to its relatively high acoustic receiver coverage; fish were unlikely to pass undetected (Fig. 1, Electronic Supplementary Material (ESM) Fig. S1). Therefore, Doghead Point and all receiver gates south were considered within the south basin, whereas anything north of Doghead Point was considered the north basin. Given that our main objective in the current study was to quantify broad-scale movement across time periods, we simplified the acoustic receiver array deployed across Lake Winnipeg to coarsen current detections to a level more comparable to past mark-recapture based studies (Fig. 1, ESM Fig. S1). A more detailed analysis of contemporary movement patterns in Lake Winnipeg is described elsewhere (Turner, 2020).

#### Historical movement study.

Walleye were tagged during the first two years of a three year historical study (Table 1). In 1974, tagging took place from May 29th to August 30th and from May 6th to October 30th in 1975 (Table 1.). Over both years of tagging, 7,991 walleye were captured and released into Lake Winnipeg at various locations across the basins (Fig. 1). About 10% of the tagged fish were reported recaptured between June 6th, 1974 and May 29th, 1977 (Table 1.). Average fork length at tagging for walleye across the north basin and



**Fig. 1.** Map of study area with insert to highlight study location within Canada. Acoustic receiver gate names: RR – Red River (3 receivers), MSB – mid south basin (6), Islands – Hecla and Black islands (4), Doghead Point (North-South division; 2), MNB – Mid north basin (3), NB – north basin (9). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1												
Historical	tag	and	recapture	values	for	each	year	of	the	study	across	basins.
N = numb	er of	indiv	iduals tag	ged, n =	nun	nber o	f indiv	/idu	ials r	eporte	d captui	ed.

	1974	1975	1976	3-year total
Ν	South: 429 North: 1,714	South: 1,489 North: 4,368	0	South: 1,918 North: 6,082
n	169	387	171	South: 234 North: 584

south basin was 385 mm and 382 mm, respectively. Of all fish tagged, 87 fish had no associated fork length recorded at tagging. Historical tag returns were exclusively from commercial fishers operating on the lake. Fishers were paid \$1.00 CDN for each tag returned; the equivalent of \$4.78 CDN in 2020. Historical reporting rates for the commercial fishery on Lake Winnipeg are unknown, but estimates determined on jaw-tagged Lake Erie walleye ranged from 10 to 17% annually (Vandergoot et al., 2012). Fish were orig-

inally captured and tagged using a combination of short set gill netting, trap, and seine netting methods. Fish were tagged with individually numbered external anchor tags (Floy<sup>®</sup> T-Bar Anchor Tag, FD-94, 25 mm monofilament; Floy Tag Inc., Seattle, WA, USA) inserted around the first and second dorsal fins between the pterygiophores. A spatial overlay grid measuring 8.5 by 8.5 km, 72.25 km<sup>2</sup> (ESM Fig. S2) was used to assign initial tagging and subsequent recapture locations.

# Contemporary movement study

In 2016, a study was initiated by Fisheries and Oceans Canada to monitor fish movement in the Lake Winnipeg basin. Acoustic receivers were placed throughout the lake in a grid style array (Kraus et al., 2018; ESM Fig. S1). To address broad-scale movement patterns at a similar coarse scale of resolution to that of the historical survey, a subset of receivers was selected to form gates across the lake. During the 2016 field season, prior to any walleye tagging activity, 31 acoustic receivers (VR2W, VR2Tx, 69 kHz; Vemco, Innovasea, Bedford, NS, Canada; ESM Fig. S1) were deployed throughout Lake Winnipeg covering the south basin from the Red River in the south to Doghead Point. Three of these receivers were deployed at Doghead Point, spaced 1.5 km and 0.5 km across the 2 km channel. This ensured a ~ 80% and ~ 96% detection probability between the receivers. During 2018, the middle receiver across the channel was lost leaving roughly a 2 km spacing between the two remaining receivers (~70% detection probability). Rough estimates of detection probability were inferred from sentinel tags located in the south basin (ESM Fig. S1); detailed descriptions of detection and spacing across the grid array have been described elsewhere (Kraus et al., 2018).

During 2017, the start of the walleye tagging study, an additional 13 acoustic receivers (VR2W and VR2Tx, Vemco; ESM Fig. S1) were deployed to cover the area north of Doghead Point. Receivers in the south basin nearest to the Red River were spaced 7 km from one another. The distance from the Red River receiver gate to the mid south basin gate was about 46 km while receiver spacing between the mid south basin gate was about 7 km. The distance between the mid south basin and island (Hecla and Black) receivers was about 40 km. Distance covered between the island receiver gates and Doghead Point was about 63 km. Distance separating the Doghead Point receiver gate and the mid north basin receiver line was about 40 km with receivers in this gate spaced 14 km apart from one another. Distance between the mid north basin line and the north basin line was about 40 km with receivers spaced approximately 14 km except for one receiver at Grand Rapids about 140 km north of the north basin receiver gate (Fig. 1).

