Received: 17 April 2020 | Accepted: 19 November 2020

DOI: 10.1111/fwb.13665

ORIGINAL ARTICLE

Freshwater Biology WILEY

Spatial distribution of lake trout (*Salvelinus namaycush*) across seasonal thermal cycles in a large lake

Silviya V. Ivanova[1] | **Timothy B. Johnson**[2] | **Brent Metcalfe**[2] | **Aaron T. Fisk**[1]

[1]Great Lakes Institute for Environmental Research, University of Windsor, Windsor, ON, Canada

[2]Ontario Ministry of Natural Resources and Forestry, Picton, ON, Canada

Correspondence
Silviya V. Ivanova, Great Lakes Institute for Environmental Research, University of Windsor, 401 Sunset Ave., Windsor, ON N9B 3P4, Canada.
Email: ivanovas@uwindsor.ca

Funding information
Canada Research Chairs; Natural Sciences and Engineering Research Council of Canada; University of Windsor; Canada-Ontario Agreement on Great Lakes Water Quality and Ecosystem Health

Abstract

1. Animal movements are influenced by the environment they inhabit and the need to maximise fitness and minimise cost. As such, seasonal thermal cycles in temperate lakes play an important role in the selection of habitat by species. Lake trout (*Salvelinus namaycush*) is a native top predator in the Laurentian Great Lakes and currently under rehabilitation in Lake Ontario. This cold, deep-water species is known to migrate to shallower depths in the autumn to spawn, but their spatial and seasonal distribution have not been examined in detail.
2. We quantified the residency and home ranges of 24 lake trout in eastern Lake Ontario across a full year (1 May 2017 to 30 April 2018) using acoustic telemetry to assess the influence of seasonal thermal cycles. Specifically, we used three thermal logging stations in the eastern basin, 164 acoustic receivers, and a total of over 1,000,000 detections to describe seasonal distribution. We also documented occurrences of long-distance movements (via 130 acoustic receivers located in the western basin of Lake Ontario), and thus the potential spatial overlap of populations from the eastern and western basins.
3. During stratification (1 July–1 November), lake trout ($n = 24$) showed a horizontally restricted distribution in regions of deeper water in eastern Lake Ontario. A variable and broad distribution was observed around the shallower Kingston Basin shoals during isothermal (1 January–30 April), spring warming (1 May–30 June; spring mix), and autumn cooling (2 November–31 December) periods. Home range sizes ranged from 0.1 to 3,966 km^2 among all thermal cycles, with the largest observed during cooling autumn mix conditions driven by four individuals. Large variation in home range area was observed among individuals, and, thus, means were not statistically different between seasons. Three individuals occupied shallower shoals even during stratified conditions, and another individual crossed the entire lake from the east to the west end of Lake Ontario, travelling over 200 linear km in 17 days.
4. Our results confirm that thermal regimes and spawning needs affect the spatial use of lake trout in Lake Ontario, but demonstrate that there are broad distributions during isothermal conditions, highly individualistic spatial utilisation, and inter-individual variation in spatial distribution and exploratory behaviour. All of these behaviours are consistent with other top predator species.

5. Defining the spatial utilisation and distribution of individuals are important steps toward a better understanding of reintroduced species ecology in freshwater ecosystems. The variation of individual lake trout distribution across seasons implies that individuals may have different influences on the overall ecosystem function and potentially different responses to increasing water temperatures. These results suggest that an adaptive management approach is required when rehabilitating populations of this native fish where populating multiple habitats in an ecosystem is an objective in the face of a changing environment.

KEYWORDS

acoustic telemetry, habitat use, home ranges, inter-individual variation, salmonids

1 | INTRODUCTION

Animal habitat use is influenced by the environment they inhabit and the need to maximise fitness and minimise cost, i.e. maximise habitat exploitation (Begon et al., 2006; Nathan et al., 2008). Animal movements and distribution across habitats represent efforts to optimise fitness (Magnuson et al., 1979), although these may be modified by other factors (Morbey et al., 2006). Predator home ranges are often large in extent, overlapping those of their prey, and areas considered good foraging grounds tend to be frequented more than areas where prey availability is scarce (Adlerstein et al., 2008). Spawning is another activity that influences fish movement and habitat use on a seasonal basis (Hunter et al., 2003). Spawning habitat is typically represented by specific features, such as substrate, depth, and hydrology, which may differ from habitats used during non-reproductive times of the year. Preference and utilisation of habitat could also be influenced by spatial competition based on density of conspecifics (Kawaguchi & Desrochers, 2018) and presence of heterospecifics (Vander Zanden et al., 1999). In all cases, thermal conditions constrain the choice of particular habitats for fish due to their thermoregulatory requirements as ectotherms (Magnuson et al., 1979), for example during stratification in lakes. The identification of distributions and home ranges throughout the year can inform our understanding of fish behaviour (Landsman et al., 2011).

It has been hypothesised that cold water species are more vulnerable to increasing temperatures in lakes associated with climate change, largely because of decreased suitable habitat within a lake due to alteration of the thermal structure and reduced oxygen concentrations (Collingsworth et al., 2017; Shuter & Lester, 2004). For large, deep lakes, changes in the horizontal and vertical home ranges and distributions are expected to occur with seasonal changes in lake thermal structure (Cline et al., 2013; Magnuson et al., 1990). Prolonged stratification, either by delayed autumn turnover, early onset of spring stratification, or both, has the potential to delay habitat switching events, migrations, and autumn spawning, and/or impair egg survival due to physiological stress imposed by suboptimal conditions (Carlson & Siefert, 1974; Garside, 1959). Similarly, adult growth rate is shown to decrease with increases in temperature above the optimal (King et al., 1999). Thus, the quantification of the seasonal home ranges and correlations with thermal cycles provides an important baseline for prediction of climate change effects on species distributions and a necessary step to updating existing bioenergetic predictions.

