Canadian Journal of
Zoology

OPEN ACCESS | Research Article

Distinct patterns of movement in monthly space use across Lake Winnipeg by a population of south basin walleye

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Abstract

Lake Winnipeg hosts North America's second largest commercial fishery for walleye (*Sander vitreus* (Mitchill, 1818)); however, little is currently known regarding walleye distribution throughout the lake. Here we identify two movement strategies for adult female walleye (migrant and resident) and describe patterns in monthly space use over 2 years. We used permissible home range estimators to determine monthly home range (95%), core range (50%), and associated mean locations. Mean locations showed that migratory walleye occupied more northern regions of the lake during late summer into fall (August and September) and were more southern during winter (November to March) and spring (April to June), overlapping residents. Migrants exhibited larger ranges during June, July, and October and shared similar ranges to residents when found at similar latitudes. Putative repeat spawning within the Red River was marginally more frequent among migrants compared to residents. This study describes two movement strategies of walleye within the south basin of Lake Winnipeg, possibly arising from multiple factors including water clarity, prey density, and temperature gradients. Results presented here provide information on the timing of movement and the spatial distribution of fish, which may be incorporated into a spatiotemporal based approach for fisheries management and stock assessment.

Key words: Percidae, migration, spatial ecology, home range estimator, acoustic telemetry, walleye

Introduction

Understanding movement patterns of highly mobile fishes is critical to the application of effective fisheries management, especially in large freshwater lakes. However, technological limitations to studying fish movement has limited these investigations historically (see Turner et al. 2021). Understanding habitat requirements across life stages for species, such as preferred habitats for foraging and reproduction and potential differential behaviour patterns among individuals can provide researchers and managers valuable insight into best management practices (Cooke et al. 2013). For instance, partial migration strategies are a relatively common phenomenon where a portion of individuals in a population demonstrate increased movement and habitat use compared with others who remain relatively resident to a particular area across their entire adult lifespan (Jonsson and Jonsson 1993; Mueller and Fagan 2008; Chapman et al. 2011). These patterns of behaviour have been previously documented in freshwater fishes and are relatively common across large, heterogenous habitats (Lucas and Baras 2000; Mueller and Fagan 2008). Understanding these movement patterns has implications for both where (in space, e.g., fish sanctuaries) and when (seasonality, i.e., periodic closures of the fishery) management boundaries are applied to fisheries.

Acoustic telemetry studies have confirmed both partial (including facultative i.e., plasticity in movement strategy year-to-year) and long distance migration behaviours in walleye (*Sander vitreus* (Mitchill, 1818)) populations (Hayden et al. 2014, 2018; Raby et al. 2018; Matley et al. 2020; Elliott et al. 2022; McKee et al. 2022). Migrations observed across these systems may be related to individuals' attempts to maximize fitness by exploiting variable resource availability in space that may provide them with benefits such as increased growth, reproductive success, or both (Elliott et al. 2022; McKee et al. 2022). Long-range migration events for walleye in the Great Lakes appears to be related to preferences for cooler, deeper waters following spring spawning, presumably reflecting behavioural thermoregulation as lakes warm, as well as the potential to access large-bodied prey (Bowlby and Hoyle 2011; Raby et al. 2018; Matley et al. 2020; Elliott et al. 2022; McKee et al. 2022). The maximum length of migratory individuals (at time of tagging) was found to be significantly larger than that of residents in Black Bay, Lake Superior, with larger females making up a greater proportion of migratory walleye (McKee et al. 2022). Furthermore, this species typically demonstrate relatively high rates of spawning site fidelity (Zhao et al. 2011; Hayden et al. 2018; Chen et al. 2020). As many walleye populations across large inland lakes are subjected to both commercial and recreational fishing activities, telemetry studies provide valuable insight on the spatial and temporal patterns of walleye. These insights can better inform management and conservation strategies by linking habitat use at time of capture to spawning areas, both of which require management to sustain populations (Crossin et al. 2017).

Lake Winnipeg walleye is an ecologically important species, both as a native top predator within the system and by supporting the most economically important fishery in the Province of Manitoba (Lumb et al. 2020). The fishery provides both sustenance and income for Indigenous communities surrounding Lake Winnipeg, supporting hundreds of jobs directly and indirectly related to commercial and recreational fishing (Heuring 1993; Nicholson 2007; Probe Reserach 2018). From 2010 to a low in 2018, total harvest and relative body condition of Lake Winnipeg walleye declined in response to multiple factors, including deteriorating water quality, an increasing frequency of species invasions, and increased harvest quotas, although walleye abundance now appears to be increasing following 2018 (Environment Canada and Manitoba Water Stewardship 2011; Schindler et al. 2012; Ocean Outcomes 2024). In 2010, reductions in mesh net sizes across the upper half of the south basin of Lake Winnipeg and throughout the north basin resulted in increased capture rates of smaller individuals (Nicholson 2007; Manitoba Sustainable Development 2019). However, mesh sizes in both the south basin and channel were increased in 2020 to reduce fishing pressure on smaller walleye (<300 mm in fork length). Currently, walleye is assessed as a single stock, although the timing of fishing seasons are staggered in the spring between the south and north basin (i.e., 2 weeks earlier in the south basin) and differences in allowable mesh net sizes exist across the basins (i.e., larger in the north). Fishing pressure also differs between the basins of Lake Winnipeg, with the majority of fishing effort occurring in the south basin (Franzin et al. 2003). Additionally, zebra mussel (*Dreissena polymorpha* (Pallas, 1771)) have established across the south basin (first detected in 2013; Enders et al. 2019), and are predicted to affect walleye production, both in Lake Winnipeg (Geisler 2015) and elsewhere (Geisler et al. 2016; Hansen et al. 2020). Similar threats across the Great Lakes historically have led to the collapse of many active and productive walleye fisheries (Schneider and Leach 1977), raising concern for the future sustainability of Lake Winnipeg walleye populations.

Several studies investigated morphological and genetic differences across Lake Winnipeg walleye and found differing conclusions as to whether or not populations in the south and north mix or remain in their respective basins (Watkinson and Gillis 2005; Moles et al. 2010; Backhouse-James and Docker 2012; Johnston et al. 2012; Thorstensen et al. 2020). Johnston et al. (2012) demonstrated a south to north increase in mean age and size across walleye, and Watkinson and Gillis (2005) effectively showed distinct differences in scale growth and morphology between south and north basin fish. While genetic studies concluded that there is little to no genetic divergence across south and north basin spawning locations throughout the lake (Backhouse-James and Docker 2012). Subsequent work using RNA sequencing detected gene flow in Lake Winnipeg walleye predominantly along a south to north gradient (Thorstensen et al. 2020). Further, low but measurable rates of movement occur between the basins for at least the past 50 years (Turner et al. 2021). However, detailed (i.e., monthly) movement patterns of walleye remain undescribed.