During the spring and fall of 2017, 204 (90% female) walleye were tagged with acoustic transmitters (V16-4H, ~6½ year tag life, Vemco) in the south and north basins (Table 2; Fig. 1) with average fork length at tagging 597 mm in the south basin and 543 mm in the north basin (range: 452-721 mm). During the spring of 2018, an additional 155 walleye (60% female) were tagged in the south and north basins using a combination of tag sizes to incorporate smaller bodied individuals (V13-1H, ~648 day tag life, Vemco; Table 2: Fig. 1). Walleve sex was determined through visually investigation during surgery. Average fork length of tagged walleye during 2018 was 482 mm in the south and 448 mm in the north basin (range: 344-735 mm). Acoustic transmitter tags had a nominal random delay range of 85-165 s to ensure equal probabilities at each random delay and to also reduce the probability of transmitter collisions on receivers and prolong tag life of the V16 and V13 tags. Walleye tagged in 2017 and 2018 were captured using an electrofishing boat (Smith-Root SR20-EH; GPP 5.0; 100-500 V). Prior to surgery, fish were placed in holding tanks filled with aerated ambient water. Fish were immobilized using a Portable Electroanethesia System (PES, Smith-Root, 100 Hz, 25% duty cycle, 40 V for ~ 5 s, Vancouver, WA, USA; Vandergoot et al., 2011). Fish were then placed in a padded trough while respiration was maintained through constant irrigation over the gills. A 3 cm incision was made midventral on the abdomen and the tag was inserted within the body cavity of the fish. Incisions were closed

Table 2

Acoustic telemetry tagging numbers across north and south basins of Lake Winnipeg. Number of individuals tagged followed by the tag type. Tagging locations in Fig. 1.

	South Basin	North Basin
Spring 2017	170 (Female = 157, Male = 13)	28 (Female = 20, Male = 8)
Fall 2017	6 (Female = 5, unknown = 1)	0
Spring 2018	73 (Female = 38, Male = 30, unknown = 5)	82 (Female = 53, Male = 7, unknown = 22)

with 2–4 interrupted sutures (standard surgical knots; 3–0 polydioxanone-II violet monofilament; Ethicon, Cincinnati, OH, USA). Fish also received an external tag (Floy<sup>®</sup> T-bar anchor; Floy Tag Inc.) inserted into the muscle between the pterygiophores below the base of the soft dorsal fin. Floy tags contained a unique identification number along with a telephone number for reporting purposes. Fish were placed into recovery holding tanks and released when they regained the ability to physically swim away from a releaser's hand. Physical recaptures of fish were reported by commercial and recreational fisheries. Fish handling, capture, and surgery were approved by Canadian Council on Animal Use Protocols administered by Lakehead University (Project ID: 1466383) and Fisheries and Oceans Canada (FWI-ACC-2017–001; FWI-ACC-2018–001).

# Multi-state live-dead modelling

A multi-state live-dead mark-recapture analysis (Lebreton et al., 2009; White et al., 2006) was chosen to evaluate fish movement and survivorship to account for both live (detections encountered through acoustic telemetry equipment) and dead (commercial and recreational recaptures) reports. Multi-state live-dead models allow for the estimation of four parameters: survival ( $\varphi$ ), movement ( $\psi$ ), resight (p), and reporting rate (r). Detailed assumptions of the model can be found in ESM Appendix S1 (Seber, 1986; White and Burnham, 1999; Pollock et al., 1990). Our main interest in using this model was to provide estimates of survival  $(\phi)$  and movement ( $\psi$ ) across the basins. Additional parameter estimates resight (p) and reporting rate (r) were used in model fitting but were not the focus of the historical and current studies and are not reported on further here. Additionally, historical survival estimates derived from the model were surprisingly low ( $\sim$ 8%) and as a result are not reported here (potentially a result of low sample size, low recapture or reporting rate, and no live resight information). We opted to independently calculate historical survival from tag and recapture data incorporating rates of tag loss, reported captures, and natural mortality reported elsewhere. For multi-state mark-recapture models, we considered two different basins for this analysis (south and north). Mark-recapture live-dead models were run using program MARK (White et al., 1999; White et al., 2006) via Rmark (Laake et al., 2019) in the R statistical programming environment (R Core Team, 2019).