Lake trout (*Salvelinus namaycush*) is a top predator native to all of the Laurentian Great Lakes (hereafter Great Lakes). The species declined in the mid 1900s due to a combination of overfishing, habitat degradation and predation by sea lamprey (Christie, 1972; Fitzsimons et al., 1999; Schneider et al., 1983) and is generally stocked to varying degrees for rehabilitation. As a native top predator, lake trout exerts a top down stabilising influence on the food web and has a key role in the cycling of energy between the benthic and pelagic offshore zones (Ives et al., 2019; Ryder & Kerr, 1990). Further, because trout thrive in pristine, oligotrophic systems, individuals are sensitive to ecosystem change and stress, and are therefore used as an indicator species of ecosystem quality (Ryder & Edwards, 1985). Lake trout is thus considered a desired component of the Great Lakes fish community and a key indicator of Lake Ontario's ecosystem health.

Lake trout is a cold-, deep-water species (Stewart et al., 1983) and has been described as both pelagic and demersal (Guzzo et al., 2016; Riley et al., 2008) because individuals feed on both types of prey (Colborne et al., 2016; Mumby et al., 2018). Trout migrate to shallower depths (<10 m, rocky shorelines and offshore shoals) in the autumn to spawn (Hansen, 1999). In Lake Ontario, lake trout spawning behaviour has been studied and physical spawning habitat described (Fitzsimons, 1995; Goodyear et al., 1982; Thibodeau & Kelso, 1990), and recently, the temperature–depth niche has been quantified for spring, summer, and autumn, but this has not been done for winter (Raby et al., 2020). However, lake trout home ranges throughout any season have never been quantified, and in particular, neither have their sizes, locations, and associated thermal conditions—a problem given the increasing warming of the Great Lakes (Zhong et al., 2019). In addition, trout from western and eastern Lake Ontario are believed to stay spatially segregated (Raby et al., 2017; Ontario Ministry of Natural Resources and Forestry and U.S. Fish and Wildlife Service, personal communication), yet new evidence suggests that may not be the case (Holden, 2019). Considering the variation of genetic strains stocked throughout the years in Lake Ontario with various habitat preferences (e.g. Seneca, Apostle Island, Klondike; Lantry et al., 2018), understanding the behaviour differences in strain performance would contribute valuable information to rehabilitation efforts, including the role of reintroduced fish in the ecosystem. In addition, understanding seasonal changes in lake trout distributions and home range sizes in Lake Ontario, and the potential for long-range movements between populations of the eastern and western basins of the lake, will, as a first step, provide a basis for predicting effects of lake trout on the lake ecosystem function as well as population responses to warming. On a broader scale, fit and function of reintroduced species in an ecosystem are important questions for any system in which species are undergoing rehabilitation or reintroduction, and contributions to this field are key to adaptive management.

With the growing use of acoustic telemetry in the Great Lakes, we had the opportunity to quantify the distribution and home ranges across seasons of an ecologically important top predator with history of rehabilitation. Since water temperature has a major influence on animal distributions and bioenergetics, we used the seasonal thermal cycles of the lake as a guide. Lake trout is a good cold-water model species and quantifying the residency and home ranges would contribute to: (a) understanding the among-season spatio-temporal ecology of a reintroduced cold-water predator in a large lake and provide clues on how such species respond to the spatio-temporal variation in the environment; (b) assessing potential thermal constraints to lake trout distributions at present; and (c) ultimately, contribute to predictions about the impact of climate change on cold-water species, and in particular lake trout distributions in a warming climate. Thus, the objectives of this study were to quantify the thermal cycles of eastern Lake Ontario over a period of one full year, relate these to and quantify the home ranges and residency of individual lake trout using acoustic telemetry, and determine if any individuals dispersed to the western basin of Lake Ontario.

2 | METHODS

2.1 | Study site

Lake Ontario is the 13th largest lake in the world, with surface area >19,000 km^2 and a maximum depth of 244 m. It is home to six salmonid species, two of which are native, supporting a valuable recreational fishery (Stewart et al., 2017). Eastern Lake Ontario is characterised by shallow offshore areas (from hereon referred to as shoals or Kingston Basin) varying in depth from 0 to *c*. 40 m (Figure 1) separated from the deep main basin of the lake by the Duck-Galloo Ridge. The larger St Lawrence Channel (*c*. 60 m deep) and two smaller