The main objective of this study was to describe monthly movement patterns across a population walleye tagged in the south basin of Lake Winnipeg to better understand how walleye distribute throughout the lake. We assessed the repeatability of movement behaviour by first categorizing individuals into two main groups: resident or migrant. We then determined and compared monthly home (95%) and core (50%) range estimates and their associated latitudinal centroid locations between these groups, considering relevant habitat features in determining movement over a 2-year period of study. Additionally, we assessed putative repeat spawning between female residents and migrants in the Red River at the southernmost extent of Lake Winnipeg.

Materials and methods

Location

Lake Winnipeg (Manitoba, Canada) is the 10th largest lake in the world by surface area (23 750 km^2; Brunskill et al. 1980) and can be subdivided into two relatively distinct basins connected by an intermediate channel area with a narrow pinch-point approximately 2 km wide (Doghead Narrows; Fig. 1). We used this pinch-point as a convenient marker to differentiate the south and north basins of Lake Winnipeg. The south and north basins differ in both biotic and abiotic features such as differing maximum summer water temperatures, turbidity, forage prey species composition and density, mean depth, surface area, as well as the timing of ice on/off due to the four degrees of latitude the lake covers (Fig. 1; Brunskill et al. 1980; Environment and Climate Change (ECCC) and Manitoba Agriculture and Resource Development (MARD) 2020).

Receivers

A grid-style telemetry array (Kraus et al. 2018) was deployed across Lake Winnipeg during the 2016 field season, prior to tagging. During 2016, 69 (VR2W, VR2Tx, 69 kHz; Innovasea, Halifax, NS, Canada) receivers were deployed across Lake Winnipeg covering the south basin from the Red River to Hecla and Black Island (Fig. 1). An additional three receivers were deployed and spaced evenly between the 2 km Doghead Narrows area. However, the middle receiver at the channel

Fig. 1. Map of Lake Winnipeg, study location. Receiver locations indicated on the map, black circles represent receivers deployed in 2016 and black triangles represent receivers deployed in 2017. Walleye (*Sander vitreus*) tagging locations are indicated by red squares (Red River, Sandy Bar, Winnipeg River). Additionally mapped is the reference tag location (open black circle; Supplementary Material Fig. S9). The basin division at Doghead Point, which divides the south and north basins is also indicated on the map. Imagery source: ESRI World Imagery (ESRI 2025). Map displayed in WGS 1984 coordinate system.

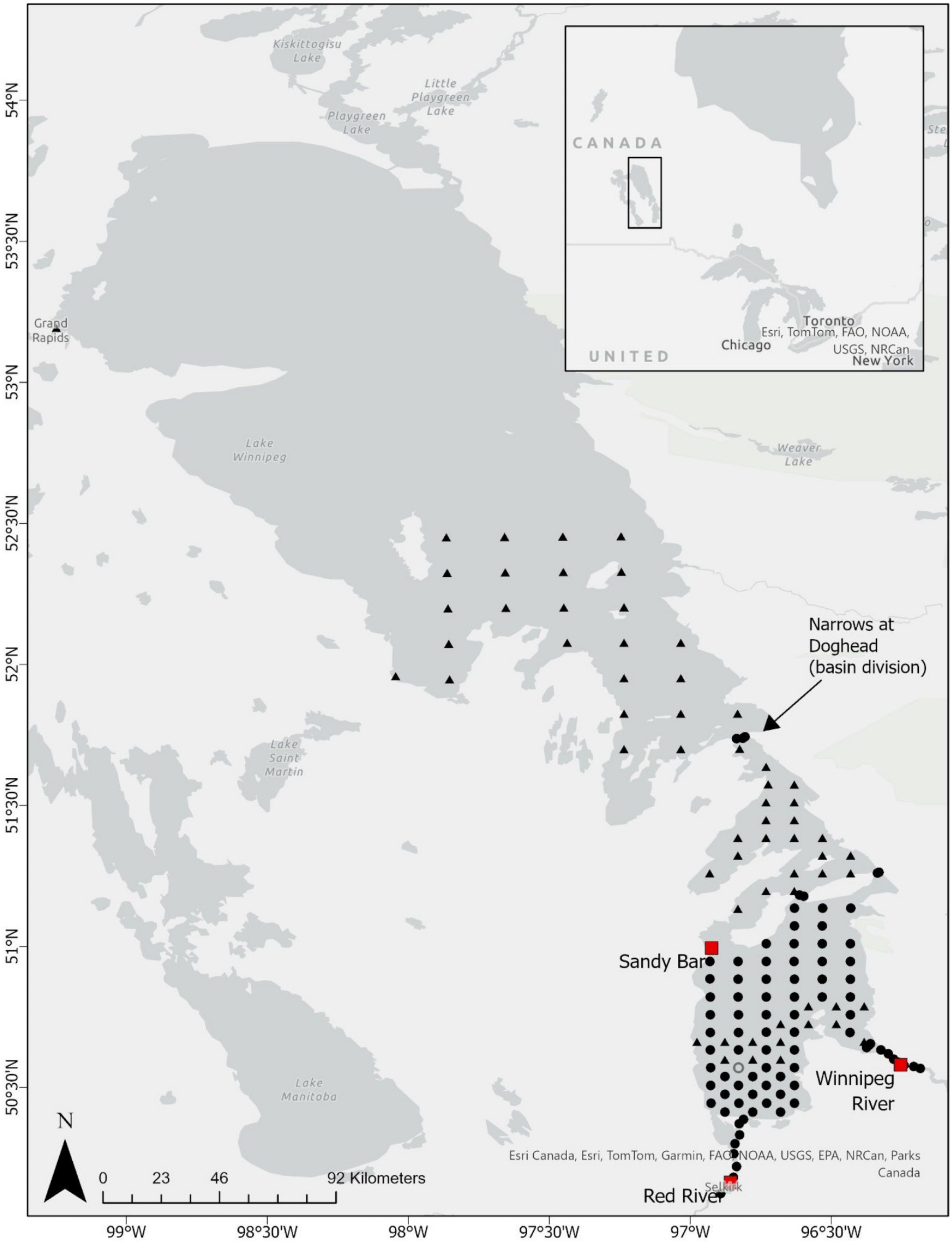


Table 1. General tagging information, sex and fork length (FL) range across all tagging locations for migrant and resident walleye (*Sander vitreus*) included in model analysis.

Movement group	Number of individuals tagged at each location	FL range at tagging (mm)	Sex
Migrant	Sandy Bar (11) Red River (20)	480–721	1 male and 30 female
Resident	Sandy Bar (2) Red River (15) Winnipeg River (1)	453–706	1 male and 17 female

Note: See Fig. 1 for tagging locations.

of Doghead Point was lost in 2018, resulting in the decline in detection probability (~90% in 2017, ~70% in 2018) based of limited sync-tag data. Receivers were spaced across the lower portion of the south basin in a 5 km grid, and from the middle of the south basin up to Hecla and Black Island at a 7 km spacing (Fig. 1). During the 2017 field season, an additional 14 (VR2W, VR2Tx, 69 kHz) receivers were added to the middle of the south basin to provide additional coverage (first week of June 2017; Fig. 1). Twenty-one (VR2W and VR2Tx, 69 kHz) receivers were deployed north of Hecla and Black Island arranged across the same grid with 7 km separating each (May 2017; Fig. 1). An additional 25 (VR2W, VR2Tx, 69 kHz) receivers were deployed north of Doghead Point along the grid array and were separated by 14 km (June 2017). A single receiver was deployed at the mouth of Saskatchewan River (24 May 2017) while two were placed in the Dauphin River (one at the mouth and 1 km up stream; 31 May 2017) to record any movement in and out of these larger river systems (Fig. 1).