### **Data preparation**

The historical mark-recapture study took place between May 30th, 1974 to March 31st, 1977 and included 148 weekly time steps (approx. 3 years) while the contemporary telemetry study took place from May 5th, 2017 until April 17th, 2019 with 103 weekly time steps (approx. 2 years). We used weekly time steps to provide a detailed temporal resolution and fit seasonal and annual groupings to balance overparameterization while implementing biologically relevant time bins. Weekly encounter histories for individual fish and fork length (mm) in both datasets were developed using program R (R Core Team, 2019) and are available on request from the authors.

Telemetry data was filtered for false detections using the R package GLATOS (Binder et al., 2019); false detections occur when multiple transmissions collide at a receiver station and need to be subsequently removed from the dataset. Additionally, individual fish abacus plots using all deployed receivers across the lake (ESM Fig. S1) were visually assessed to evaluate if tag failure or mortality (natural, tag loss, or fishing mortality both reported or unreported) occurred. We removed one individual in 2017 and ten individuals in 2018 tagged at Sandy Bar (south basin) with zero

detections recorded, indicating likely tag failure, or mortality through removal or following surgery. The fate of individuals (i.e., probable deaths) were also assessed using the full array grid (ESM Fig. S1). Individuals that were frequently detected on multiple receivers on the array south of Doghead Point and then suddenly were no longer detected for the duration of the study were assumed to have been removed (i.e., harvested), or died away from a receiver and assigned dead at the time and place of the last detection. Given the extensive array in the south basin, the probability of being alive and unsighted on any receiver in this basin were deemed to be extremely low. Receiver coverage extended into the Red River and no fish were documented moving and remaining in this river system. Similarly, walleye that were subsequently detected multiple times on the same receiver for more than two weeks (excluding winter months when fish were observed to be more lethargic) were assessed as dead or having dropped a tag. In both cases, we noted the first-time bin this occurred and the location and added this information to the encounter history file (e.g., as 'known' dead). Fish that went undetected north of Doghead Point and were not observed again were assumed to be at liberty due to the lack of receiver coverage across the north basin as it was not possible to determine at what point in time they may have been removed from the study, if at all.

We opted to group the weekly encounter history data into seasonal time bins in order to address questions of movement and survival on a seasonal basis across a given year in the contemporary dataset. Seasonal time bins varied slightly during the spring in the contemporary dataset due to restrictions associated with the timing of tagging and receiver downloads. Seasons were determined using ice-on/ice-off events, ambient air temperatures, and knowledge of relative walleye spring spawn and fall run events to encapsulate biological meaningful events. We chose a longer time bin for winter consisting of 24 weeks to ensure that we were able to capture short but effective fall and spring seasons when walleye have been documented elsewhere to be relatively active in their movement behaviour (Hayden et al., 2017; Kirby et al., 2017; Mckee, 2018; Peat et al., 2015; Raabe et al., 2020; Wang et al., 2007). During initial data investigation, individual walleye were observed overwintering close to known spawning locations indicating pre-spawn movement activity was significantly less than that of post-spawn activity. Based on these patterns, the spring grouping incorporated behaviours associated with spawn and post-spawn movement off the spawning grounds. As walleye are known to have increased periods of movement during spring and fall, well documented in other movement studies (Hayden et al., 2017; Kirby et al., 2017; Mckee, 2018; Peat et al., 2015; Raabe et al., 2020; Wang et al., 2007), we included models with interactive effects to capture inter-basin movement and its potential to vary seasonally. Based on these considerations, spring consisted of seven weekly bins in 2017 (May 5th-June 18th), and eight for spring 2018 (April 24-June 18th). In 2017 and 2018, summer consisted of 12 weekly bins (June 19th-September 10th), fall consisted of eight weekly time bins (September 11th- November 5th), and winter consisted of 24 weekly time bins (November 6th-April 23rd).

Historical data were grouped on an annual basis. Given the lack of detail across the historical dataset (only release and recapture data at most for each individual) and to avoid overparameterization, models were constrained to assess the data on an annual basis only; May 30th, 1974 to May 22nd, 1975 (52 weekly time bins), May 29th, 1975 - May 20th, 1976 (52 weekly time bins), May 27th, 1976 - March 31st, 1977 (45 weekly time bins). To allow for more direct comparisons between historical and contemporary datasets, we also considered yearly time bins for the contemporary telemetry data (ignoring seasons). Weekly telemetry data in the contemporary dataset was binned by year from May 5th, 2017 to April 24th, 2018 (53 weekly time bins) and from May 1st, 2018 to May 7th, 2019 (54 weekly time bins). Historically, fish were assigned a basin location based on initial tag and final recapture locations determined through a reported location on the grid layout (ESM Fig. S2). For contemporary telemetry data, fish were assigned a basin location of either south or north. This location was determined based off the weighted average of detections across the gates within a given week (either seasonally or annually). Weekly basin locations were defined as the individual weighted average of detections across the gates, assigning a basin location of south, north, or no location if not detected.