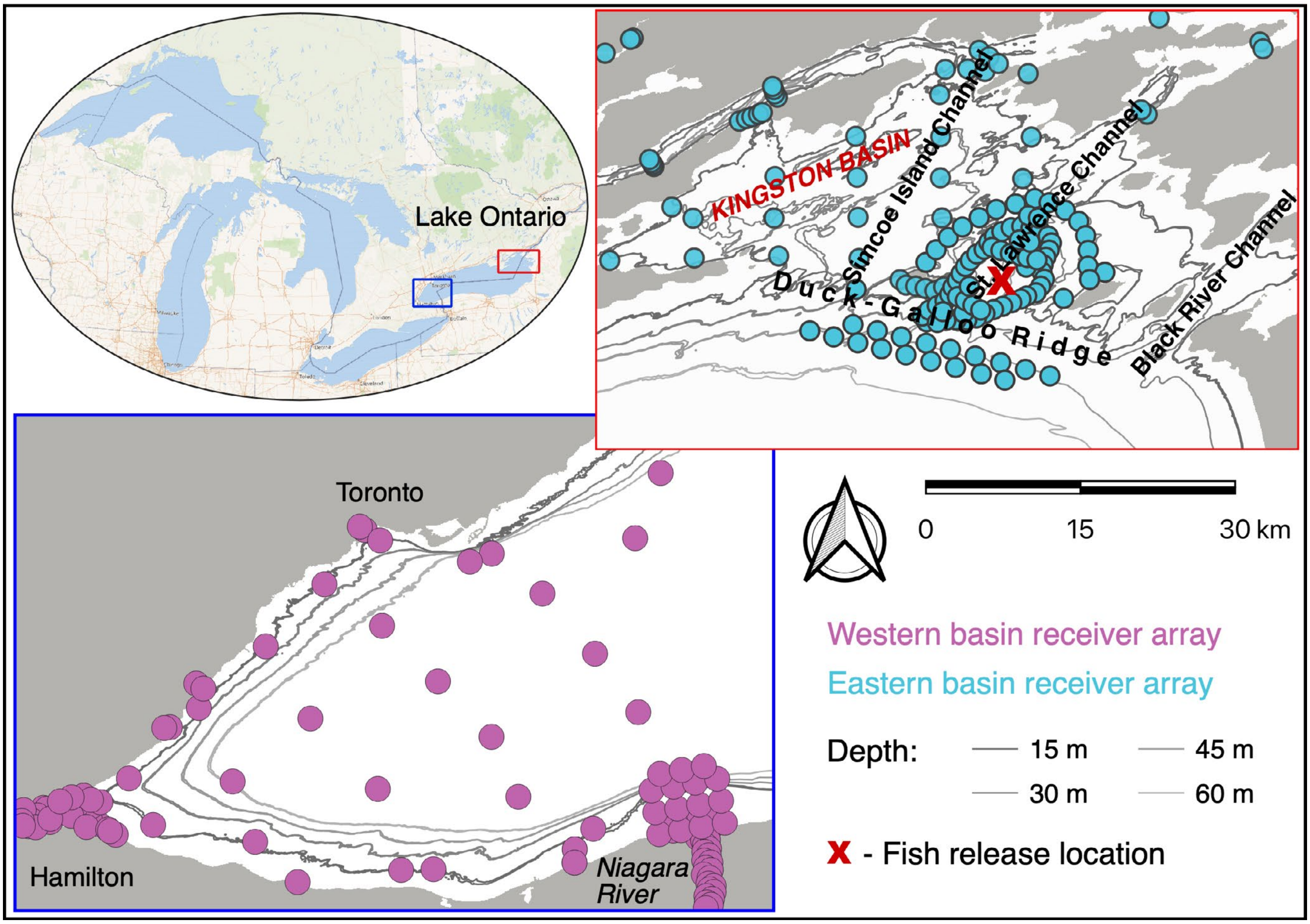


FIGURE 1 Map of receiver locations and bathymetric features for the western basin and eastern Lake Ontario used to examine the habitat use of lake trout

Simcoe Island and Black River channels bisect the Duck-Galloo Ridge to provide deep water connections between the Kingston Basin and the main basin of Lake Ontario. The western basin of Lake Ontario is defined here as the area west of a line running north from the Niagara River mouth to Toronto (Ontario, Canada; Figure 1). The main basin is generally considered the area between the Duck-Galloo Ridge and the western basin and for the purposes of this study the term would be used to identify these deeper areas (max depth 244 m) in eastern Lake Ontario. The term eastern Lake Ontario is used here to refer to the eastern basin, Duck-Galloo Ridge and eastern quarter of the main basin (as per extent shown in Figure 1). It is important to note that we use lake bathymetry (i.e. restriction in the depth range available for occupancy in the shoals [0–40 m] versus the main basin [0–244 m]), and not position within the water column, to describe the two-dimensional horizontal spatial distribution of lake trout.

2.2 | Description of thermal cycles

To describe the seasonal thermal dynamics in eastern Lake Ontario, three strings of temperature loggers (HOBO TidBit v2 Temperature Data Logger; Onset Computer Corporation) spaced every 2 m from 10 m depth to the lake bottom collected data over the study period of 1 May 2017 to 30 April 2018 (logger 1 coordinates: 43.979233, −76.49645; logger 2: 43.961675, −76.586484; and logger 3: 43.826748, −76.661223; Figure 2). Temperature was recorded every 15 min, with a resolution of 0.02°C at 25°C, and accuracy of ±0.21°C from 0° to 50°C. To quantify the thermal seasons we calculated mean daily temperature at depth, examined temperature change in relation to depth to determine the position of the thermocline across locations, and used the following definitions: (a) stratified—when >5°C temperature differential occurred above versus below the thermocline; (b) autumn mixing and cooling (from here on referred to as autumn mix)—when the thermocline broke down, temperatures from the 10-m logger and the bottom had <5°C difference, and the overall temperature rapidly declined until it reached a relatively constant value; (c) isothermal—when temperatures varied <5°C among all loggers and were neither cooling nor warming; and (d) spring mixing and warming (spring mix)—when temperatures started to warm rapidly until a thermocline was established with temperature difference above and below the thermocline of >5°C.