Walleye tagging

Walleye were tagged in 2017 across the south basin of Lake Winnipeg. A total of 166 walleye were tagged during the 2017 field season during the spring (May) in the Red River ($n = 110$) and Sandy Bar ($n = 60$) and an additional tagging effort occurred at the Winnipeg River in October ($n = 6$; Fig. 1). Fish were captured using an electrofishing boat (Smith-Root SR20-EH; GPP 5.0; 100-500 V, Vancouver, WA, USA) and placed in live wells filled with aerated ambient water. Walleye were immobilized prior to surgery using a Portable Electroanethesia System (PES, Smith-Root, 100 Hz, 25% duty cycle, 40 V for ~5 s, Vancouver, WA, USA). Fish were placed in a padded trough while a constant flow of water was provided over the gills during surgery. A small 3 cm incision was placed mid-ventral and a V16-4Hacoustic tag (diameter = 16 mm, dry mass = 24 g, min. delay = 85 s, max. delay = 270 s, est. battery life = 6.67 years, Innovasea) was inserted into the body cavity. Two to four interrupted sutures (standard surgical knots' 3-0 polydioxanone-II violet monofilament) were administered to close the incision. External T-bar tags were inserted into the muscle at the base of the soft dorsal fin for external identification. 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). Acoustic transmitter tags had a nominal random delay range of 85–165 s to reduce the probability of transmitter collisions on receivers.

Data filtering and management

All data preparation and analyses were conducted using program R version 3.0.2 (R Core Team 2019). Raw detection data were filtered to remove any false detections (Pincock 2012). Filtered data were then plotted for each tagged individual using abacus plots to visually identify fish that were detected and remained in the array for the duration of the study period. After assessing which individuals remained alive over the duration of the study (15 May 2017 to 31 March 2019; $n = 49$; Table 1), clear patterns of movement behaviour became evident. To determine the maximum extent an individual may have achieved within a given year, all receiver detections within the south and the north basin were each grouped as a single functioning unit. Migratory fish were defined as individuals that both (a) recorded both south and north basin detections (i.e., detected at or past the Narrows at Doghead point) locations across a single calendar year, and (b) demonstrated this behaviour repeatedly over two consecutive years of observation. Resident fish were categorized as individuals that remained south of Doghead point for the entire duration of the study period, over both years.

To compare putative repeat spawning between the migrant and resident walleye in Lake Winnipeg, abacus plots of female walleye tagged in 2017 in the Red River were used. Individuals recorded on any receiver within the Red River during the following spring (2018) were assumed to be present to spawn (Supplementary Material Fig. S1).

As we had already determined that a subset of walleye were travelling large distances (see above), we opted to use a 1 h time interval, which has previously been suggested for relatively active and mobile species (Simpfendorfer et al. 2002). We gathered a mean hourly location and further subjected detected data locations to a randomized ±500 m to both latitude and longitude; this randomization ("jittering") ensured that the model had enough unique locations required ($\geq$15) to calculate a range estimate for each year and month (see Supplemental Material Table S1 for the number of individuals included in each group, month, and year for range estimates).

Home, core range, and centroid location estimation

Individual monthly home and core range estimates for migrant and resident walleye were calculated using a permissible home range estimator (PHRE; Tarjan and Tinker 2016), adapted here for estimates of monthly walleye home (95%) and core (50%) range (code adapted from Tarjan and Tinker

2016). Briefly, the PHRE model is a kernel density estimator (non-parametric method to estimate the probability of data distribution) and was developed to allow for the inclusion of relevant habitat and landscape features (i.e., depth and exclusion areas) that may have some influence on animal space use, while also restricting estimates within the bounds of a specific area, an important consideration for fish, who are limited to the bounds of a body of water. Habitat elements incorporated into the model are based on a priori information (Tarjan and Tinker 2016). Here, we incorporated three habitat features; a northing line, substrate, and depth (detailed below). Habitat features in the PHRE model are incorporated as values associated to the gridded overlay of the lake. The model then transforms unique fish locations by applying it to a new coordinate system that incorporates the transformed habitat features and set smoothing parameters. Kernel density estimators are then back-transformed to reflect geographic coordinate locations and polygons are output to reflect home and core range space use (see Tarjan and Tinker 2016 for further details on PHRE model methodology).

Due to the primarily latitudinal orientation of Lake Winnipeg and prior knowledge of limited walleye movement between basins (Turner et al. 2021), a northing line was incorporated to more effectively capture and integrate movements along this axis. The northing line was represented by a number of set points that were evenly distributed at 9.75 km intervals (based on a balance of fine scale detail and model computation) across 390 km of the lake latitudinally (similar to the "ATOS" description in Tarjan and Tinker (2016)). Lake depth was also included in the PHRE model using recent and detailed bathymetric surveys (see fig. 3A in Rudolfsen et al. 2021). To improve model run time, a random subsample of 5000 grid points evenly spaced across the lake was created, and depths between points were linearly interpolated. Points that fell along the edge of the lake were given a depth value of zero. Depth was chosen as a habitat element as previous studies focusing on walleye habitat preference have demonstrated a seasonally-dependent association with depth, with walleye showing preference for mid-range depths in the summer and associations with shallower depths in the winter, likely related to thermal-optical habitat availability (Lester et al. 2004; Rudolfsen et al. 2021). Depth is likely also associated with different life history processes utilized throughout a given year (e.g., spawning during spring and foraging during summer). Most importantly, depth best describes limitations of "permissible habitat" by ensuring range estimators take into account non-permissible features such as shorelines and islands. Finally, substrate was the last habitat element incorporated into the PHRE model. Detailed sediment information was gathered at each acoustic receiver location (Fig. 1.) with the dominant substrate type assigned to each receiver location as described in Rudolfsen et al. (2021; Fig. 3*b*). We selected fine substrate type for use throughout the PHRE model as walleye have been previously shown to be more closely associated with this substrate type within Lake Winnipeg (Rudolfsen et al. 2021). Although model estimates of core and home range were confined to the limits of the lake, the inclusion of habitat features like sediment used here assisted in estimating ranges that may be more closely associated with preferred walleye habitat use.

