






Divergent migration within lake sturgeon (*Acipenser fulvescens*) populations: Multiple distinct patterns exist across an unrestricted migration corridor

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Abstract

1. Population structure, distribution, abundance and dispersal arguably underpin the entire field of animal ecology, with consequences for regional species persistence, and provision of ecosystem services. Divergent migration behaviours among individuals or among populations are an important aspect of the ecology of highly mobile animals, allowing populations to exploit spatially or temporally distributed food and space resources.
2. This study investigated the spatial ecology of lake sturgeon (*Acipenser fulvescens*) within the barrier free Huron-Erie Corridor (HEC), which connects Lake Huron and Lake Erie of the North American Laurentian Great Lakes.
3. Over 6 years (2011–2016), movements of 268 lake sturgeon in the HEC were continuously monitored across the Great Lakes using acoustic telemetry (10 years battery life acoustic transmitters). Five distinct migration behaviours were identified with hierarchical cluster analysis, based on the phenology and duration of river and lake use.
4. Lake sturgeon in the HEC were found to contain a high level of intraspecific divergent migration, including partial migration with the existence of residents. Specific behaviours included year-round river residency and multiple lake-migrant behaviours that involved movements between lakes and rivers. Over 85% of individuals were assigned to migration behaviours as movements were consistently repeated over the study, which suggested migration behaviours were consistent and persistent in lake sturgeon. Differential use of specific rivers or lakes by acoustic-tagged lake sturgeon further subdivided individuals into 14 “contingents” (spatiotemporally segregated subgroups).

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5. Contingents associated with one river (Detroit or St. Clair) were rarely detected in the other river, which confirmed that lake sturgeon in the Detroit and St. Clair represent two semi-independent populations that could require separate management consideration for their conservation. The distribution of migration behaviours did not vary between populations, sexes, body size or among release locations, which indicated that intrapopulation variability in migratory behaviour is a general feature of the spatial ecology of lake sturgeon in unfragmented landscapes.

KEYWORDS

acoustic telemetry, behaviour, GLATOS, metapopulation, migration variability, movement, partial migration

1 | INTRODUCTION

Divergent migration, defined here as the coexistence of distinct migration behaviours within a population or among sympatric populations, is an important aspect of the ecology of mobile animals (Bowler & Benton, 2005; Dingle, 2014), and has been documented across several taxa (e.g. Cagnacci et al., 2011; Doherty et al., 2017; Herman et al., 2005; Sanz-Aguilar, Béchet, Germain, Johnson, & Pradel, 2012). Divergent migration can increase the ability of individuals or populations to exploit spatially or temporally distributed food resources, and maximize spatiotemporal overlap with favourable growth conditions (Brönmark et al., 2013; Chapman et al., 2012; Jonsson & Jonsson, 1993; Smith & Skúlason, 1996).

Divergent migration is a common form of life-history diversity in fish (Secor, 1999). The most frequently observed form of divergent migration in fish is partial migration, in which individuals of a population are either residents or migrants (reviewed by Chapman et al., 2012). Divergent migration consisting of more than two distinct behaviours also has been observed due to recent advancements in fish tracking technologies (e.g. acoustic telemetry) that enable continuous observation of multiple individuals for long time periods (years; Altenritter, Zydlewski, Kinnison, Zydlewski, & Wippelhauser, 2017; Dionne, Zydlewski, Kinnison, Zydlewski, & Wippelhauser, 2013; Hayden et al., 2014). Cohorts showing the same primary migration behaviour also may differ in their use of specific habitats, which results in the formation of migration subgroups or “contingents” (Secor, 1999). Contingent behaviour has been observed in striped bass (*Morone saxatilis*) and summer flounder (*Paralichthys lethostigma*), and likely contributes to species persistence in environments where disturbance, exploitation and resource depletion cause local extinctions (Gahagan, Fox, & Secor, 2015; Kerr & Secor, 2012; Secor, 1999, 2015). The movements of contingents also may provide clues to the geographical organization of populations that potentially interact as metapopulations.

Widespread fragmentation of the world's large rivers has made it difficult to determine the nature and basis of divergent migration in anadromous and potamodromous fish species. Fish movements in most large rivers across the globe are restricted by man-made barriers

(Dynesius & Nilsson, 1994; Nilsson, Reidy, Dynesius, & Revenga, 2005). Although many native species manage to complete their life cycles under such circumstances, fish populations inhabiting fragmented landscapes may no longer express the full range of migration behaviours characteristic of populations in more pristine environments. Populations living in fragmented landscapes may not represent useful models for understanding the natural level of habitat and population connectivity needed to conserve or restore native species.

The extent of migration divergence shown by lake sturgeon (*Acipenser fulvescens*) in ecosystems free of man-made barriers to fish movement has not been described. The common perception of lake sturgeon breeding ecology is that spawning-ready individuals migrate into rivers to spawn in the spring and summer, but reside in lakes when not reproductively active (Bemis & Kynard, 1997; Pollock, Carr, Kreitals, & Phillips, 2014; Rusak & Mosindy, 1997). Alternative behaviours, however, have been suggested and observed. For example, some lake sturgeon populations may contain a river-resident form that completes its life cycle entirely in the spawning river (Boase, Diana, Thomas, & Chiotti, 2011; Thomas & Haas, 2002). Lake sturgeon populations in the Lake of the Woods and the Rainy River system, located on the border between Minnesota (US) and Ontario (Canada), included a second migratory form that summered in the lake and overwintered in the river (Rusak & Mosindy, 1997).

Tracking individual movements at the spatiotemporal scale and resolution required to determine the extent of divergent migration is complicated by the unique life history of lake sturgeon. Lake sturgeon are long-lived (up to a maximum of 154 years) and spawn only intermittently, with females reproducing once every 4–9 years and males every 1–3 years (Peterson, Vecsei, & Jennings, 2007); therefore, seasonal or short-term observation is insufficient to document the diversity of migratory behaviours shown by lake sturgeon. Observation periods in previous studies of lake sturgeon spatial ecology (generally ≤ 2 years) have been much shorter than the average lake sturgeon life span of 25–30 years or even long enough to document multiple spawning periods (Probst & Cooper, 1955; Thomas & Haas, 2002). Describing divergent migration in lake sturgeon occupying ecosystems lacking barriers to fish movement may require the ability to track movements of individuals at spatial scales of up to 10^4 km² given that

some lake sturgeon have been observed to migrate hundreds of km between feeding grounds and spawning sites in rivers (Auer, 1996).

The lake sturgeon populations inhabiting the St. Clair River, Lake St. Clair and Detroit River, which together form the Huron-Erie Corridor (HEC), may provide an important case study in conservation as these free-ranging fish are more likely than other populations to express the range of phenotypic diversity and population connectivity characteristic of pristine populations (Figure 1). In contrast to most spawning rivers used by lake sturgeon, the Detroit and St. Clair rivers are among few large rivers in which sturgeon use of the mainstem rivers is completely unrestricted by dams or other man-made barriers. Lack of barriers provides lake sturgeon with unimpeded access to over 86,000 km² of habitat that includes deep, oligotrophic lakes (e.g. Lake Huron); shallow, fluvial lake environments (e.g. Lake St. Clair); and a variety of river habitats (e.g. the mainstem Detroit River, the St. Clair

River delta; Hondorp, Roseman, & Manny, 2014). The diversity of available habitats present in this river-lake ecosystem could promote divergent migration in lake sturgeon populations if, as was observed in the Rainy River-Lake of the Woods system, specific individuals or groups of individuals tend to use different habitats (spatial segregation), or use the same habitats in a different sequence (temporal segregation). Lake Michigan also could be included as part of the system as it is connected to Lake Huron via the 8 km wide, 30 m deep Straits of Mackinac. The lake sturgeon that spawn in the Detroit and St. Clair rivers are believed to be among the largest remaining self-sustaining populations in the Great Lakes, and number c. 45,000 fish for the St. Clair system alone (Thomas & Haas, 2002). The number, geographic organization and connectedness of lake sturgeon populations in the HEC have not been described. Although two or more populations are suspected based on identified spawning sites in the Detroit and St.