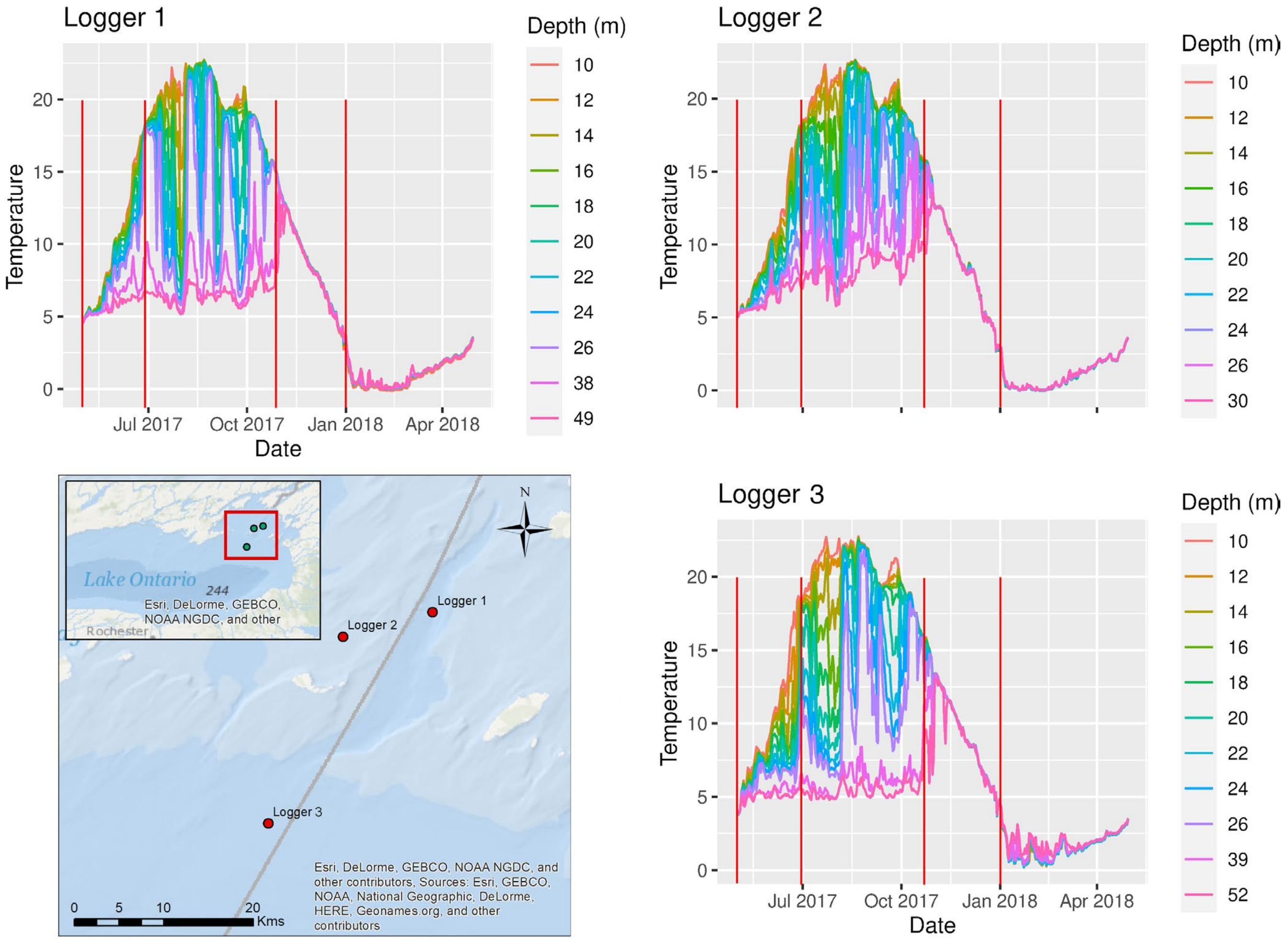


FIGURE 2 Eastern Lake Ontario thermal profiles (daily mean water temperatures) from 1 May 2017 to 30 April 2018 at three locations near the St. Lawrence Channel. Red vertical lines denote the starts and ends of the four thermal periods