Consistent with the methods of Tarjan and Tinker (2016), smoothing parameters were used in the model and determined through visual assessments. A random sub sample of six migrants and six residents were run through the model independently and the average smoothing parameters for substrate and depth variables were determined and held constant for final model analysis across both groups (substrate: 0.0009 and depth: 0.057). Given our prior knowledge of the variation in movement distances between migrant and resident groups throughout a given year, we used an adaptive smoothing parameter (h) for the northing line axis similar to Tarjan and Tinker (2016). The smoothing parameter (h) varied as a function of the mean nearest neighbour distance (d) between the detection locations through the following equation

$$h_{\mathrm{b}}(d/4)^{2.5} \tag{1}$$

where h_{b} represented the standard smoothing parameter of five northing line units, determined through a random sub sample of individuals to avoid over or under smoothing for either movement group. Through the PHRE model and its subsequent creation of range polygons representative of the space use for each fish across each year and month, we obtained a centroid location to determine a mean centralized location for each range estimate.

Statistical analyses

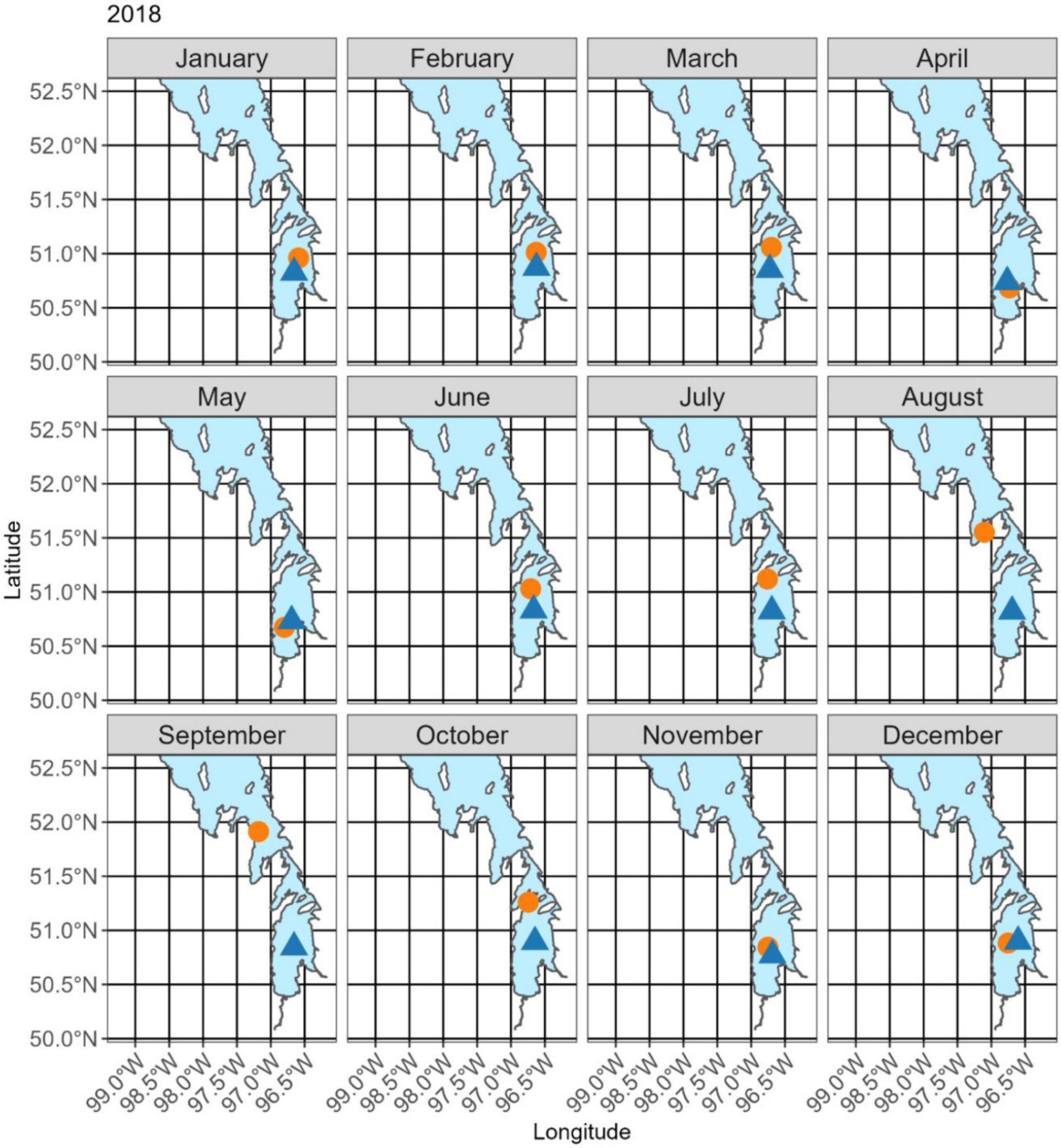
Equality of the proportion of repeat Red River spawners between migrant and resident female walleye was tested with an exact binomial test. A generalized linear mixed model (GLMM) in the R package glmmTMB (Brooks et al. 2022) was applied to evaluate home and core ranges of migrant and resident walleye estimated from the PHRE model. Home and core range values were log transformed to meet assumptions of normality and homogeneity of variance. Individual walleye tag numbers were included as a random effect to account for non-independence of individuals through time while month, movement group (resident and migrant), year, and the interaction between month and movement group were all included as fixed effects. Model comparisons conducted using log-likelihood ratios revealed that the interaction term between month and group always explained more variation than additive models ($p = <0.001$); as such, all models were interpreted at the level of the interaction. A Tukeys post-hoc analysis was also completed to determine significant differences across months and group means of estimated by the GLMM.

Results

Identification of migrant and resident walleye

A total of 31 migrants (30 female) and 18 residents (15 female) were identified and included in the analysis (Table 1).

Fig. 2. Map of 95% seasonal home range mean centroid locations derived from permissible home range estimation (PHRE) model. Orange circle indicates migrant walleye (*Sander vitreus*) location while the dark blue triangle indicates resident walleye location during each month in 2018. See Supplementary Material for home range (95%) centroid locations for 2017 (Fig. S2) and 2019 (Fig. S3) and core range (50%) 2017 (Fig. S4), 2018 (Fig. S5), and 2019 (Fig. S6). Shapefile data courtesy of Government of Manitoba (2025), projection in NAD 1983 (National Geodetic Survey 1986). See Supplementary Material Table S1 for number of individual fish included in monthly PHRE model estimates.