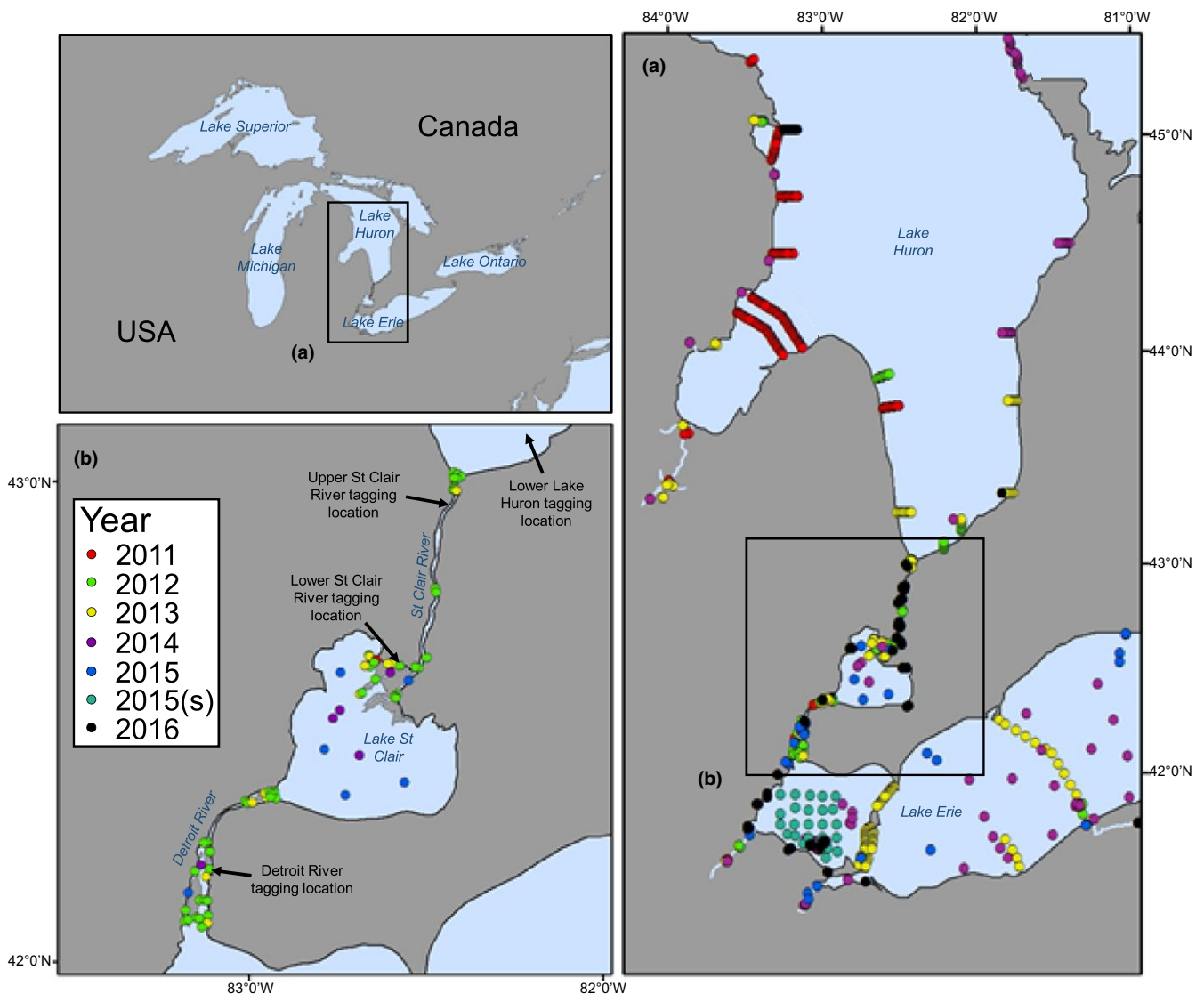


FIGURE 1 Location of study site relative to the Laurentian Great Lakes region; (a) Great Lakes Acoustic Telemetry Observation System (GLATOS) network as established over the period from 2011 to 2012; (b) Huron Erie Corridor (HEC) core network, established over the same time period. Monitors coded as 2015(s) were only deployed during the summer months of that year. Tagging locations of lake sturgeon are indicated by black arrows

Clair rivers, genetic differentiation among individuals collected from different spawning sites was not detected with analyses of neutral microsatellite markers (Marranca, Welsh, & Roseman, 2015; Welsh, Hill, Quinlan, Robinson, & May, 2008; Welsh et al., 2010a).

The goals of this study were to determine whether lake sturgeon, in an environment free of barriers to fish movement, show divergent migration and contingent behaviour, and how migration behaviours help define population structure within the HEC. Study objectives were to: (1) describe population-scale movement patterns of lake sturgeon that spawn in the Detroit-St. Clair rivers, and possible contingents within behaviour groups; (2) determine if particular movement behaviours were associated with size, sex or tagging location; and (3) determine if the distribution of migration behaviours among groups of individuals using specific spawning rivers and sites suggests that lake sturgeon in the Detroit-St. Clair river system are comprised of two or more populations. Our approach was to use acoustic telemetry to provide continuous multi-year observations of a large sample (>250 individuals) of adult-sized lake sturgeon.

2 | MATERIALS AND METHODS

2.1 | Study site

This study focused on lake sturgeon using the Lake Huron-to-Lake Erie Corridor (HEC), which included the St. Clair River, Lake St. Clair and the Detroit River (Figure 1). The HEC spans 135 km from Lake Huron to Lake Erie and discharge from Lake Huron into the St. Clair River averages 5,150 m³/s (Holtschlag & Koschik, 2002). No barriers exist upstream of the St. Clair River between Lake Huron and Michigan; however, a set of shipping locks exist 450 km away at the head of the St. Marys River, which interrupts the pathway to Lake Superior. The outlet of Lake Erie is the Niagara River that contains Niagara Falls about mid-way between Lake Erie and Lake Ontario. The mainstem rivers in the HEC are free of any man-made barriers to fish movement, providing fish with over 86,500 km² of continuous lake and river habitat. Though the HEC formed the main area of focus for this study, our study also was able to record lake sturgeon movements across large areas of Lake Erie and Lake Huron (Figure 1a).

2.2 | Fish capture and tagging

Lake sturgeon were captured from four distinct locations around the HEC to ensure that individuals from suspected local populations were included in the study. Three of these locations were associated with known spawning sites in the Detroit River, the lower St. Clair River and the upper St. Clair River (Figure 1b). Lake sturgeon from these sites were sampled during May and June during the spawning season each year from 2011 to 2014, except during 2011 when only the lower St. Clair River was sampled. Sampling was conducted as part of annual population surveys conducted by the Michigan Department of Natural Resources (MDNR; lower St. Clair River) and by the U.S. Fish and Wildlife Service (USFWS; upper St. Clair River and Detroit River). Individuals were captured using baited set lines

as described by Thomas and Haas (1999). Sturgeon were dehooked and then placed in a holding tank on the vessel prior to tagging. Lake sturgeon were also captured in lower Lake Huron (Figure 1) between June and July, in the years 2012, 2014 and 2015, using trap nets with soak times ranging from 2 to 5 days. Captured individuals were removed from the net and placed in onshore raceways fed by lake water until processed (usually the day after capture). Individuals collected in trap nets were released into the upper St. Clair River after processing.

Lake sturgeon were tagged by removing them from the holding tank and placing them ventral side up in a soft mesh cradle. Inverted in the cradle, the specimens showed the conditions associated with tonic immobility, which facilitated surgical tag implantation (Kessel & Hussey, 2015). During processing, gills were ventilated by keeping the head submerged. Fork [F_L] and total [T_L] lengths were measured to the nearest mm and total weight [W_T] measured to the nearest 0.01 kg. A small mid-ventral incision (c. 30 mm) was made anterior to the pelvic fins and a 69 KHz Vemco® V16-6L transmitter (tag) inserted into the body cavity. Acoustic tags were 16 mm in diameter, 95 mm length, weighed 34 g in air, transmitted a unique ID code every 60–180 sec, and had a 10-year battery life. Tag to body weight ratio was <0.35% for all tagged fish ($M = 0.17 \pm 0.003$ SE). The incision was closed with three independent coated vicryl sutures (Ethicon PDS-II size 0 with OS-6 half-circle reverse cutting needle or MONO-DOX size 0 with NCP-1 half-circle reverse cutting needle) tied with a double surgeon's knot. Prior to surgery, all surgical equipment, including the transmitter, was sterilized in a 10% betadine solution and incision site swabbed with the same solution. When possible, maturity was assessed by gonad inspection during the tagging procedure, either visually through the incision, or with an ultrasound (Chiotti, Boase, Hondorp, & Briggs, 2016). North American sturgeon generally are difficult to sex unless captured in spawning-ready condition (Vecsei, Litvak, Noakes, Rien, & Hochleithner, 2003). Spawning-ready individuals have large, conspicuous gonads that are easily observed through the small incision that was made to insert the acoustic transmitter. Conversely, in vivo visual inspection of gonads and ultrasound were not effective tools for sex determination of individuals that were more than 12 months from their next spawning event. Thus, sex for reproductively inactive individuals was often listed as unknown.