We evaluated a pre-defined set of models that were tested against the most general model. We chose three sub models for movement and survival and two sub models for resight and reporting rate parameters for a total of 36 possible parameter combinations across historical and contemporary datasets (ESM Table S1; Table S2). Top models from pre-defined model parameters were evaluated for model fit, with the top models with the lowest AICc values reported for historical and contemporary datasets, compared using  $\triangle$ AICc where a  $\triangle$ AICc >2 was used to indicate that model fits were not the same (Table 3; Table 4; Burnham and Anderson, 2002). The top two models across the historical analysis therefore are considered to equally fit the data. Using the top model fits for the historical and contemporary data, we additionally evaluated the added explanatory effect of fork length at tagging (as a fork length by basin interaction term in the model) as a continuous covariate on movement. Additionally, because weekly time bins were used to originally bin data in the encounter histories files, model estimates of survival and movement were estimated on a weekly basis across a given season.

To determine survival and movement on an annual time scale, we adjusted the weekly estimates from the models to represent annual estimates of movement and survival. Furthermore, to compare the historical and contemporary datasets and their estimated parameter values using a similar model parameterization, we fitted the historical top model structure (excluding the fork length covariate) to the contemporary acoustic telemetry dataset.

## Adjusted movement and independent survival estimates

Annual historical movement was estimated and adjusted to account for tag loss, as the model used to evaluate movement assumes 100% tag retention (White et al., 2006). The number of fish remaining in the lake each year after tag shedding (N') was

Table 3

Top five models from historical tag-based movement study using multi-state live-dead mark recapture models.  $\varphi$  = survival, p = resight,  $\psi$  = movement, r = reporting rate, Npar = number of parameters in model.

φ	р	ψ	r	Npar	AICc	ΔAICc	AIC weight
Constant	Year	Basin	Basin	8	20745.53	0.00	0.47
Year	Year	Basin	Basin	10	20746.58	1.04	0.28
Constant	Year	Year	Basin	9	20747.84	2.31	0.14
Year	Year	Year	Basin	11	20748.73	3.19	0.009
Year	Basin	Basin	Basin	9	20789.15	43.6	1.6e-10

#### Table 4

Toi	o three models from contemporary	v telemetrv-based	movement study us	sing multi-state live-o	lead mark-reca	pture models. S	vmbols as in Table 2.
		,					

φ	р	ψ	r	Npar	AICc	ΔAICc	weight
Basin *Season	Basin	Basin *Season	Basin	40	19397.66	0.000	0.99
Basin *Season	Basin	Basin + Season	Basin	32	19414.13	16.47	2.6e-4
Basin *Season	Basin	Basin *Season	Constant	39	19564.09	166.43	0

estimated as the number of fish tagged in each year (N; Table 1) adjusted for annual tag loss at 21.9% (SD = 0.02;  $\hat{\tau}$ ; 0.781; Koenigs et al., 2013) and individuals reported captured (n; Table 1; Eq. (1)). We then calculated the number of tagged fish that did not move across the basin (f) as ( $N' - \psi * N$ ), where  $\psi$  is the movement estimate derived from mark-recapture models (Eq. (2)). We then used Eq. (3) to determine the percent of fish that remained in each basin (*%res*). This then allowed us to use Eq. (4) to determine the adjusted annual movement estimate  $(\hat{\psi})$  accounting for tag losses. Both the unadjusted and adjusted estimates for model estimated historical movement are reported here for comparison (Table 5).

$$N' = (N * \hat{\tau}) - n \tag{1}$$

$$f = N' - (\psi * N) \tag{2}$$

$$\% res = f/N' \tag{3}$$

$$\widehat{\psi} = 100\% - \% res \tag{4}$$

Given the design of the historical study (e.g., no observations of live resights), the model was poorly suited for estimating survival. We therefore opted to independently calculate survival while accounting for tag loss, natural mortality, and reported captures across the study. We considered accounting for commercial reporting rate using an estimate derived from a Lake Erie walleye study (10-15%; Vandergoot et al., 2012), however, this produced unrealistically small estimates of survival (7-9%) and were not considered further. We used Eq. (5) to determine the number of individuals that retained their tags ( $N_{TL}$ ) in a given year where  $\widehat{ au}$ is annual tag retention (0.781; Koenigs et al., 2013). We additionally removed the reported individuals each year (n, or loss to the fishery) from total individuals remaining after tag loss to determine the number of fish at liberty ( $\omega$ ; Eq. (6); Table 5). We then applied an estimate of annual instantaneous natural mortality (*M*) as 0.29 (Vandergoot and Brenden, 2014). We selected natural mortality estimates from Lake Erie, as this lake is similar in many respects to Lake Winnipeg in size, mean depth, and productivity (Dove and Chapra, 2015; ECCC and MARD, 2020; Rawson, 1952). Survival was then estimated as the number of fish remaining in each year (Eq. (8)).