2.3 | Acoustic telemetry

A total of 164 fixed-station acoustic telemetry receivers (69-kHz VR2W; Innovasea) in eastern Lake Ontario were used to track and record lake trout movements for one full year (Figure 1; 1 May 2017–30 April 2018). Receivers were spaced *c.* 1 km apart in the St. Lawrence Channel. Receivers outside the channel and at the Duck-Galloo Ridge were spaced *c.* 2.5 km apart, and in the Kingston Basin *c.* 5–10 km apart. Receiver detection efficiency at 80% was *c.* 1,600 m (Klinard et al., 2019). Moorings consisted of concrete cylinders (*c.* 62 kg) as the anchors connected to two 28-cm trawl floats by a 3-m length of 1.1-mm polypropylene rope with inline galvanised swivels. Receivers were attached to the riser *c.* 2 m above the lake bottom with the hydrophone pointing upwards. An approx. 30-m weighted rope was attached to the concrete anchor at one end and a cinder block at the other end to serve as a drag line for grappling when retrieving the receivers for download. In addition, receivers ($n = 130$, 69-kHz VR2W) in the western end of Lake Ontario were used to identify any cross-lake movement. From here on, the receivers are collectively referred to as an *array*. Two tagging events took place in 2016: 26 October at Main Duck Island (43.927653, −76.618055, $n = 9$) and 3 November at Charity Shoal (44.042179, −76.483863; $n = 21$). In both cases, fish were caught using gill nets set overnight (30 m each of 64-, 76-, and 89-mm stretch monofilament mesh) and held in 600-L holding tanks continuously resupplied with aerated lake water until tagged; fish were held <2 hr total following removal from nets. A tank filled with lake water and MS-222 mixture (4 g of MS-222 with 8 g of baking soda buffer per 10 L of water) was used as anaesthetic to prepare the fish for surgery. Once nonresponsive, fish were placed in a foam cradle and their gills continuously irrigated with lake water. Total length was measured, and fin clips and marks recorded (to confirm stocked or wild); 10 fish were female and 20 were male, all adult. A small incision (*c.* 20 mm) was made posterior of the pelvic fins, a V16 acoustic transmitter (hereafter tag; 68 mm length × 16 mm diameter; 10.3 g weight in water; nominal delay 180 s; estimated battery life 3,650 days; Innovasea) was inserted into the peritoneal cavity, and the incision was closed with three Vicryl sutures (Ethicon VCP423, 2-0 FS-2 cutting). An external floy tag was also attached to provide angler awareness of the internally tagged fish. Surgery took <3 min, after which fish were allowed to recover in a holding tank until able to swim upright, and then released within the receiver array in the St. Lawrence Channel in water >20 m depth (Figure 1). All tagged fish were similar in size with mean total length of 766 ± 9 mm.

2.4 | Data analysis

Data were analysed for the period 1 May 2017–30 April 2018, during which all acoustic receivers were present. R statistical software (version 0.98.1103) was used for all analyses and ArcMap (version 10.3.1) for graphing. White–Mihoff filtering tools were used to filter out any false detections (White et al., 2014), where a detection range of 1,600 m was used based on 80% detection efficiency (Klinard et al., 2019). A total of six lake trout were removed from the analysis: IDs 16871 and 16875 were removed due to tag expulsion or death; four other individuals, although detected for a number of months after release, had no detections during the period of data analysis and were presumed to be either out of the array and/or dead. Of the remaining 24 individuals, partial data were used for IDs 16853, 16859, and 16876 due to eventual tag expulsion or fish mortality—this was determined based on the changed pattern of detections, where the tags were continuously detected by a single receiver for the remainder of the study; thus, any detections 24 hr prior to the onset of such changed pattern were removed from analysis. A 24-hr cut off was chosen based on examination of individual movement tracks and comparison to the other tagged fish in our study to ensure the observed behaviour included in the analysis was not out of the ordinary. Partial data inclusion is not likely to bias our results as all calculations were performed separately for each individual and then means taken where necessary (see below). A total of 1,050,469 detections were used for further analysis based on 24 individuals. Detection data were separated into four thermal seasons (defined in results) based on observed thermal cycles in eastern Lake Ontario.

The receivers in the eastern basin are not uniformly distributed and therefore may introduce bias based on density of spacing, and/or if simultaneous detections occurred on different receivers. None of these were considered to be a problem for our residency index because calculations were based on presence/absence (not number of detections) per receiver and since fish move, the detections at a particular receiver would represent presence of the fish in the vicinity of that receiver within detection range. Thus, although some regions had more receivers than others, they all provide a general locality of the fish in a consistent manner (i.e. Kingston Basin vs. St. Lawrence Channel vs. main basin). For home range calculations that are based on density estimates, bias is more likely, especially when true spatial data (i.e. x, y positions) are not available. For this reason, we chose to calculate centres of activity (a position averaging calculation of all detections at receivers over a particular time interval) and use that for estimation of home ranges. To further verify that there was no bias based on receiver distribution, we examined the trajectories of each individual over time against the generated home ranges and confirmed the results. Inference has not been made, nor should it be, for areas without receiver coverage, or periods when the fish were outside the array.