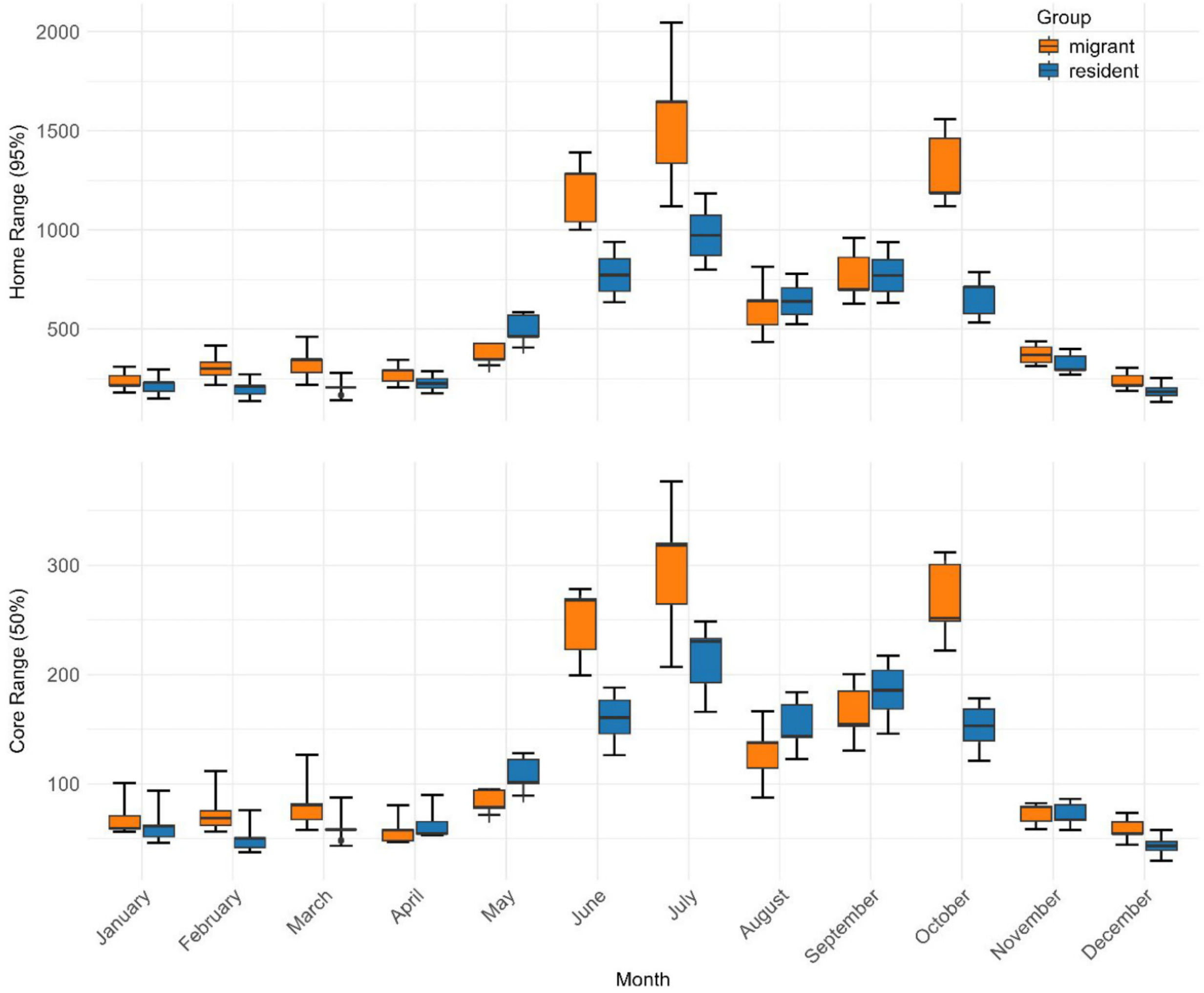


Residents remained within the south basin (between 50.5° and 51° of latitude) for the duration of the 2-year study while migrants recorded both southern (~50.5° latitude) and northern (~52° latitude) detections within a 1-year timeframe which was also repeated in the second year of the study. Two individuals were categorized as "others" and demonstrated varied movement patterns over the 2-year study (i.e., migrant 1-year, resident the next), and were dropped from further analysis.

Latitudinal centroid locations of range estimates

Resident walleye latitudinal home range centroids were generally stable through the year, always positioned within the south basin between 50.5° and 51° of latitude (Fig. 2; also see Supplementary Material Figs. S2 and S3). By contrast, migrant latitudinal home range centroids demonstrated much greater variation, with a major, sustained and significantly more northward distribution from July (~51.3° latitude) to

Fig. 3. Mean 95% home range (top panel) and 50% core range (bottom panel) estimates of migrant and resident walleye (*Sander vitreus*) in Lake Winnipeg predicted from generalized mixed effects models (GLMMs). Plotted values are back-transformed (expressed as km^2). Error bars indicate upper and lower 95% confidence intervals. See Tables 2 and 3 for model output results.



October (~51.7° latitude), extending past the Doghead Narrows in August (~51.56° latitude) and September of 2018 (~51.9° latitude; Fig. 2) and in August (~51.6° latitude) and September (~52° latitude) of 2017 (see Supplementary Materials Fig. S2). The southernmost extent of the distribution for both migrants and residents occurred during April and May (coinciding with spawning aggregations). Latitudinal home range centroids were most similar between migrants and residents during November to January (~50.75) and April to May (~50.6; Fig. 2). Latitudinal core ranges indicated essentially the same trends documented in the home range locations (Supplementary Materials Figs. S4 and S5).

Home range

The interaction between group (migrant and resident) and certain months was significant in models for both 95% and 50% ranges. In both models, migrant walleye demonstrated similar home ranges across the winter months of December (estimate = 229.5 km^2, 95% CI: 179.7–293.2 km^2) to February (estimate = 353.7 km^2, 95% CI: 252.5–495.5 km^2) and spring months of March (estimate = 368.4 km^2, 95% CI: 250.2–542.4 km^2) to May (estimate = 369.3 km^2, 95% CI: 321.1–424.9 km^2; Fig. 3 and Table 2). Home range increased significantly for migrants during the summer months of June (estimate = 1107.9 km^2, 95% CI: 939.2–1306.8 km^2) and July (estimate = 1420.6 km^2, 95% CI: 1044.1–1932.9 km^2), as well as during the fall in October (estimate = 1262.1 km^2, 95% CI: 1070.1–1487.5 km^2; Fig. 3 and Table 2). Similar to migrants, resident walleye demonstrated similar home range use during winter months of December (estimate = 147.9 km^2, 95% CI: 125.4–243.8 km^2) to February (estimate = 225.6 km^2, 95% CI: 158.7–320.6 km^2) and spring months of March (estimate = 219.1 km^2, 95% CI: 154.6–310.2 km^2) to May (estimate = 492.5 km^2, 95% CI: 412.6–587.8 km^2; Fig. 3 and Table 2). Resident home range also increased significantly during the summer months of June (estimate = 736.2 km^2, 95% CI: 604.5–896.7 km^2) to August (estimate = 609.8 km^2, 95% CI = 500.7–742.7 km^2) and from September (estimate = 734.2 km^2, 95% CI: 602.9–894.2 km^2) to October (estimate = 615.8 km^2, 95% CI: 507.0–747.9 km^2; Fig. 3 and

Table 2. 95% Home range model output results from the generalized mixed effects models (GLMMs; also see Fig. 3).