$$N_{TL} = N * \hat{\tau} \tag{5}$$

$$\omega = N_{TL} - n \tag{6}$$

$$\mathbf{N}' = \boldsymbol{\omega} * (1 - \mathbf{M}) \tag{7}$$

### Table 5

Historical unadjusted and adjusted movement estimates annually and across the duration of the study.  $\hat{\phi}$  = Independent survival calculation determined using equations (5) through (8) (see methods).  $\hat{\psi}$  = annual historical movement corrected for tag losses.

	Year 1	Year 2	Year 3
Model Annual $\psi$ Corrected Annual $\widehat{\psi}$	0.2% 0.3%	0.9% 1.2%	0.3% 0.4%
Independent Annual $\widehat{\phi}$	50%	69%	54%

$$\widehat{\phi} = \mathbf{N}' / \mathbf{N}_{\mathrm{TL}} \tag{8}$$

For comparison, we also derived survival estimates via catch curve analysis. Fishery survey data from 1979 to 2018 was obtained from the Government of Manitoba (2018). For comparison to the historic tagging study (1974–77), we selected the three earliest years in the dataset (1979-81). For comparison to the contemporary telemetry study (2017–19), we selected the three most recent years in the dataset (2016-18). Differences related to collection methods between the historical and contemporary fish survey data do exist through differences in gillnet mesh sizes as well as effort across each of the basins. So the number of fish in each age class was summed per year, and a linear regression of age on log(catch) was then fitted from the age class in each data set that was fully recruited to the fishery (e.g., highest mean catch over the 3year time period) along the descending arm of the catch curve. Annual survival was estimated as the antilog of the slope of the descending arm of the catch curve (Krebs, 2014).

# Results

# Historical movement

Movement probability estimates for the historical survey varied among years or by basin with none of the top models including a basin by time interaction. The top model indicated movement varied by basin and was not time dependent (Table 3). Annual south to north basin movement probability was estimated at 1.1%  $(\beta = -4.48 \text{ SE} = 0.212)$  while north to south movement was estimated at 0.35% ( $\beta$  = -1.14 SE = 0.243) across the duration of the study. The inclusion of fork length at capture as a stratum covariate resulted in a better model fit ( $\Delta$ AICc -99.75). The effect of fork length at tagging positively affected movement in a south to north direction ( $\beta_{FL}$  = 0.005 SE = 0.002) and was negative in a north to south direction ( $\beta_{FL}$  = -0.014 SE = 0.003). Historically, larger fish (>300 mm) in the south basin were more likely to move to the north basin, whereas small individuals (<300 mm) had similarly low rates of movement in either direction, and were higher in a north to south direction for only the smallest body sizes encountered (Fig. 2).

#### **Historical survival**

Parameterization of survival probability estimates for the historical tagging study varied among the top five models (Table 3); estimates were either constant across basins and over the course of the study or varied on an annual basis. Independent survival estimates, which accounted for tag loss, natural mortality, and reported captures (see methods) were 57.6% on average across the three-year study (Table 5).

#### **Contemporary movement**

Movement models in the contemporary dataset were tested for basin (north and south) by time (season) interactions and additive effects (Table 5). Probability of travelling from the south to north basin were consistently higher than in a north to south direction (Fig. 3). Travel between basins tended to be lowest in winter and



**Fig. 2.** Effect of fork length at size of tagging on estimated movement probability for north basin fish moving south (red, solid line) and south basin fish moving north (blue, dashed line) for both the historical (left) and contemporary (right) movement studies. Confidence intervals (95%) are shown (shaded). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

summer and highest in fall and spring (Fig. 3). As with the historical data, the inclusion of fork length at tagging as a covariate improved model fit ( $\Delta$ AlCc -22.8), but in an opposing pattern. Unlike historical estimates, a small negative effect of fork length on movement probability from the south to north basin was noted ( $\beta_{FL} = -0.0004$  SE = 0.0006), while a strong positive effect of fork length on travel probability from the north to south basin was observed ( $\beta_{FL} = 0.005$  SE = 0.0008; Fig. 2). However, movement was consistently greater in a south to north direction across all lengths of tagged fish, being similar only at the largest fork lengths (Fig. 2).

#### **Contemporary survival**

Survival models were fit with either a basin by time interaction or with additive effects (Table 5). Survival estimates among the top three models all included a basin by season interaction (Fig. 3). Fall weekly survival estimates in both years tended to be higher in the south basin compared to the north basin. While winter survival was greater in the north basin in 2017, this was not observed in 2018. In both basins, survival appeared to increase from spring to winter, declining again from winter to spring (Fig. 3).