Duration of each procedure was 2–4 min, after which fish were placed in a recovery tank and monitored for 10–20 min prior to release to ensure they showed no negative signs of stress associated with surgery. Changes in behaviour after surgery were not observed (Hondorp, Holbrook, & Krueger, 2015). The Federal, Provincial and State agencies that were responsible for the field portion of the project were not required by statute to establish formal institutional animal care and use committees. However, sampling and handling of lake sturgeon was conducted in accordance with guidelines for the care and use of fishes in research developed by the American Fisheries Society, the American Society of Fishery Research Biologists and the American Society of Ichthyologists and Herpetologists (Jenkins et al., 2014).

2.3 | Acoustic monitoring

Acoustic-tagged lake sturgeon were monitored throughout the HEC and broader Great Lakes region with a network of Vemco® VR2W 69 KHz acoustic receivers. Receivers were initially deployed within the HEC at the start in 2011, and the network expanded over the course of the study (Figure 1a). Collaboration with the Great Lakes Acoustic Telemetry Observation System (GLATOS; <http://glatos.glos.us>) increased the geographical area monitored for tagged lake sturgeon by providing access to detection data from an additional 1,155 receiver sites in Lake Erie and Lake Huron (Figure 1b). The GLATOS database was queried for our lake sturgeon tag ID codes (on 22 November 2016) and the resulting detection dataset formed the raw data for this study.

2.4 | Data analysis: Suspected false detection filtering

Detections were recorded from 281 of the 282 tagged Lake Sturgeon from 2011 to 2016. To identify and remove suspected false detections created by acoustic tag ID code collisions (Simpfendorfer et al., 2015), the GLATOS raw data export was filtered using the White-Mihoff Filtering Tool (White, Mihoff, Jones, Bajona, & Halfyard, 2014). Detections were considered potentially false and removed if they were isolated by 1 hr or more from the closest detection of the same ID anywhere on the acoustic network. This identified 63,949 potentially false detections (0.6%) out of a total of 10,627,572 raw detections. All potentially false detections were excluded from further analyses. The remaining detections were assessed for minimum swimming speeds between chronologically sequenced detections. Calculated swimming speeds were assessed for feasibility based on maximum sustained swimming speed and a maximum effective receiver detection range of 1,500 m. Detection range values were based on detection range test results from past studies in this system (Hayden et al., 2016). Feasible maximum swimming speed was calculated using the average size of the tagged sturgeon (147.3 cm) and the body lengths per second provided for similar sized fish in Peake, Beamish, McKinley, Scruton, and Katopodis (1997). This provided a maximum sustained swimming speed of 109.66 cm/s (Peake et al., 1997); thus, any transitions between receiver stations that exceeded this speed were removed. This filtered and removed an additional 5,330 suspected false detections. In total, 69,279 (0.7%) suspected false detections were identified and removed from the original dataset.

2.5 | Data analysis: Detection efficiency assessment

Classification of sturgeon movement behaviours required us to estimate the locations of tagged lake sturgeon on days when individuals were not detected (see *Data analysis: Estimated daily locations* section), therefore, it was necessary to assess the probability of detecting tagged animals moving past receiver groups at geographic bottlenecks within the network (DE_{mig} ; Kessel et al., 2014).

Assignment of estimated locations assumed that tagged individuals were not able to pass river entrance and exit receiver sections without detection (i.e. DE_{mig} 100%), due to multiple overlapping detection ranges and tag transmission rates of c. 2 min. To test this assumption, the individual detection histories were visually assessed for incidences of receiver network sections being passed without representation in the detection record. A total of 2,140 transitions from rivers to lakes were recorded, but not a single instance was observed in which an individual was not detected on the acoustic receiver group separating a river and a lake. As such, it was justifiable to assume 100% DE_{mig} for sturgeon moving between lakes and major rivers. This value was greater than estimated by Hondorp et al. (2015), an average DE_{mig} of 92.3% from three receiver sites in the lower St. Clair River. The disparity is most probably due to the necessity in this study to document movement between geographic regions rather than specific receiver sites.

2.6 | Data analysis: Estimated daily locations

Lake sturgeon tracked for less than 30 days ($n = 13$) were not considered for further analysis as their detection histories were too short to provide a meaningful contribution. This left individuals tracked for a minimum of 288 days, with the vast majority tracked in excess of 2 years ($M = 1,050$ days \pm 28 SE). For the remaining 268 lake sturgeon, continuous (i.e. daily) locational histories for each tagged individual were used to identify distinct migration behaviours. The HEC geography provided geographical bottlenecks to movement at the inlets and outlets to the lakes that were well monitored by extensive receiver coverage, established to effectively capture transitions between lakes and rivers predicted to occur in association with spawning migrations (Figure 1b). Receiver coverage at each bottleneck location allowed for ingress and egress of the rivers by lake sturgeon to be inferred from the detection records before and after any gaps within an individual's detection dataset. To classify different lake sturgeon movement behaviours, the study area was divided into two categories, river and lake, and five regions based on geography. The regional categories were (from north to south): Lake Huron, St. Clair River, Lake St. Clair, Detroit River and Lake Erie (Figure 1). For any day, an individual was not detected within the acoustic network, up to the date of their last detection in the database, the fish's location was assigned to one of the five regions, and thus river or lake, based on the profiles of the surrounding detections.

2.7 | Data analysis: Migration behaviour designation

Agglomerative hierarchical clustering (Kaufman & Rousseeuw, 2008) was used to identify potential migration behaviours and contingents within behaviours (objective 1). To aid grouping, detection histories were arranged along a continuum of similarity. Detection histories were comprised of a categorical state variable, z_{it} , representing the location (z) of the i th fish on the t th day of the study. For days when a fish was not detected at any location during that day, z_{it} was inferred

based on locations of the previous and next detections. Clustering was performed on a matrix of dissimilarity coefficients, d_{ij} , using the “agnes” function in the R package “cluster” (Maechler, Rousseeuw, Struyf, Hubert, & Hornik, 2017). Dissimilarity coefficients were calculated in two steps. First, similarity, s_{ij} , was calculated between each pairwise combination of detection histories using only the set of K_{ij} days during which a location was determined (i.e. z_{it} was not null) for both the i th and j th fish, such that:

$$s_{ij} = \frac{\sum_{k=1}^{K_{ij}} \begin{cases} 1 & \text{if } z_{i,k} = z_{j,k} \\ 0 & \text{otherwise} \end{cases}}{K_{ij}}$$

thus, s_{ij} was the proportion of days, among those days where location was determined for both fish, during which location was the same for both fish. Similarities were then weighted by the number of days used in each comparison (K_{ij}) to give more weight to fish with more data, and subtracted from 1, such that:

$$d_{ij} = 1 - \left(s_{ij} K_{ij} \times \left(\frac{K}{T} \right)^{0.2} \right),$$

where T was the total number of days in the study. The exponent (0.2) results in a nonlinear weighting (penalty) such that the incremental change in penalty decreases as K increases. This specific value was chosen so that for a given level of overlap, longer histories would be weighted more than shorter histories, but, given the nature of the analysis, to sharply penalize comparisons of histories shorter than 1 year. The cluster analysis algorithm started by treating each of 268 fish as a unique group and then, in a stepwise fashion, sequentially combined the two most-like groups (smallest d_{ij}) until only a single group remained (Kaufman & Rousseeuw, 2008). When groups contained more than one fish, the unweighted pair-group average method cluster analysis (Kaufman & Rousseeuw, 2008) was used to calculate dissimilarity between groups. Analysis was performed using R v.3.3.1 (R Core Team, 2017).

2.8 | Data analysis: Predictors of migration behaviour membership

A Kruskal–Wallis test was used to determine (Hollander & Wolfe, 1973) if total length or weight differed among movement behaviour groups. A nonparametric test was used because the data were not normally distributed. Analysis was performed using the `kruskal.test` function in the “stats” package in R v.3.3.1 (R Core Team, 2017).