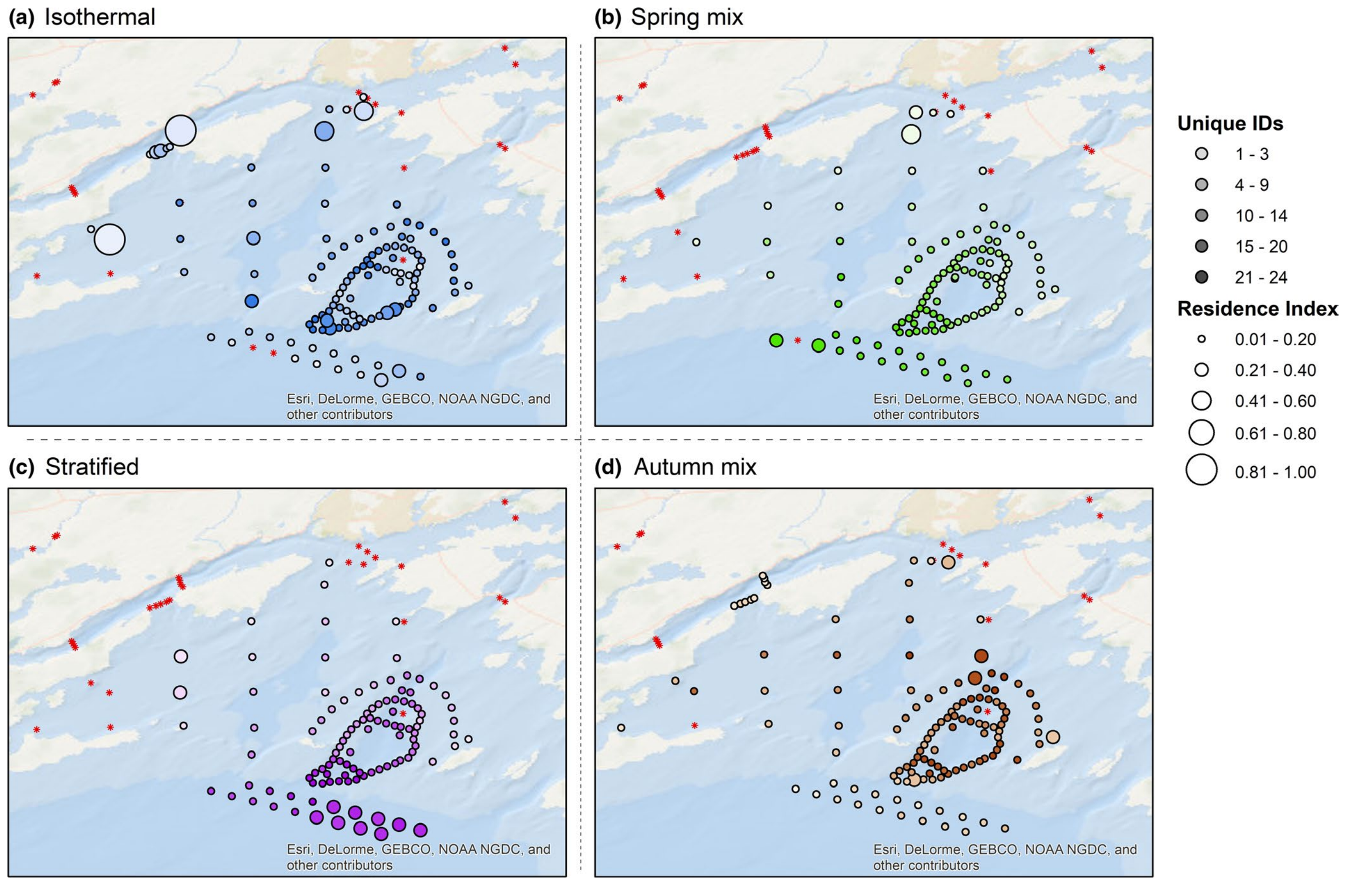
Lake trout distribution preferences were determined using a residency index (Kessel et al., 2015). Individual residence was calculated as the number of days an individual was detected per receiver divided by the total number of days the same individual was detected in the array, and then mean residence index (RI) was obtained from the mean of all individuals' residence results. The numbers of detections used for RI calculations by thermal period were: stratified—687,508; autumn mix—59,539; isothermal—86,347; and spring mix—217,075. Centres of activity (Simpfendorfer et al., 2002), were used to approximate locations of individuals at a given time for the calculation of home ranges. For centres of activity, simultaneous detections on multiple receivers are not allowed, but only successive detections. Considering our tags had a large detection range of *c.* 1,600 m at 80% detection efficiency (Klinard et al., 2019), receivers located in the St. Lawrence channel showed such tendency, thus we removed from analysis every second receiver and associated detections from this receiver array. Approximate locations were then calculated for each individual using position averaging of the detections occurring over a 30-min period. These locations were then used to infer individual home ranges using Kernel utilisation distribution (KUD) at 50% (core) level (adeHabitatHR package; Calenge, 2006). The numbers of locations and IDs used to infer home ranges by thermal period were as follows: stratified—66,651 based on 24 IDs; autumn mix—8,548 and 20 IDs; isothermal—10,311 and 17 IDs; and, spring mix—18,583 and 22 IDs. CalcHR.R and Indices.txt (Fieberg & Kochanny, 2005) were used to quantify Hurlbert Index of overlap (Hurlbert, 1978) on core KUDs between all periods.

3 | RESULTS

The following four thermal cycle periods were identified for eastern Lake Ontario based on our temperature logger data: (a) stratified—1 July to 1 November; (b) autumn mix—2 November to 31 December; (c) isothermal—1 January to 30 April; and (d) spring mix—1 May to 30 June.

Tags had a nominal delay of 180 s and maximum possible daily detections were *c.* 480. Mean (±*SD*) of observed detections across individuals was 43,770 (±3,314), with daily mean (±*SD*) 119.9 (±9.1). There are a variety of reasons why the maximum detections per day were not observed, such as the spacing between receivers in the Kingston Basin for example, or individuals that spend time in the main basin but outside of the receiver range. Number of detections per individual were normally distributed (Shapiro–Wilk normality test $p = 0.98$).

Based on the residence index (RI) method, lake trout showed a preference for the St. Lawrence Channel and the main basin during periods of thermal stratification. However, during isothermal, autumn, and spring mix conditions, individuals dispersed throughout the shallower Kingston Basin and St. Lawrence Channel (Figure 3). The greatest RI values for the autumn mix period were observed at known spawning locations of Galloo Island and Charity Shoal, whereas RI values during the isothermal period were greatest at what we believe may be the wintering grounds throughout the Kingston Basin. The number of individuals that contributed to an RI calculation per receiver varied between 1 and 7 on any given date for all four periods (mean of 3.8 individuals per day for isothermal and autumn mix periods, and 4.1 for spring mix and stratification).