Month	Movement group	SE	Estimate	Lower CI	Upper CI	Group
January	Migrant	0.14	282.7	212.1	376.8	abcd
January	Resident	0.17	246	173.1	349.5	abcd
February	Migrant	0.17	353.7	252.5	495.5	abcde
February	Resident	0.17	225.6	158.7	320.6	ab
March	Migrant	0.19	368.4	250.2	542.4	abcdef
March	Resident	0.17	219.1	154.6	310.2	ab
April	Migrant	0.13	311.2	237.4	407.8	abcd
April	Resident	0.12	265.4	206.1	341.7	abc
May	Migrant	0.07	369.3	321.1	424.9	bcd
May	Resident	0.09	492.5	412.6	587.8	def
June	Migrant	0.08	1107.9	939.2	1306.8	hi
June	Resident	0.10	736.2	604.5	896.7	fgh
July	Migrant	0.15	1420.6	1044.1	1932.9	hi
July	Resident	0.10	926.6	760.9	1128.5	ghi
August	Migrant	0.16	554.6	403	763.3	cdefg
August	Resident	0.10	609.8	500.7	742.7	efg
September	Migrant	0.10	743.2	600.4	920.1	efgh
September	Resident	0.10	734.2	602.9	894.2	efgh
October	Migrant	0.08	1262.1	1070.7	1487.5	i
October	Resident	0.09	615.8	507	747.9	efg
November	Migrant	0.08	352.8	298.7	416.5	bcd
November	Resident	0.10	314.1	257.1	383.6	abcd
December	Migrant	0.12	229.5	179.7	293.2	ab
December	Resident	0.16	174.9	125.4	243.8	a

Note: For each combination of Month and Movement group estimate, the standard error (SE), lower and upper confidence intervals (CI), and letter group are provided. The estimate and confidence intervals are derived from back-transformed values. Combinations that do not share the same letter groups are interpreted as significantly different based on α of <0.05.

Table 2). Late fall (November) resident home ranges overlapped significantly with migrants as well as during the winter (December, January, and February) and spring (March, April, and May; Fig. 3 and Table 2). Migrant and residents did share overlap as well between the summer months of June through to September (Fig. 3 and Table 2) and only differed significantly across the month of October. There was a significant negative effect of year ($p < 0.001$) indicating that home ranges decreased over the study period for both groups (Supplemental Materials Table S2), which reflects that summer-fall period is captured in 2017 and 2018 when home range estimates for both groups are highest, but 2019 date end prior to summer. See Supplemental Materials Figs. S6 and S7 for an example of the 95% home range PHRE output map for a migrant and resident individual.

Core range

Estimates of 50% core range use had similar patterns as home range estimates. Migrant core range was generally elevated June (estimate = 235.4 km^2, 95% CI: 174.5–317.6 km^2), July (estimate = 279.1 km2, 95% CI: 235.5–330.7 km2), and October (estimate = 263.1 km^2, 95% CI: 222.1–311.6 km^2), and lower during winter and spring (November to May; Fig. 3 and Table 3). Resident core range showed a more similar pattern as home range with significantly lower space use from November (estimate = 70.5 km^2, 95% CI: 58.1–85.5 km^2) to April (estimate = 69.2 km^2, 95% CI: 48.5–98.6 km^2) and was significantly elevated during June (estimate: 154.1 km^2, 95% CI: 125.8–188.5 km^2) to October (estimate = 147.1 km^2, 95% CI: 120.1–179.9 km^2; Fig. 3 and Table 3). Core range overlapped significantly between residents and migrants except during October when migrant core range was significantly larger (Fig. 3 and Table 3). There was a significant negative effect of year ($p < 0.001$) indicating that home ranges decreased over the study period (Supplemental Materials Table S3), again likely reflecting reduced core range estimates during summer and fall which were absent in 2019.

Repeat spawning

Female walleye tagged during Spring 2017 within the Red River were assessed for repeat spawning (20 migrants and 15 residents, see Table 1). As we considered only individuals tagged in Red River, 13 of 20 migrant walleye (65%) re-entered the Red River in 2018. By contrast, 6 of 15 resident walleye (40%) re-entered the Red River in spring 2018. An exact binomial test indicated that difference in repeat spawning ratios of residents compared to migrants was marginal ($p = 0.056$).

Table 3. 50% Core range model output results from the generalized mixed effects models (GLMMs; also see Fig. 3).

Month	Movement group	SE	Estimate	Lower CI	Upper CI	Group
January	Migrant	0.07	75.3	65.1	87.1	abcd
January	Resident	0.09	65.8	54.7	79.1	abc
February	Migrant	0.13	79.4	60.4	104.4	abcdef
February	Resident	0.13	53.3	41.1	69.4	a
March	Migrant	0.16	85.7	62.1	118.4	abcdefg
March	Resident	0.10	61.6	50.1	75.6	ab
April	Migrant	0.14	61.2	45.8	81.8	abc
April	Resident	0.18	69.2	48.5	98.5	abcde
May	Migrant	0.10	82.4	66.5	102.2	abcd
May	Resident	0.10	106.9	87.6	130.4	cdefg
June	Migrant	0.15	235.4	174.5	317.6	hi
June	Resident	0.10	154.1	125.8	188.5	gh
July	Migrant	0.08	279.1	235.5	330.7	i
July	Resident	0.10	203.2	166.5	247.9	hi
August	Migrant	0.17	120.4	85.7	169.1	bcdefgh
August	Resident	0.18	150.3	105.5	214.1	defghi
September	Migrant	0.12	161.5	125.5	208.1	ghi
September	Resident	0.17	177.9	127.3	248.6	fghi
October	Migrant	0.08	263.1	222.1	311.6	i
October	Resident	0.10	147.1	120.1	179.9	efgh
November	Migrant	0.08	69.5	58.7	82.4	abc
November	Resident	0.09	70.5	58.1	85.5	abc
December	Migrant	0.19	56.9	38.5	84.1	abc
December	Resident	0.17	41.4	29.1	58.8	a

Note: For each combination of Month and Movement group estimate, the standard error (SE), lower and upper confidence intervals (CI), and letter groupings are provided. The estimate and confidence intervals are derived from back-transformed values. Combinations that do not share the same letter groups are interpreted as significantly different based on α of <0.05.

Discussion

Our study demonstrated clear patterns of partial migration in Lake Winnipeg walleye tagged in the south basin of Lake Winnipeg. During most winter months and the spawning season of this population (April to May; Stewart and Watkinson 2004), latitudinal centroids were most similar for both migrant and resident walleye. During this time, both groups were concentrated in the south basin, with the maximum southern extent for both populations occurring in May. After putative spawning, latitudinal centroid locations shifted northward for migrant walleye over several months (primarily during summer to fall) but remained within half a degree of latitude in the south basin for resident walleye over all time periods. Typically, migrant walleye had larger home and core ranges compared to those of the resident walleye (significantly so during October as migrants returned from the north basin) and total range overlapped between the groups during the winter and spring months. Increases in space use for both residents and increased from May to October, though were most apparent for migrants during June and July. While our study is the first to clearly document partial migration in Lake Winnipeg walleye, this pattern has been documented in Laurentian Great Lakes populations (Wang et al. 2007; Bowlby and Hoyle 2011; Peat et al. 2015; Hoyle et al. 2017; Raby et al. 2018; Hayden et al. 2019; McKee et al. 2022). Additionally, the incorporation of habitat features in our model (i.e., northing line, substrate, and depth) that likely influence walleye habitat selection in the current study may represent a more accurate assessment of overall space use for this species within Lake Winnipeg.