Year	Number					Mean L (cm)	Mean W (kg)
	Total	DR	LSC	USC	LH		
2011	8	0	8	0	0	145.0	20.5
2012	75	11	28	26	10	144.4	23.8
2013	77	25	24	28	0	147.8	22.8
2014	108	40	26	31	11	148.7	22.8
2015	14	0	0	0	14	150.5	24.0

2.9 | Data analysis: Spatial extent of populations

To further assess geographical organization and spatial structure of lake sturgeon populations present in the HEC (objective 3), Residence Index (RI) from the filtered detection records of all individuals was calculated as the number of days detected at each receiver station group (i.e. lower Detroit River) divided by the total number of days the fish was detected anywhere within the acoustic receiver network. Station group RI calculations were normalized for the amount of time each station group was deployed relative to the tracking period of each individual. The total number of individuals within the group that were detected at each station was then calculated. Mean RI values were plotted by tagging location as graduated symbols in ArcMap 10.2®. The distribution of mean RI values was clearly similar between individuals tagging in the St. Clair River (both locations) and Lake Huron, and distinct from those tagged in the Detroit River (see Figure S1). As such, individuals tagged in the lower St. Clair River, upper St. Clair River and Lake Huron were combined and the mean RI plotted on one map.

3 | RESULTS

3.1 | Tagging and detection summary

A total of 282 adult-sized lake sturgeon were tagged in the months of May–June between 2011 and 2014, ranging from 117.4 to 180.3 cm total length (L_T ; $M = 147.3 \pm 0.01$ SE), and from 9.8 to 63.0 kg total weight (W_T ; $M = 23.1 \pm 0.5$ SE; Table 1). Between 19 July 2011 and 24 August 2016, a total of 10,558,293 filtered lake sturgeon detections were recorded on the GLATOS acoustic receiver network. Receivers deployed in minor tributaries to the St. Clair River and Lake St. Clair (e.g. Black, Pine, Belle, Clinton, and Thames rivers) in 2014 did not detect any lake sturgeon, which suggests that lake sturgeon do not use these habitats (Figure 1), and no movement into Lake Michigan through the Straits of Mackinac or into the St. Marys River or downstream through the Welland Canal or over Niagara Falls past Lake Erie was observed.

3.2 | Migration behaviours and contingent structure

Acoustic-tagged lake sturgeon released into the HEC showed five distinct migration behaviours based on the duration and timing of river and lake use. Specific behaviours included year-round

TABLE 1 Lake sturgeon tagging summary by sampling year, total number tagged, number tagged in the Detroit River (DR), lower St. Clair River (LSC), upper St. Clair River (USC), and southern Lake Huron (LH), mean total length (L_T ; cm) and mean total weight (W_T ; kg)

river residency (Figure 2-1) and multiple lake-migrant behaviours (Figure 2-2 to 2-5) that involved movements between lakes and rivers. “River residents” (behaviour 1; Figure 2-1) were individuals that spent between 78% and 100% ($M = 95 \pm 1\% SE$) of the observation period in either the Detroit River or St. Clair River. The second, third and fourth behaviours consisted of individuals that migrated between rivers and lakes (“lake-migrants”), but periodicity and duration of use of these habitats varied among groups. “Seasonal river (summer)-lake (winter) migrants” (behaviour 2) were individuals detected annually in rivers during the spring and summer months (May to September), but moved into one of the lakes during the winter (Figure 2-2), whereas “lake-dominant migrants”

(behaviour 3) were individuals that spent the majority of their time in one of the lakes, but made brief trips into rivers every 1–4 years, usually during April–June, coincident with spawning season (Figure 2-3). “Seasonal lake (summer)-river (winter) migrants” (behaviour 4) showed the same movement behaviour as individuals in behaviour 2 except that lakes were used in the spring-summer and rivers were used as overwintering habitat (Figure 2-4). Lastly, “lake skipper migrants” (behaviour 5) were individuals that made seasonal transitions between a river and multiple lakes in a repeatable order (Figure 2-5). For example, eight individuals released in the Detroit River in the spring, moved into Lake Erie during the early summer, returned to the Detroit River in late summer, and

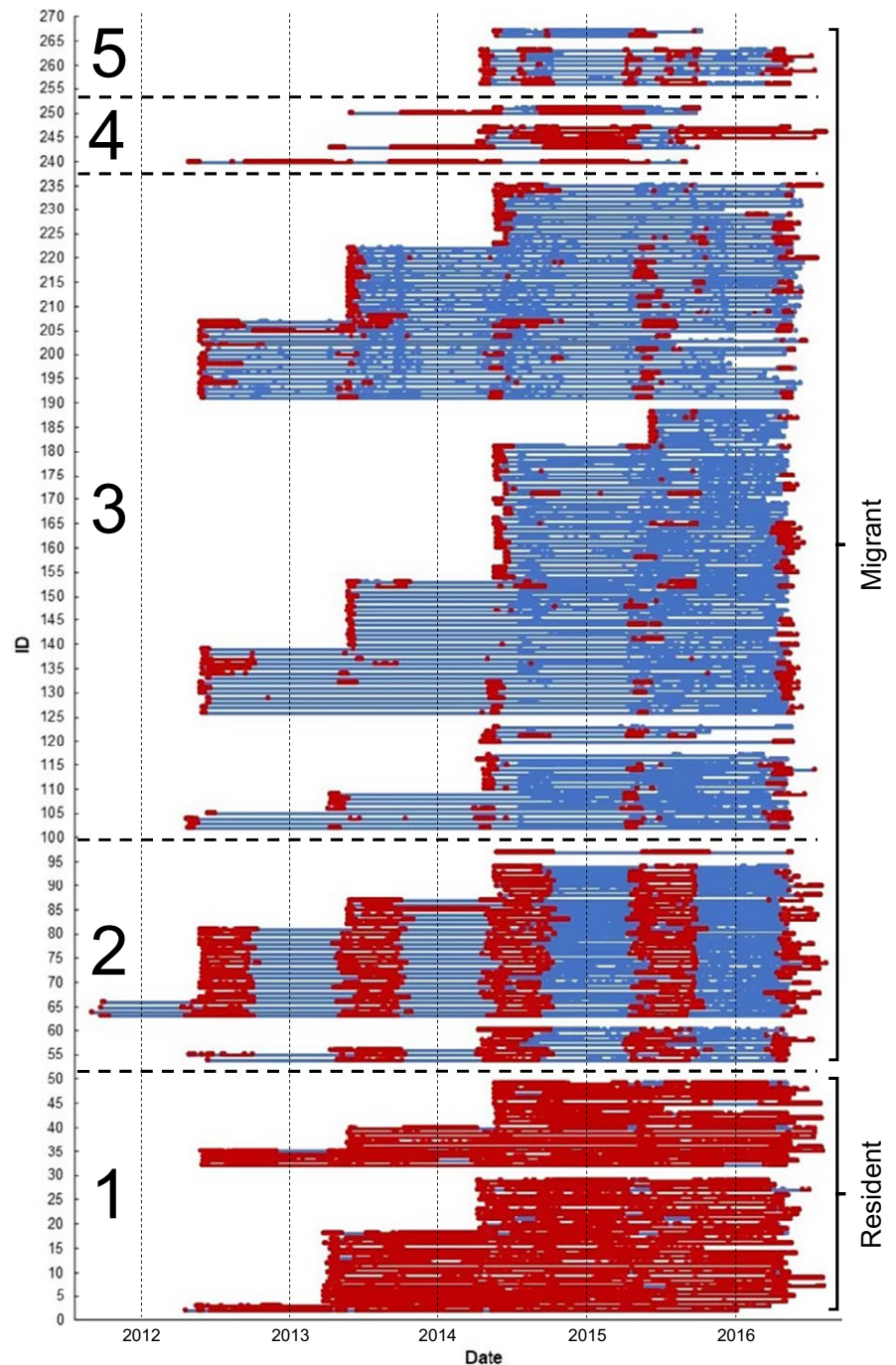


FIGURE 2 Abacus plot of all individuals grouped by cluster analysis. Behaviours (1–5) were determined by agglomerative hierarchical clustering at >0.40 time-weighted difference. Daily locations are represented by thick lines for detections and thin lines for predicted locations, with red representing river presence and blue representing lake presence. Grouped individuals are separated by dashed lines. Behaviours are: (1) River resident; (2) Seasonal river (summer) and lake (winter) use migrant; (3) Lake-dominant making short duration river trips migrant; (4) Seasonal lake (summer) and river (winter) use migrant; and (5) Lake skippers, using rivers to transition between lake, migrant

then quickly moved into Lake St. Clair, where they overwintered. These individuals then repeated this sequence of movements the following spring. For all individuals assigned to a migration behaviour group (>85%), movement patterns of group members were consistently repeated over the course of the study.