(a) Isothermal
(b) Spring mix
(c) Stratified
(d) Autumn mix

Esri, DeLorme, GEBCO, NOAA NGDC, and other contributors

FIGURE 3 Mean residence index for all individual lake trout in eastern Lake Ontario for the period of May 2017–2018. Hue and size represent the number of unique IDs and the residence index the results were based on, respectively. Note, lake trout were not detected at all receivers (denoted with red stars)

The core home ranges (50% KUD) showed similar pattern to the residence index results. Nearly all individuals (21 of 24) showed a preference for the main basin and southern end of the St. Lawrence channel during stratification; whereas distribution of home ranges for the remaining three periods were spread throughout the shallower Kingston Basin (example shown in Figure 4). Three individuals (IDs 16855, 16856, and 16876) occupied multiple core home range areas during stratified conditions of which at least one was in the shallower (in comparison to the main basin) Kingston Basin (Figure 4), suggesting use of the shoals during that period. Seasonal individual core home range area sizes varied between 0.1 and 3,966 km^2 (Table 1) with the smallest and largest occurring during isothermal and autumn mix conditions, respectively. Home ranges averaged 72.5 km^2 (±58.7 standard deviation) across the four seasons. While home range sizes were generally below 220 km^2, four individuals, namely IDs 16869, 16860, 16865, and 16867, contributed to the large mean and variance during autumn mix with core home range area sizes of 3966, 511, 283, and 279 km^2, respectively. Excluding these first two individuals' home ranges, there were no statistical differences between the mean home range sizes of any thermal periods ($p > 0.05$, ANOVA). The number of individuals with home range sizes falling within the first

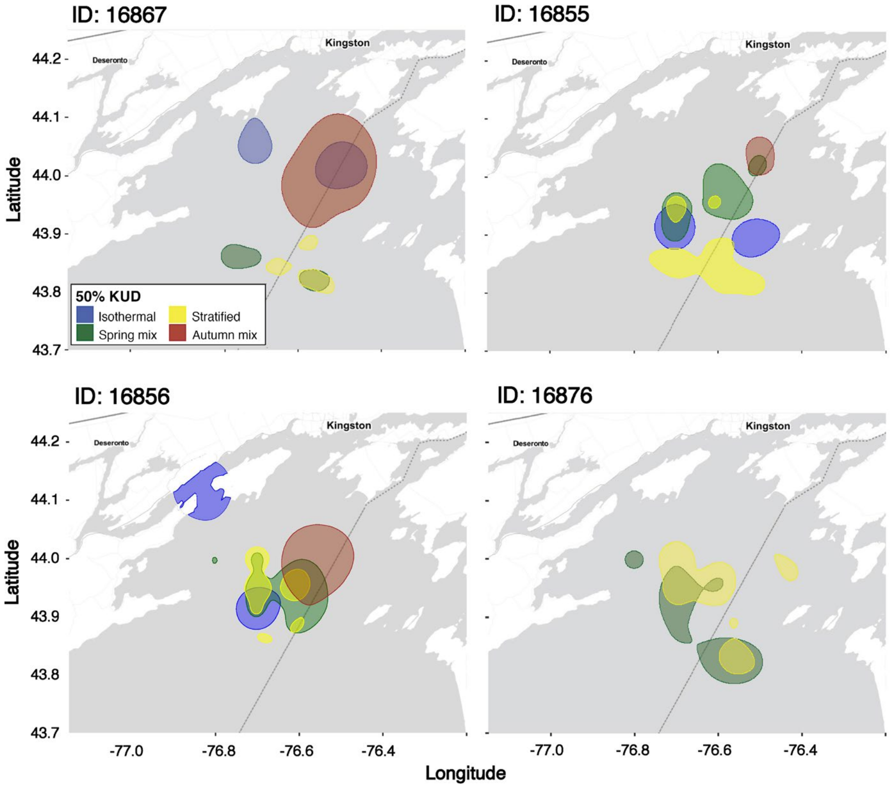


FIGURE 4 The home ranges of individual with ID 16867 are shown as a representative example for the majority of tagged lake trout. Shown are also the home ranges of the three lake trout individuals (IDs 16855, 16856, and 16876) that spent at least part of the stratified period into the Kingston basin shoals. KUD, Kernel utilisation distribution

TABLE 1 Lake trout mean, standard error, minimum, and maximum core home range (50% KUD) area sizes (km^2) for eastern Lake Ontario

	KUD (mean ± *SE*)	Min	Max	Number of IDs with KUD size between the 1st and 3rd quartile/all IDs	Mean number of HR cores between individuals (range)	Number of days
Autumn mix[a]	297 ± 195.1	2.2	3,966	8/20	1.6 (1–3)	60
	81.2 ± 20.9[a]		282.6[a]		1.5 (1–2)[a]	
Isothermal	74.1 ± 16.4	0.1	215.5	9/17	2.05 (1–3)	120
Spring mix	77.8 ± 9.5	3.2	178.4	8/22	1.05 (1–3)	61
Stratified	60 ± 7.6	14.7	169.7	12/24	2.13 (1–4)	124
IDs with outlier KUD sizes for fall mix[a]						
16869	3,966	—	—		2	
16860	510	—	—		3	

Note: Also shown are the number of IDs with home range size within the first and third quartiles out of the total number of IDs with a home range per thermal season. Two lake trout IDs with outlier values for the autumn mix period KUDs are also shown.