**Fig. 3.** Mean probability of weekly movement (top panel) and survival (bottom panel) by season from spring 2017 to winter 2018. South basin movement estimates are weekly seasonal movement into the north basin in a given season (blue, dashed) and north basin movement estimates are weekly seasonal movement into the south basin in a given season (red, solid). Confidence intervals (95%) are shown in grey. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

# Comparison of historical and contemporary movement and survival

The historical top model structure included constant survival across basins and basin-specific movement rates, with no temporal effects of season or time. Independent yearly estimates of survival were estimated at 50% during the first year, 69% during the second, and 54% during the third year of the study. Historical survival estimates derived from catch curve analysis were somewhat lower at 45.5% (95% CI, 38–55%; Fig. 4). After adjusting the model estimates of weekly survival to a standardized annual survival estimate, contemporary annual survival was estimated at 37% ( $\beta$  = -2.58 SE = 0.056) across the duration of the study; 44.9% ( $\beta$  = -0.20 SE = 0.127) during the first year, and 26.8% ( $\beta$  = -0.798 SE = 0.204) during the second year (Table 4). Contemporary survival estimates derived from catch curve analysis were somewhat higher at 64.3% (95% CI, 58-71%; Fig. 4). Annual movement transition probability across the lake (with no directionality considered) for the contemporary dataset was 7% ( $\beta$  = -2.57 SE = 0.055) during 2017 and 8.6% ( $\beta$  = 0.22 SE = 0.083) in 2018, compared to annual historical estimates of < 1% (Table 5). However, after adjusting annual historical movement to account for tag loss, historical movement transition probability ranged from 0.3 to 1.2% (Table 5).

# Discussion

In the historical and contemporary movement studies, our models revealed a small but measurable proportion of tagged walleye moving between basins in north and southward directions, but with movement primarily occurring from south to north. This



**Fig. 4.** Catch curves for Lake Winnipeg walleye during historical (1977–1979) and current (2016–2018) time periods, used to estimate instantaneous mortality which were then used to estimate annual survival rates (see text).

consistency in movement patterns between studies was observed despite differences in study design and five decades separating the two studies. Furthermore, we demonstrate variable but generally low annual survival over both studies, perhaps not surprising as commercial walleye harvest in Lake Winnipeg during the past 20 years has frequently exceeded maximum sustainable yield estimates (Lumb et al., 2020). Seasonally, walleye movement was highest during fall in the contemporary dataset, with the lowest movement between basins occurring in summer and winter (occurring in 2017). These results present the first direct measurements of walleye movement across the south and north basin of Lake Winnipeg.

Previously documented morphological differences between north and south basin walleye (Johnston et al., 2012; Sheppard et al., 2018; Watkinson and Gillis, 2005) has led to speculation that walleye in each basin are distinct stocks. However, documented movement of walleye between basins reported here do not support this conclusion. Further, if we assume that movements reported here provide an opportunity for genetic mixing, our results also support previous molecular studies indicating low genetic differentiation between basins (Backhouse-James and Docker, 2012), as well as recent work showing gene flow occurring between basins primarily in a south to north direction (Thorstensen et al., 2020). The sum of evidence between both previously reported genetic studies and movement patterns reported here would seem to suggest that reported morphometric differences between basins are likely due to phenotypic plasticity related to habitat differences between the basins rather than population divergence.

Morphological differences between fish in the south and north basins have also likely informed differences in management between basins historically, but our results suggest that these morphological differences may be, at least in part, a consequence of walleye movement patterns. Larger mesh sizes are applied in the north basin (95 mm in the summer and fall, 108 mm in the winter) than in the south basin (until recently 76 mm year round, increased to 89 mm in 2020; Manitoba Sustainable Development, 2020). However, our study shows that larger walleye tended to contribute to the predominant direction of movement from the south to the north basin during both time periods. Thus, mesh sizes employed in the north are likely in part also targeting larger walleye originating from the south basin. Size-dependent migration has been documented in other movement studies on walleve (Bowlby and Hoyle, 2011; Mckee, 2018; Wang et al., 2007); larger fish tend to travel longer distances than smaller individuals as they are better able to account for the associated negative bioenergetic costs (Minns, 1995; Woolnough et al., 2009). In the contemporary dataset, larger fish appear to be primarily responsible for the majority of both northward and southward movement, which may partly contribute to the higher contemporary rates of movement observed in our study (though direct comparison of movement rates are impossible due to differences in study design). However, it is also worth noting that the historical patterns of larger fish contributing to north to south movement rates is likely also a consequence of larger commercial mesh being fished in the north basin, which were the source of recaptures in this study.