Lake sturgeon were unevenly distributed among the various movement behaviours. Migration behaviour 3, "lake-dominant migrants," had the largest number of individuals ($n = 128$) and behaviour 4, Seasonal lake (summer) and river (winter) use migrants, the smallest ($n = 8$; Table 2). The movement profiles of 36 individuals (13.4%) did not conform to any of the defined migration behaviours and were, therefore, left unassigned (plot of profiles available in Figures S2 and S3). It is possible for some individuals that switching between migration behaviours may have negated group designation, but further analysis would be needed to test this. Also, a larger sample size and longer study period than used here may have elucidated their movement patterns.

Among the five main movement behaviours identified above, 14 subgroups or "contingents" were identified using cluster analysis based on lake sturgeon use of specific rivers and lakes (Table 2; Figure 3). The river-resident behaviour (behaviour 1) was separated into two contingents (1a, 1b) by river (Detroit vs. St. Clair). Three contingents were identified within migration behaviour 2. Lake use within these contingents was restricted to Lake St. Clair except for

one individual that used Lake Huron. Individuals in contingent 2a spent the spring and summer in the Detroit River and overwintered in Lake St. Clair, whereas individuals in contingents 2b and 2c spent the spring and summer in the St. Clair River and overwintered in Lake St. Clair (2b) or Lake Huron (2c). The lake-dominant pattern was represented by four distinct contingents that inhabited a unique lake-river subsystem. Lake use among these contingents was primarily restricted to Lake St. Clair (contingents 3a, 3c) or Lake Huron (3d). Comparatively, few individuals ($n = 3$) were observed to migrate between the Detroit River and Lake Erie (3b). Contingents 3a and 3c were not statistically separable due to their common use of Lake St. Clair, but were considered distinct based on the primary river of use. One individual was removed (designated as unassigned; included in Figures S2 and S3) from each of the groups 3a and 3b based on highly contrasting proportions of their movement profiles, undetected by the analysis due to a small amount of temporal overlap. Behaviour 4 individuals were represented by three contingents, with most individuals (six of eight fish) overwintering in the Detroit River (4a, 4b). Only two individuals (contingent 4c) overwintered in the St. Clair River. The lake skipper group (behaviour 5) consisted of two contingents that both overwintered in Lake St. Clair, but spent the remainder of the year in the Detroit River-Lake Erie systems (5a) or the St. Clair River-Lake Huron system (5b).

TABLE 2 Lake sturgeon movement group composition. Sex composition is displayed as Male (M), Female (F) and Unidentified (U). Lengths (L) are given in cm and Weights (W) in kg. Grey bars represent main movement groups 1 to 5, with regional subgroups described below

Group	Total	M	F	U	Mean L	Min L	Max L	Mean W	Min W	Max W
1	46	18	10	18	146.9	122.2	176.6	21.5	9.8	51
1a	28	16	10	2	150.5	124	176.6	24.4	13.5	51
1b	18	2	0	16	141.5	122.2	160.5	17.1	9.8	27
2	40	8	6	26	147.5	120.7	179.3	23	11.4	45
2a	7	2	2	3	155	138.5	177.1	29.1	17	39
2b	32	6	4	22	146.4	120.7	179.3	22	11.4	45
2c	1	0	0	1	129.3	129.3	129.3	15	15	15
3	128	65	22	41	147.7	122.6	180.3	23.1	10	49.5
3a	16	11	4	16	146	123.4	180	23.3	15	49.5
3b	4	3	1	4	150.3	135.2	164.9	27.1	16	36.5
3c	63	26	13	63	149.4	122.6	180.3	23.6	10	48
3d	45	25	4	45	145.6	129.3	177.8	22	13	37
4	8	3	1	4	147.05	130.2	167.1	22.6	13.5	36
4a	1	1	0	0	130.2	130.2	130.2	13.5	13.5	13.5
4b	5	1	0	4	149.2	139.6	163.8	23.4	20	32
4c	2	1	1	0	150.2	133.3	167.1	25.3	14.5	36
5	10	8	2	0	146.5	137.2	170.1	23.12	15	40.5
5a	8	7	1	0	146	137.2	170.1	22.9	15	40.5
5b	2	1	1	0	148.4	138.6	158.2	24.1	17	31.2
NA	36	10	9	17	146.4	122	174	24.2	12.5	45.6
NAa	9	1	4	4	149.5	137.8	170.3	25	14	38.5
NAb	27	9	5	13	145.4	122	174	24	12.5	45.6