Seasonal changes in temperature conditions in Lake Winnipeg may have contributed in part to the divergent movement patterns of walleye. Lake Winnipeg covers 4° of latitude, resulting in dramatic temperature gradients along its south–north axis. Differences in summer surface temperatures between basins approach 3–4 °C but are less so in late summer when differences fall to around a one degree (ECCC and MARD 2020). Additionally, the duration of ice cover in the north basin typically exceeds that of the south basin by about 2 weeks (ECCC and MARD 2020). Preferential temperatures for walleye lie between 20 and 23 °C (Hokanson 1977; Barton and Barry 2011) and movement associated at least partially with optimal water temperatures and optimal thermal-optical habitat have been hypothesized in other systems (Wang et al. 2007; Hayden et al. 2014; Peat et al. 2015; Raby et al. 2018; McKee et al. 2022). Similarly, lower summer temperatures may lead to slower growth in walleye based on bioenergetics modelling (Kershner et al. 1999); south basin summer surface water temperatures ranged from approximately 18–24 °C between 1999 and 2016 (ECCC and MARD

2020), which periodically may exceed thermal optima. By contrast migrant females may experience optimal thermal temperatures for an extended period due to their migratory behaviours as they follow warmer water conditions north slowly across May, June, July, August, and September when their most northern locations were noted, then return to the south as the basins start to collectively cool in October.

Repeatable patterns of long-range movement are expected when affording migrants some fitness advantage over residency, presumably related to increased growth, fecundity, survival, or some combination of these factors (Roff 1988; Chapman et al. 2012) as has been proposed in other migrating walleye populations (Wang et al. 2007; Hoyle et al. 2017; McKee et al. 2022). Similarly, populations of lake whitefish (*Coregonus clupeaformis* (Mitchill, 1818)) with the greatest migration distances displayed the highest growth and consumption rates compared to less migratory populations (Rennie et al. 2012*a*). Though areal prey density and availability is reported to be more than 7-times higher in the south basin than in the north during the ice free period, so too are walleye densities, by similar or greater magnitude (Lumb et al. 2018, 2020). As such, summer per capita prey densities for walleye may actually be greater in the north basin than in the south basin providing reduced competition for migrants, this may also occur across other systems such as Lake Erie and Saginaw Bay, Lake Huron (Brenden et al. 2015; Hayden et al. 2019). Studies on fish prey densities across Lake Winnipeg have confirmed a near disappearance of rainbow smelt (*Osmerus mordax* (Mitchell, 1814)) across the north basin which first invaded in the early 1990s and were the dominant prey fish up until 2009 (Remnant 1991; Lumb et al. 2020), and were readily consumed by walleye captured across the north basin previously (Sheppard et al. 2015). As such, walleye movement in pursuit of this prey species cannot be attributed to the documented migration strategy given their virtual disappearance from the north basin. Cisco (*Coregonus artedi* Lesueur, 1818) have been captured more frequently in the south basin during more recent surveys; however, prior to the invasive of rainbow smelt, cisco were historically found in greater abundance in the north basin (Olynyk et al. 2017). Currently, little is known about the spatial ecology of cisco throughout Lake Winnipeg. It is expected that walleye moving into deeper, cooler areas during the summer or early fall into the narrows (max depth of ∼38 m) (Brunskill et al. 1980) or north basin have a greater opportunity to exploit cold-water fishes like cisco have been linked to greater asymptotic growth for female walleye across other lake systems (Kaufman et al. 2009; Noring et al. 2021) and may be an important forage prey species for walleye within Lake Winnipeg. Further work on walleye diets following the collapse of rainbow smelt in the north basin is warranted, particularly to determine differences in diet during the summer and fall between the basins and to determine if the main motivation of walleye migration is associated with prey availability as has been suggested elsewhere (Raby et al. 2018; Mckee et al. 2022).

Marginal differences in putative repeat spawning activity between resident (40%) and migrant (65%) walleye observed in the Red River may also reflect differences in resource acquisition between the two groups. Energy acquisition towards reproductive output in walleye likely occurs around August and September (when migrant walleye were at their most northern locations in the current study) and continues through the winter until the following spring spawn event (Henderson et al. 1996). Alternatively, it is possible that the reduced occurrence of resident walleye was due to the use of alternative spawning locations in the south basin with similar spawning success, though it is not immediately clear why residents should display variable spawning fidelity compared to migrants. Regardless, our study provides observations to support further research into walleye spawning fidelity and spawning success required to test these hypotheses, particular as they relate to behavioural strategies that optimize reproductive opportunities.

Differences in water clarity between basins may also potentially impede walleye foraging in the south basin during the summer feeding season, despite higher areal prey densities, as the south basin of Lake Winnipeg is more shallow, turbid, and subjected to more frequent algae blooms throughout the summer months compared to the relatively clearer and deeper north basin (Brunskill et al. 1980; ECCC and MARD 2020). Optimal water clarity expressed as Secchi depth for walleye is approximately 2 m (Lester et al. 2004) and more recent work has demonstrated turbidity in the form of algae likely further impairs walleye vision (Nieman et al. 2018; Nieman and Gray 2019). Comparatively, average annual Secchi depths measured from 1999 to 2016 varied between 0.8 and 1.4 m across the north basin compared to only 0.4–0.9 m in the south basin (ECCC and MARD 2020). Additionally, Lake Winnipeg experiences seasonal variation in turbidity, where the south basin experiences increased turbidity during the summer and fall (Secchi depth < 0.7 m), compared to that of the north basin (Secchi depth ∼1.5 m).

The northward movement in migratory walleye was also paired with generally larger monthly home and core ranges compared with resident walleye during migration over the open water season, but similar home and core ranges during the typical period of ice cover. Generally, both groups occupied more space after spawning (May) through the fall (October), then contracted significantly during winter months. Given the much higher prey densities in the south basin, smaller ranges among resident fish may be expected due a higher encounter rate with prey compared with migrants. Furthermore, receiver spacing was sparser in the north basin beyond the Doghead Narrows, resulting in lower migrant detection probabilities during August and September. This likely contributed to smaller range estimates for migrants during these months compared with residents which occupied a region of the lake with more dense receiver coverage.

Considering together (a) suboptimal turbidity, optical habitat, and warmer water temperatures in the south basin, (b) differences in both areal and per capita prey densities between basins, and (c) larger home and core ranges observed in migrant walleye during the summer months, these differences may reflect inert differences in foraging strategies between groups, independent of prey density. Other research has demonstrated both theoretical (Giacomini et al. 2013) and empirical evidence (e.g., Madon and Culver 1993; Rennie et al. 2012*b*) displaying the importance of foraging activity in driving patterns of prey consumption and life histories. While we did not have data on growth of tagged walleye from this study, migrant walleye have been shown in Black Bay, Lake Superior to demonstrate larger asymptotic size compared to resident fish (McKee et al. 2022), however contrary to this result, Bihun et al. (2024) found no difference in home range size between smaller male and larger female walleye tagged in Lake Erie. Larger home and core ranges for migrant walleye in our study may reflect a greater probability of prey encounter rate, offsetting any additional expended energy in migration, potentially leading to more rapid/efficient growth in migrants. Similarly, marginal differences in putative repeat spawning activity between migrant and resident may also reflect differences in resource acquisition between the two groups.