Differences in collection methods and study motivations between historical and contemporary time periods likely resulted in differences in the mean length of fish tagged. Given that the mean length of tagged walleye in the historical dataset was smaller, lower south to north movement rates historically could in part be due to smaller mean lengths and larger gillnets employed throughout the north basin (108 mm north basin; 76 mm south basin). However, the directionality of movement probabilities with length were opposite between time periods, making the impact of mean length differences between time periods on overall movement rates difficult to discern. Furthermore, individuals across the historical dataset were recaptured exclusively by the commercial fishery and we therefore recognize temporal and spatial biases likely exist (Holst et al., 1998; Millar, 2000). Specifically, differences in gillnet mesh sizes historically likely led to lower recaptures of smaller bodied individuals in the north basin and suggests our estimates of movement rates from south to north are likely conservative. Despite this potential bias in the recapture of larger tagged fish in the north basin, we were still able to detect greater movement rates in the south to north direction historically, opposite what would be excepted if the pattern were solely a consequence of differences in commercial gear used between basins.

Consistent inter-basin movement patterns across historical and contemporary studies from the south to north basin may reflect environmental gradients between the north and south basins of Lake Winnipeg. The south basin of the lake is more shallow and turbid, and does not stratify during summer months compared with that of the deeper, cooler north basin where stratification does occur, though infrequently (Brunskill et al., 1980). Additionally, Lake Winnipeg extends just over 4° of latitude, which maintains a north-south gradient of water temperature (McCullough, 2020). Ice on dates for the two basins generally occur within a day or two of each other (ECCC and MARD, 2020), with delays in ice off during the spring across the north basin roughly two weeks offset from the south basin (Brunskill et al., 1980; ECCC and MARD, 2020). South to north walleye movement may result from individuals seeking out cooler waters as temperatures in the south basin during the summer typically reach an average daily mean of ~ 23 °C with maxima reaching upwards of ~ 26 °C (~23 °C thermal optima for walleye; Kitchell et al., 1977; Lester et al., 2004; McCullough, 2020). Similar movement behaviour in walleye that appears to be related to thermal preference has been observed in both Lake Erie and Lake Huron (Hayden et al., 2014; Raby et al., 2018; Wang et al., 2007). An interesting by-product of selection

for northward movement in some Lake Winnipeg walleye (perhaps related to thermal physiology) is that these individuals will also experience reduced vulnerability to commercial and recreational gear in the south basin, where fishing effort is most intense.

These low but consistent movement rates of walleye between basins appear to reflect a behaviour known as partial migration (Bronmark et al., 2014; Chapman et al., 2011, 2012), an adaptive strategy which may evolve over time to provide benefits such as increased body growth, survival, and reproduction in response to environmental gradients that ultimately influence an individual's life history strategies (Bowlby and Hoyle, 2011; Bronmark et al., 2014; Roff, 1988). Partial migration in walleye populations is not uncommon and has been documented elsewhere, though in greater proportions (Hayden et al., 2014; McKee, 2018). The greater distances across the basins in Lake Winnipeg compared to these other systems may help to explain the lower observed proportions of fish movement between the south or north basins of Lake Winnipeg.

Walleye movement was highest during fall and lowest in the summer across both basins, as observed in the contemporary dataset. Higher rates of movement in the fall may reflect the pursuit of schooling and or fall-spawning prey (e.g., cisco). Movements of walleye into the Red River are noted in the fall (Stewart and Watkinson, 2004) and movement into tributaries during fall has also been documented in the Laurentian Great Lakes (Bowlby and Hoyle, 2011; Hoyle et al., 2017; Wang et al., 2007). During the observed summer decline in movement behaviour, fish may have been constrained by increased energetic costs of travel through sub-optimal warmer water temperatures, making them less likely to undergo large-scale migrations.

Contemporary walleye survival rates appeared to vary between basins depending on season and may in part be due to differences in the timing and intensity of commercial fishing activities related to our seasonal time bins. Low fall survivorship in the north basin (relative to the south) may be correlated with increased northsouth movement in the fall; cooling water temperatures in the north basin may promote the movement of walleve southward. allowing them to occupy waters closer to optimal temperatures for a longer duration of time. However, this behaviour may increase vulnerability to commercial fishing activity which opens September 1st across the lake; fish moving between basins during this time may be particularly vulnerable around the narrow channel at Doghead Point where commercial fishing activity has been known to be fairly substantial. Further investigation into the degree to which walleye movement is driven by spatial thermal gradients (e.g., Raby et al., 2018) may aid fisheries managers in better determining the timing of walleye movements and therefore better predict particular time periods and/or locations in the lake where vulnerability to commercial harvest is highest (and therefore potentially require more carefully regulated management).