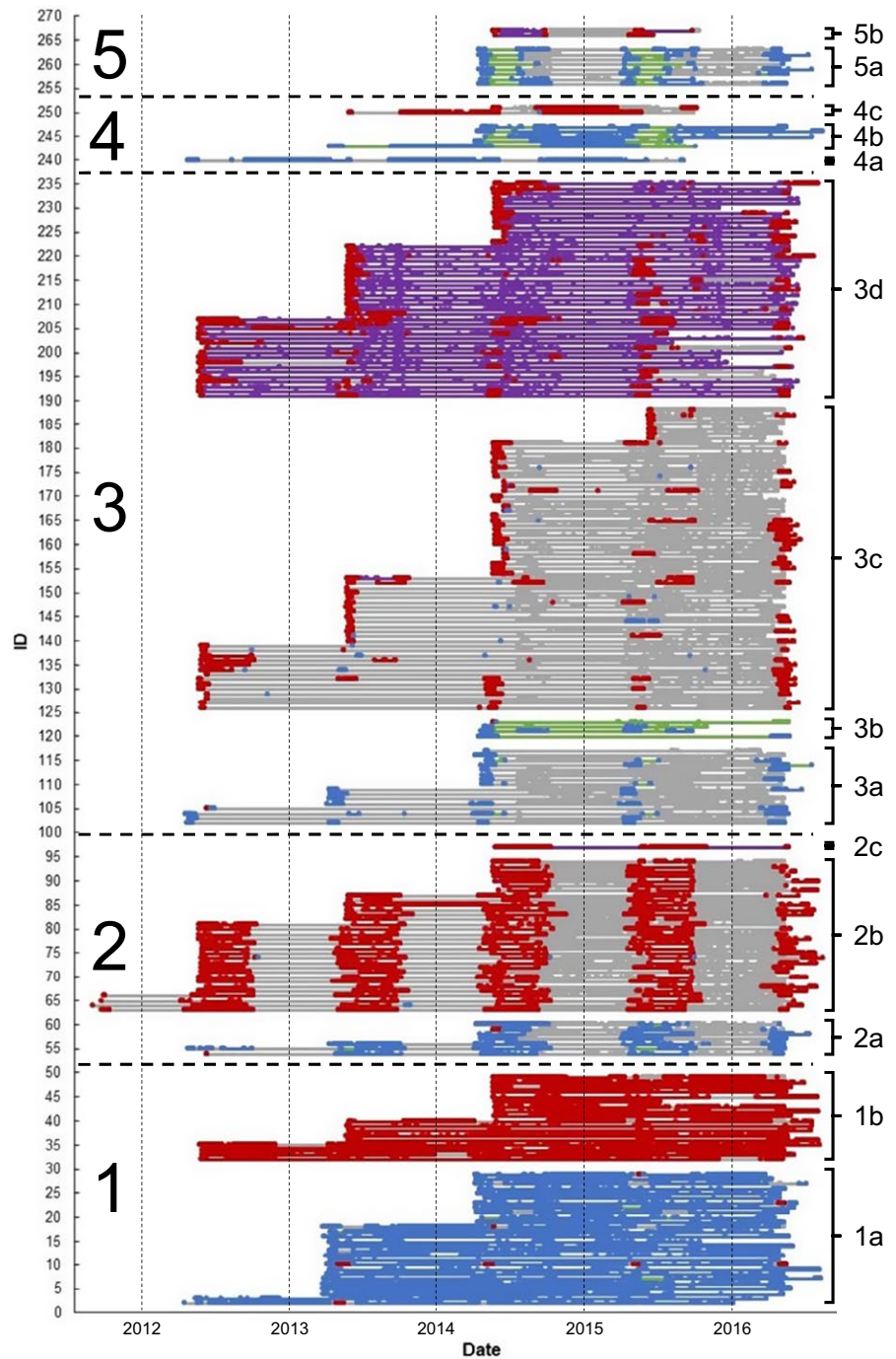


FIGURE 3 Abacus plot of all individuals grouped by cluster analysis. Behaviours (1–5) were determined by agglomerative hierarchical clustering at >0.40 time-weighted difference. Contingent subgroups are based on regional and temporal use. Daily locations are represented by thick lines for detections and thin lines for predicted locations, with colour representing Lake Erie (green), Detroit River (blue), Lake St. Clair (grey), St. Clair River (red) and Lake Huron (purple). Contingents are; 1a) Detroit River; 1b) St. Clair River and Lake St. Clair; 2a) Detroit River and Lake St. Clair; 2b) St. Clair River and Lake St. Clair; 2c) St. Clair River and Lake Huron; 3a) Detroit River and Lake St. Clair; 3b) Detroit River and Lake Erie; 3c) St. Clair River and Lake St. Clair; 3d) St. Clair River and Lake Huron; 4a) Detroit River and Lake St. Clair; 4b) Detroit River and Lake Erie; 4c) St. Clair River and Lake St. Clair; 5a) Lake Erie, Detroit River and Lake St. Clair; and 5b) Lake St. Clair, St. Clair River and Lake Huron

3.3 | Predictors of migration behaviour

Body size, sex, spawning river and release site were not associated with migration behaviour. Lake sturgeon total length ($H = 0.18302$, $df = 4$, $p = .9961$) and weight ($H = 1.2895$, $df = 4$, $p = .8632$) did not differ among different migration behaviours (Figure 4a,b; Table 2). Likewise, sex ratios did not differ among the five behaviours, although the true sex ratios of each group were unknown due to a large number of individuals with undetermined sex (Figure 4c; Table 2). Finally, the distribution of migration behaviours did not differ between spawning rivers (Detroit vs. St. Clair) or among potential spawning sites (Detroit River vs. lower St. Clair River vs. upper St. Clair River; Figure 4d).

3.4 | Lake sturgeon geographical organization

Use of spawning rivers organized contingents into two main populations using either the Detroit River or St. Clair River (Figure 5). One putative population consisted of contingents tagged and detected in the Detroit River and that primarily resided within Lake Erie, the Detroit River and Lake St. Clair. The other putative population consisted of contingents detected in the St. Clair River and that primarily used within Lake St. Clair, the St. Clair River and Lake Huron. Individuals associated with one river were rarely detected in the other river. For example, only eight (10.3%) acoustic-tagged Lake sturgeon from the Detroit River segment and four individuals (2.1%) from the St. Clair River segment were detected past the receivers

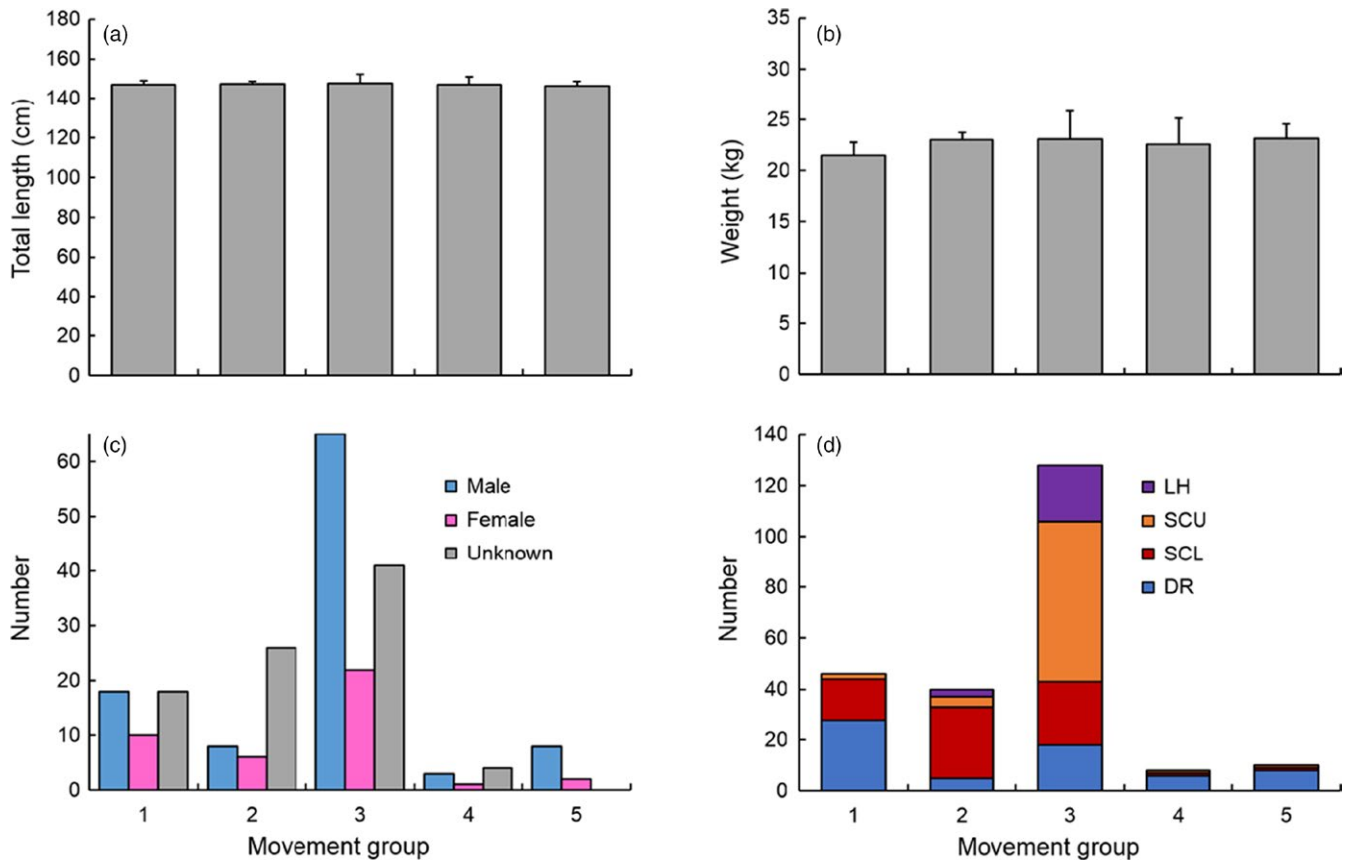


FIGURE 4 Biological characteristics of individuals assigned to each movement behaviour group, showing: (a) mean total length (cm); (b) mean weight (kg); (c) sex ratios and (d) number by tagging location. DR, Detroit River; SCL, St. Clair River lower; SCU, St. Clair River upper; LH, Lake Huron. Error bars represent 1 SE

at the outlet and inlet to Lake St. Clair (Figure 5). Only four (1.5%) individuals primarily used the alternative river relative to their tagging location. All tagged individuals associated with the St. Clair River, whether tagged in the lower St. Clair River, upper St. Clair River or lower Lake Huron, showed similar patterns of habitat use based on RI (mean residence index) across the GLATOS receiver network (Figure S1). Lake St. Clair was important habitat for acoustic-tagged lake sturgeon from both rivers. For example, Lake St. Clair was primary habitat for eight of the 14 contingents (57%) and 69.9% of all acoustic-tagged individuals were detected in Lake St. Clair on at least 1 day. In addition, Lake St. Clair was important as overwintering habitat for putative populations within the Detroit River and St. Clair River.