The use of the PHRE model allowed us to consider impassible habitat features (e.g., islands and shorelines) in assessing walleye movement. Other traditional home range estimators like kernel density estimation (Worton 1989) and local convex hull analysis (Getz and Wilmers 2004) do not estimate an animals space use around constraints set by defined areas (Tarjan and Tinker 2016) nor do they consider relevant habitat features (i.e., depth and substrate) when producing range estimates. Typically, these estimators are completed and then "clipped" to a shapefile of the study lake, ultimately underestimating estimated ranges by failing to explicitly model movement around such features. The assessment of movement and overall space use of aquatic species in waterbodies that have complex shorelines, islands, and other impassable features requires methods such as the PHRE approach which provide a more realistic estimate of habitat and space use. However, it is important to note that including habitat data based on a priori information can be challenging for a number of reasons including data availability limitations, and selecting layers that may truly be informative to habitat use. The inclusion of habitat layers based on a priori selection could therefore risk both type I and type II error where estimates exclude space that is used and include space that is unused (see Tarjan and Tinker 2016 for further details). We were unable to incorporate variation in detection efficiency into the model, as such data were not available for the duration of walleye movement data included in the current analysis. However, such data could be included in future work where detection efficiency is measured for the duration of the study as model covariates. Generally, detection efficiency varied primarily by season (Supplemental Materials Fig. S9). Detection efficiencies on receiver arrays can vary with numerous environmental conditions (Kessel et al. 2014; Kraus et al. 2018) and should be considered when interpreting results. For instance, though detection probabilities were variable, means were largely similar during open water conditions during 2016 and 2017. By contrast, winter detection probabilities during winter were greater than during summer; however, this was associated with a period where walleye ranges were generally constricted, suggesting a minor impact on our winter and early spring range estimates.

Our study also supports evidence presented elsewhere that the south basin provides a significant source of fish and genetic material to the north basin (Thorstensen et al. 2020; Turner et al. 2021). Due to sparse receiver coverage, our rate of disappearance in the north basin was relatively high (31% of all tagged fish), which may not necessarily represent mortality, but simply movement outside of the north basin acoustic array. Additionally, four fish overwintered and spent the following spring-summer in the north basin, which gives some indication that straying, partial emigration or some combination of both is present in the system. Recent genomic data supports a subtle but consistent south to north direction in the transmission of genetic material (Backhouse-James and Docker 2012; Thorstensen et al. 2020). Further expansion of the receiver array into the north basin may help resolve existing uncertainty regarding between-basin emigration.

Facultative migration was found in only six fish across this study, whereas the majority ($n = 45$) displayed repeatable patterns of behaviour; the four migrants mentioned previously and two additional individuals who survived the duration of the study but displayed variability in their movement behaviour, previously categorized as "others" appeared to alternate movement strategies (resident one year and migrant the next). Similarly low rates of facultative migratory behaviour in walleye have been reported elsewhere in the Great Lakes (McKee et al. 2022). Facultative migration may develop across a population for a number of different reasons and may be a learned behaviour, fixed through an individuals experiences during early conditions, or alternate depending on environmental cues (Chapman et al. 2011). Further research would be required to better determine factors contributing to varying patterns of movement described here.

Previous results assessing inter-basin movement of tagged fish demonstrate that south to north movements of walleye are generally low, but on average double those in a north to south direction (Turner et al. 2021). These findings as well as those reported in the current study suggest that the north basin walleye population is likely a mixed stock, which includes a significant proportion of south basin spawning individuals for a large proportion of the ice-free period. Migrating individuals may be more likely to encounter passive commercial fishing gear in the south basin and the narrows, potentially making this group more susceptible to harvest than residents. Determining differences related to spatial and temporal movements of the south basin spawning stock walleye (as well as other spawning groups not addressed here) could contribute to addressing their susceptibility to mortality through fishing pressure and adjusting management related to the timing of commercial open seasons or mesh net size limits. Our findings suggest that a more integrated cross-basin approach to walleye management versus that of a one-stock fits all approach may be required to sustainably manage walleye across the lake. Expanding studies to include north basin spawning individuals and their subsequent movement behaviour are needed to help complement the patterns reported here for south basin spawning stocks.

In conclusion, our study provides evidence of distinct movement patterns for walleye tagged across the south basin of Lake Winnipeg. Heterogeneity between the south and north basins in turbidity, temperature, and prey densities likely play the greatest role in driving these different patterns, potentially affording energetic benefits to migrants (i.e., marginally higher rates of repeat spawning compared to residents). These insights have the potential to lead to more informed approaches to walleye management on Lake Winnipeg and contribute to a growing body of literature that demonstrates alternative migration strategies in this species, particularly in large lake ecosystems. Given the collapse of rainbow smelt in the north basin and commercial and recreational fisheries that operate largely in the absence of current fishery-independent surveys suggests significant threats to the sustainability of walleye in this ecosystem.

Acknowledgements

The authors would like to thank Fisheries and Oceans Canada staff, specifically Doug Leroux, Colin Kovachik, Sarah Glowa, Camille Macnaughton, Henry Hansen as well as Jennifer Jeffery, Matt Thorstensen, and Ken Jefferies from the University of Manitoba for assistance in the field. Thanks to Brian Shuter and Constance O'Connor for their guidance and assistance throughout this work. Funding for this work was generously provided by the Manitoba Fisheries Enhancement Fund to GK and MDR (grant FES 18-034), and to EE and DW (grant FES 17-040), by Fisheries and Oceans Canada to EE and DW, the Lake Winnipeg Research Consortium, the Canada Research Chairs program, the Canadian Foundation for Innovation, and an NSERC discovery grant to MDR. We thank the careful and thoughtful suggestions from several anonymous reviewers who helped improve the published version of the manuscript.

Article information

History dates

Received: 5 December 2024
Accepted: 27 June 2025
Version of record online: 5 November 2025

Notes

This paper is part of a collection in honour of Prof. Louis Bernatchez, co-founder of the Ressources Aquatiques Québec network.

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Data availability

Data generated or analyzed during this study are available from the corresponding author upon reasonable request.

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Competing interests

The authors declare there are no competing interests.

Funding information

Funding for this work was generously provided by the Manitoba Fisheries Enhancement Fund to MDR and GK (FES 18-034), EE and DW (grant number FES 17-040), Fisheries and Oceans Canada to EE and DW, the Lake Winnipeg Research Consortium, the Canada Research Chairs program, the Canadian Foundation for Innovation, and an NSERC discovery grant to MDR.

Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjz-2024-0184.

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