Annual rates of survival across both studies were generally low. Contemporary annual survival determined by mark-recapture models (2017, 44.9%; 2018, 26.8%) were slightly lower than those derived from catch curve regression estimates (64.3%) whereas historical survival estimates (1974, 50%; 1975, 69%; 1976, 51%) were slightly higher than those determined by catch curves (45.5%). These annual survival estimates are comparable to others reported for Lake Winnipeg, ranging from 30% in the mid-1990's to 52-46% between 2013 and 15 (derived from annual mortality estimates, Lumb et al., 2020). Generally, it has been suggested that for total mortality rates to be sustainable, fishing mortality should be no>0.75-times natural mortality, and should be set to 0.5-times natural mortality when immature individuals are harvested (Lester et al., 2014) as is likely the case in the Lake Winnipeg fishery given reported lengths at maturity for Lake Winnipeg walleye (Johnston et al., 2012) and minimum mesh sizes of 76 mm

employed in the south basin (Lake Winnipeg Quota Review Task Force, 2011) until very recently (ECCC and MARD, 2020). While estimates of natural mortality do not currently exist for Lake Winnipeg, if our assumption of instantaneous natural mortality rate of 0.29 is correct, then sustainable instantaneous total mortality should be 0.45, which translates into annual survival estimates of 64%. Lumb et al. (2020) estimated sustainable annual survival to be 56% (44% annual mortality), slightly lower than our estimates. Regardless, the majority of the survival estimates reported in this study fall below sustainable survival estimates from either our study or that of Lumb et al. (2020). Our findings regarding survival support recent changes to the fishery implemented by the Government of Manitoba, including a quota buy-back and increased gillnet mesh sizes, as measures to help alleviate fishing pressure on this population. Clear recommendations to help better assess and manage the fishery are outlined elsewhere (Lake Winnipeg Quota Review Task Force, 2011).

We are confident that our telemetry results regarding fish movement and survival are robust, based on our receiver layout and number of fish sampled. Similar conclusions regarding longrange movement patterns of walleye have been made in other large lake systems with fewer numbers of tagged fish than reported in this study (Hayden et al., 2014; Raby et al., 2018). While it is likely that the contemporary acoustic telemetry dataset is likely biased towards larger female walleye (75% of the tagged fish during the study were female), whether this has biased our survival results is not clear. Though walleye display sexual dimorphism, longevity of male and female walleye are similar (Rennie et al., 2008). However, male and female walleye survival may differ based on differential vulnerability to commercial fishing gear related to size or activity. Bioenergetic comparisons of male and female percids indicates that females have higher metabolic costs (Rennie et al. 2008), which may reflect higher activity rates or differences in movement patterns in females (e.g., Raby et al., 2018). Higher female walleye activity compared to males could result in increased encounter rates with commercial fishing gear. By contrast, survival estimates based on catch curve analysis may be more representative of both adult male and females.

Contemporary movement rates presented here might be interpreted as conservative, based on our decisions regarding what constituted movement into the north basin. Individual walleye that moved into the north basin detected at Doghead could have evaded detection on north basin receiver gates due to the increased spacing in that part of the lake. To evaluate this potential bias, we determined that an additional 12 individuals over the duration of the study would have been documented as moving from the south basin to the north basin if we had included the Doghead receiver gate as part of the north basin. Additionally, only one individual across the duration of the study was not detected on the Doghead receiver gate but was subsequently detected on north basin receivers. Based on this, annual rates south to north movement could be ~4% greater annually than those reported here, still modest, and not dramatically different than our model reported estimates. However, detection on the Doghead receiver line does not guarantee movement of fish into the north basin of the lake, therefore a 4% annual increase in estimated movement rates would likely be on the higher of estimated movement into the north basin, based on our study design.

In summary, low but consistent movement rates of walleye between the north and south basins of Lake Winnipeg reported here have provided significant insights into the ecology of walleye in the lake. Specifically, movement between basins may explain molecular-based similarities between walleye from both basins, and morphological differences observed between basins may be (at least in part) a function of dominant size-dependent migration patterns. Migration patterns were shown to vary seasonally and are likely driven by fish seeking out optimal thermal conditions annually, and perhaps by prey availability at specific times of the year. The majority of estimated survival rates for walleye in Lake Winnipeg appear to be below sustainable thresholds, supporting current management actions by the Government of Manitoba. In order to evaluate the outcome of these management interventions and to determine if additional actions are required to achieve a sustainable fishery, additional monitoring and data collection efforts are likely required.

# **Declaration of Competing Interest**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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#### Appendix A. Supplementary data

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#### Journal of Great Lakes Research 47 (2021) 614-625

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