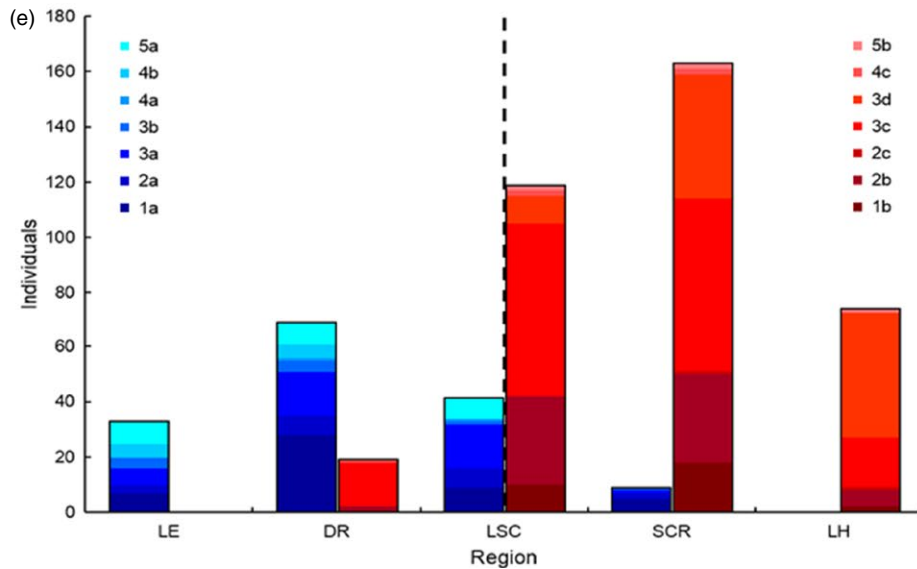
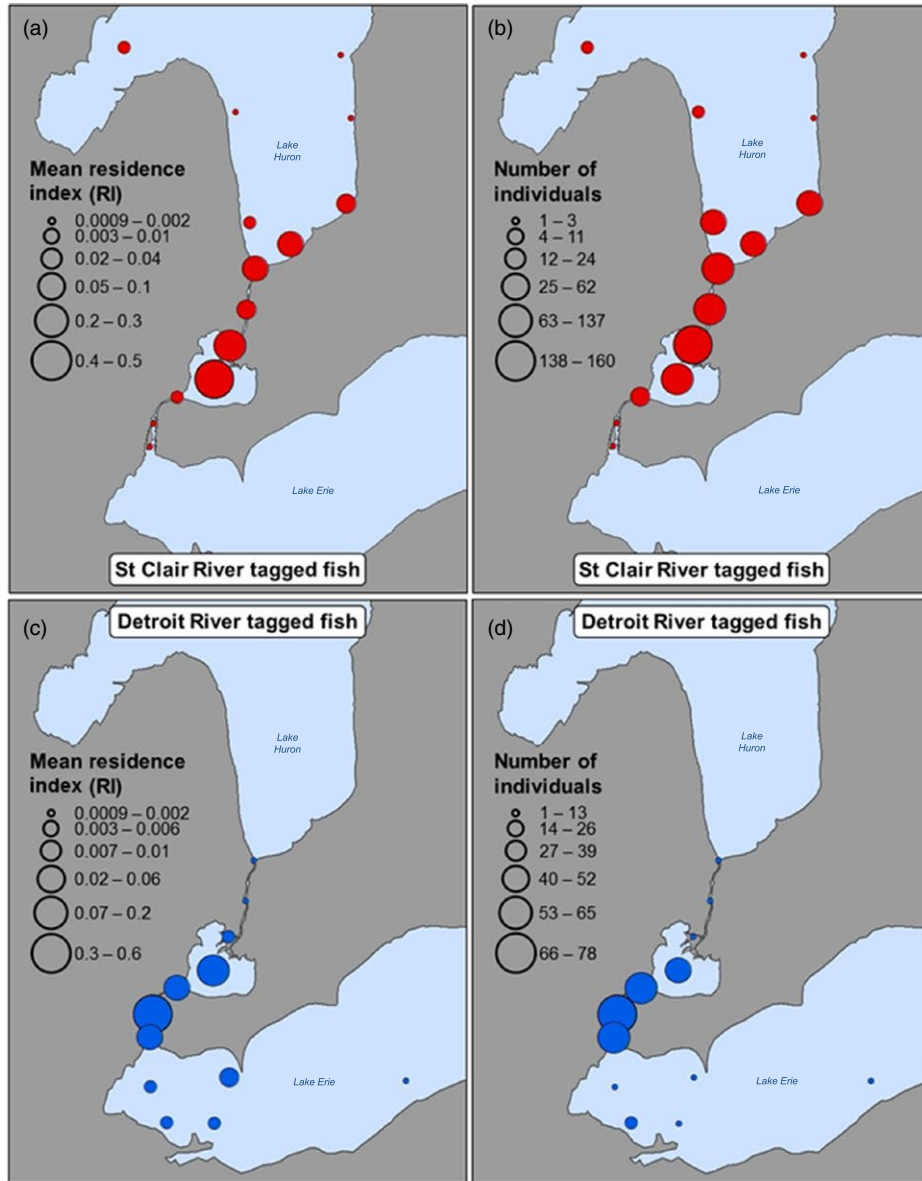
4 | DISCUSSION

Migration behaviours of lake sturgeon in an unfragmented landscape were consistent within individuals, but varied among individuals

within the same populations. Five distinct migration behaviours were identified based on phenology and duration of river and lake use. Specific behaviours included year-round river residency and multiple lake-migrant behaviours that involved movements between lakes and rivers. Individual movements were consistently repeated during the 6-year study period, suggesting that these behaviours were persistent phenotypic expressions in lake sturgeon. The frequency/occurrence of migration behaviours did not differ between the two river-associated putative populations, sexes, body size or among release locations, which indicated that intrapopulation variability in migration behaviour may be a general feature of lake sturgeon in unperturbed environments.

The results presented in this study constituted an important advancement in the understanding of lake sturgeon movements, distribution and population structure that may aid assessment of past restoration efforts and help guide future management and conservation initiatives. Differential use of specific rivers or lakes by

FIGURE 5 Distribution of detections of St. Clair River (a and b) and Detroit River (c and d) tagged lake sturgeon across the GLATOS network. Circles (a and c) represent graduated symbols for mean Residence Index (RI—number of days detected at each receiver group divided by the number of days detected anywhere on the network), and (b and d) the number of individuals detected at each receiver group; (e) number of individuals with predominant use of the Detroit River (blue) and St. Clair River (red) by study site region. LE, Lake Erie; DR, Detroit River; LSC, Lake St. Clair; SCR, St. Clair River; LH, Lake Huron. Bars are colour coded by the number of individuals from each contingent (1a through 5b). Dashed line represents the geographical separation of the two putative populations



acoustic-tagged lake sturgeon further subdivided individuals into "contingents" (Gahagan et al., 2015; Secor, 1999). Contingents associated with one river (Detroit or St. Clair) were rarely detected in the other river, which suggested that acoustic-tagged lake sturgeon in the Detroit and St. Clair rivers represent semi-independent populations that may require separate management considerations. While not directly observed, some limited exchange of spawners between rivers probably occurs and would account for the lack of genetic differentiation between the Detroit and St. Clair rivers based on neutral microsatellite markers (Welsh et al., 2008, 2010b).

Divergent migration may increase the resilience of lake sturgeon populations to natural and anthropogenic stressors. As in other lake sturgeon spawning rivers, navigational dredging, gravel mining and shoreline development have reduced the quality and availability of lake sturgeon spawning and nursery habitats in the Detroit and St. Clair rivers, and partly for this reason, the U.S. Environmental Protection Agency listed both rivers as areas of concern in 1987. Yet, lake sturgeon spawning in both rivers have retained full access to most, if not all, of their historical range, and perhaps not coincidentally, are the largest remnant lake sturgeon populations in the Great Lakes basin (Pollock et al., 2014; Thomas & Haas, 2002). We speculate that construction of barriers to fish movement in the HEC would harm lake sturgeon, as four of the five main migration behaviours required that lake sturgeon be able to move freely between lake and river habitats. Lake sturgeon in this study also required access to habitats not previously identified as important, such as Lake St. Clair. Repeated use of fluvial lakes has previously been described (e.g. Rusak & Mosindy, 1997), but not when deeper alternative lake habitats were available, in this case Lake Erie and Lake Huron.

The large sample size and long continuous observation period revealed both known and previously undescribed movement behaviours for lake sturgeon. Of the migration behaviours described for lake sturgeon in this study, migration behaviour 3 (predominant use of lakes with brief trips to the river during spawning season) was consistent with lake sturgeon migration movements previously described by others (Pollock et al., 2014; Rusak & Mosindy, 1997), and was the behaviour that contained the largest number of individuals. Two contingents (3a and 3d) undertook downstream movements into the spawning rivers (indicating the potential for outlet spawning), rather than the more typical upstream movement shown by contingents 3b and 3c. Different behaviours were also identified based on the timing and duration of use of the same habitat. For example, behaviour 2 members made similarly timed trips from lake to river habitat in the spring, but, unlike behaviour 3 members, remained in the river for prolonged periods after the spawning season. All behaviour 2 members travelled to river habitat annually, which was inconsistent with the intermittent spawning behaviour characteristic of the species. One explanation for this behaviour is that this migration behaviour in lake sturgeon may have a social component, with movements of spawning-ready individuals initiating movement of the entire group, both spawners and non-spawners. Co-occurrence of active and non-active spawners has been documented in other rivers (Thiem, Hatin, Dumont, Van Der Kraak, & Cooke, 2013), which suggests movements

influenced by social behaviour may be common in lake sturgeon. The motivation for prolonged river residence after the spawning season for all behaviour 2 members is unclear. Consistency of departure timing from the rivers amongst members indicated the potential for environmental cues triggering departure, though identification of such cues will require further investigation. Behaviour 4 members showed a pattern counterintuitive to what would be expected for migrations associated with river spawning (i.e. overwintering in the rivers and moving to the lakes during the spring and summer). This behaviour is not likely anomalous given that a proportion of lake sturgeon in the Rainy River and Lake of the Woods showed a similar behaviour (Rusak & Mosindy, 1997). The most complex of the identified migration behaviours was behaviour 5, the lake skippers, which were individuals that used more than one of the lakes on a consistent basis, a movement behaviour previously undescribed in any other lake sturgeon population.

This study confirmed prior speculations that lake sturgeon in the HEC showed both resident and migratory life-history behaviours. The relatively large number of individuals that showed river residence (20% of classified individuals) was unexpected considering the availability of productive foraging habitats in nearby lakes (e.g. western Lake Erie; Caswell, Peterson, Manny, & Kennedy, 2004). The existence of residents and migrants in the same population(s) suggested that lake sturgeon inhabiting the HEC show partial migration. Partial migration is a form of population diversity in which some individuals in a population migrate, while others do not (Dingle, 2014; Jonsson & Jonsson, 1993). We speculate that partial migration benefits a lake sturgeon population by reducing reliance on a single habitat, thereby buffering lake sturgeon against local extinction if one habitat becomes degraded while others remain intact and viable (Chapman et al., 2012). If true, then partial migration provides access of specific population segments to differential habitat and trophic resources and would promote population stability and resilience under changing environmental conditions. Migrants to the lakes during the summer may benefit from being able to behaviourally thermal regulate by using thermally stratified lake waters, and by having access to different trophic resources (Bowler & Benton, 2005). For example, migrant shortnose sturgeon inhabiting rivers in the Gulf of Maine were found to have a higher body condition relative to residents, and it was suggested that access to additional resources for migrants may constitute an adaptive reproductive advantage (Altenritter et al., 2017). Alternatively, residents may out-compete migrants for space and food in the rivers, thus, forcing their displacement to lakes. The different migration behaviours employed by lake sturgeon also may be a product of trophic polymorphisms (Smith & Skúlason, 1996), which could be tested through stable isotope analysis.

Partial migration is common in mobile species, and has been documented in a wide variety of taxa from invertebrates to vertebrates, including insects (Rankin & Burchsted, 1992), birds (Lundberg, 1988) and ungulates (Cagnacci et al., 2011). Divergent migration has been previously identified in both shortnose (*Acispenser brevirostrum*) and lake sturgeon populations and may be a common life-history

characteristic. Similar accounts of divergent migration have been observed for shortnose sturgeon inhabiting the coastal waters of the Gulf of Maine and surrounding river systems, which showed several distinct migration behaviours including residency and multiple migratory forms (Altenritter et al., 2017; Dionne et al., 2013). In the Lake of the Woods and Rainy River system, lake sturgeon showed two distinct migration behaviours based on the timing of river and lake use (Rusak & Mosindy, 1997). Half of radio-tagged lake sturgeon in this system overwintered in rivers, similar to behaviour 4 individuals in our study; the remainder showed a behaviour similar to our migration behaviour 2, which involved overwintering in lakes followed by movement into the river during the spring (spawning season).

Regulation of divergent migration in lake sturgeon was not associated with selective pressures that vary with body size, sex or location. All lake sturgeon tagged were adults and seemed to have established consistent migration behaviours, not switching to alternative behaviours over the course of the study. Size of lake sturgeon did not differ between the resident and lake-migrant behaviours, nor among the different classes of lake migrants. Intrinsic variables such as developmental stage, body size and sex have been proposed in other studies as correlates of resident and migration behaviours (Altenritter et al., 2017; Bowler & Benton, 2005; Chapman et al., 2012; Rikardsen & Elliott, 2000). In shortnose sturgeon, individuals at the same point in their reproductive development showed similar movement behaviours (Dionne et al., 2013). Here, it was not possible to determine the effects of sexual maturity or ontogeny on lake sturgeon migration behaviour given that all fish were adult-sized, and due to the difficulty of assessing earlier stages of gonad development through the small incision made to insert the acoustic tag. No association with sex on the migration behaviour of acoustic-tagged lake sturgeon was observed. Variability among individuals in migratory behaviour in lake sturgeon may be unrelated to sex. All behaviour groups were comprised of individuals from multiple tagging locations, suggesting that divergent migration is a natural feature of lake sturgeon life history in any unperturbed system, and not defined entirely by the features of the specific system they inhabit.

The existence of multiple migration behaviours and contingents identified spatial structuring in HEC lake sturgeon that could be important for conservation and management considerations, and was not previously evident from prior genetic analysis (Welsh et al., 2008, 2010a). The migration patterns of most individuals included use of only one spawning river, which can be interpreted as the existence of two populations, and thus these two ecological populations may require separate management consideration (e.g. catch regulations, abundance estimation). Here, acoustic telemetry provided a comprehensive account of lake sturgeon geographic organization, well beyond the resolution of genetic differentiation based on neutral markers. These results highlighted the importance of direct observation of movements in studies where the goal is to understand fish population structure and connectivity.

With examples from multiple fish species and other animal taxa, divergent migration is increasingly being recognized as an important form of life-history diversity that may require explicit consideration in future restoration and conservation initiatives. European roe deer

(*Capreolus capreolus*) showed four distinct migration behaviours between their summer and winter habitats (Cagnacci et al., 2011). Similar to the timing of movements by the lake sturgeon in behaviour groups 2 and 3, variation in the timing of roe deer migrations was most pronounced on their return leg in the autumn, with spring migrations probably synchronized through reproductive timing (Cagnacci et al., 2011). Three distinct migration behaviours were described for greater flamingo (*Phoenicopterus roseus*) around southern Europe and northern Africa, with inferred direct influence on survival probability (Sanz-Aguilar et al., 2012). Differences in life-history traits of migration behaviour groups, within partially migrating populations, have been regularly overlooked in evolutionary and population models (Bowler & Benton, 2005). Increasing recognition of the existence intrapopulation divergent migration should cement the concept as a key component for spatial ecology focused investigations.

5 | CONCLUSIONS

A historical shortfall in ecology is to inaccurately assume that a given species in a given region will show one common behaviour, void of group and individual variation (Conrad, Weinersmith, Brodin, Saltz, & Sih, 2011). Identification of partial migration, distinct migration behaviours and contingents, and distinct geographic units, provided essential insight into lake sturgeon spatial ecology in the HEC. Through the use of acoustic telemetry, this study addressed important data voids particularly in relation to population-scale movement and dispersal patterns at ecologically relevant temporal scales, not discernible from genetic analyses alone. Regionally, information relating to spatial ecology, such as that presented in this study, is critical for the assessment of management and restoration efforts, population abundance (Bowler & Benton, 2005), and to guide the direction for future lake sturgeon conservation behaviours. Population persistence, resilience and recovery potential can be maximized by protecting novel migration phenotypes (Brönmark et al., 2013) and by removing barriers to movement that potentially suppress expression of multiple movement behaviours.

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AUTHORS' CONTRIBUTIONS

S.T.K., D.W.H. and C.C.K. conceived the ideas and designed methodology; D.W.H., J.C.B., J.A.C., M.V.T., T.C.W., E.F.R. and R.D. collected the data; S.T.K., D.W.H., C.M.H. and C.C.K. analysed the data; S.T.K., D.W.H. and C.C.K. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data used in this manuscript are available in data publication "Acoustic telemetry detection data for acoustic-tagged lake sturgeon (*A. fulvescens*) in the Lake Huron-to-Lake Erie corridor (20161122)" on the USGS ScienceBase Catalog <https://doi.org/10.5066/f769722z> (Hondorp, 2017).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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