Abbreviations: KUD, kernel utilisation distribution; *SE*, standard error.

[a] Mean and *SE* values calculated without outliers, which are shown in the bottom part of the table.

and third quartiles throughout all seasons varied and was approx. half or less of the total (Table 1). Hurlbert index of overlap of core home ranges was low between stratified and isothermal periods 0.008 ± 0.005 (mean ± *SE*), and between autumn and spring with 0.001 ± 0.0008.

A single individual (ID 16869) travelled from eastern Lake Ontario to the western basin (Figure 5). While the individual was consistently detected on receivers in eastern Lake Ontario during the stratified and autumn season (*n* = 47,653 detections) it was last detected there on 5 December before showing up on western Lake Ontario receivers 17 days later on 22 December. The individual remained in the western basin until 13 March (a total of 556 detections) and was not detected again during the study period.

4 | DISCUSSION

Lake trout distribution and home ranges in eastern Lake Ontario determined using acoustic telemetry over the span of 1 year were generally correlated to the lake's seasonal thermal cycles based on the different basins examined and provided novel insights into the species spatiotemporal ecology. Previous studies have largely relied on catch data to infer lake trout distribution in Lake Ontario (Olson et al., 1988). Such data are often prone to spatiotemporal bias because the catchability of fish is dependent on the presence of gear in that location, vertical and horizontal, during that period and the gear's efficiency (Jagielo et al., 2003; Thorson et al., 2017; Walker et al., 2017; Walsh, 1996). Such bias may be amplified if the species of interest exhibit inter-population and/or inter-individual variation in habitat use and swimming activities. In this study, we also uncover and document important variation between individual lake trout based on multiple underlying factors when selecting habitat or in terms of exploratory behaviour. Such individualistic behaviour is consistent with other top predators, such as northern pike (*Esox lucius*), leopard seals (*Hydrurga leptonyx*), and sharks (Casselman & Lewis, 1996; Findlay et al., 2016; Hiruki et al., 1999; Wilson, 1905).

Residence index and home range results confirmed that lake trout generally used the main basin, the region with greater depth, during the stratified period, which has been suggested to be due to a physiologically driven need to inhabit colder, deep water below the thermocline, yet other factors have also been cited to contribute. Thermoregulation requirements seem likely if we consider the broader distribution into the shallower Kingston Basin for the remainder of the year when no thermal limitation was occurring. However, Raby et al. (2020) reported that in October and November lake trout occupied waters with temperature ranging between 8 and 14°C, and suggested that thermal stratification may be only one of the factors driving their habitat use. Studies have reported dissolved oxygen and competition as other factors influencing lake trout distribution (Morbey et al., 2006; Sellers et al., 1998; Vander Zanden et al., 1999). Dissolved oxygen has been used to define lake trout habitat quality (Evans, 2007; Plumb & Blanchfield, 2009), and lake trout perform better at higher dissolved oxygen levels (6–7 mg/L; Evans, 2007). The lowest recorded dissolved oxygen level in the Kingston Basin during our study period occurred in August and was >5.9 mg/L. This is well within the preferred range recorded by Evans (2007), suggesting that dissolved oxygen was not a driving factor for lake trout occupying areas outside the Kingston Basin. However, five other salmonid species and walleye (*Sander vitreus*) are present in Lake Ontario, all of which forage on the same prey (i.e. alewife, *Alosa pseudoharengus*; Hoyle et al., 2017; Mumby et al., 2018), and lake trout prey consumption rates peak during adulthood (Negus et al.,

Esri, DeLorme, GEBCO, NOAA NGDC, and other contributors

FIGURE 5 Lake trout ID 16869 Lake Ontario cross-lake movement. This individual left the eastern Lake Ontario arrays on 5 December 2017 and was detected on the western basin at the mouth of the Niagara River on 22 December 2017—a distance of >200 km. The last detection for our study period (1 May 2017–30 April 2018) occurred on 13 March 2018 in the west basin. A subset of dates and detection locations are also shown

2008). Given these, competition may be a plausible additional factor influencing lake trout distribution during the stratified period.

Species seasonal distributions may also be strongly influenced by their prey (Guzzo et al., 2016) and lake trout have the largest trophic (isotopic) niche of any of the six salmonid species of Lake Ontario, feeding on both pelagic and benthic species, with alewife and round goby being the dominant prey (Colborne et al., 2016; Mumby et al., 2018; Rush et al., 2012; Yuille et al., 2015). Seasonal movement and distribution of alewife and round goby are poorly quantified in the Great Lakes, yet inferences from other studies suggest that variable horizontal seasonal overlap exists with lake trout. Alewife are found farther offshore in the autumn and winter when compared to other seasons to avoid stressfully low temperatures at shallower depths (Bergstedt & O'Gorman, 1989; Colby, 1973; Smith, 1968), and in shallower regions to spawn in the summer (O'Gorman et al., 1991), suggesting a reverse horizontal distribution to that of lake trout. This is consistent with reports that lake trout consume alewife in the spring, but partially replace them with other species in the summer due to their reduced availability in deep, cooler waters (Dietrich et al., 2006; Luo et al., 2019). Conversely, round goby in their native habitat are reported generally to occur at depth <60 m (Miller, 1986) in the autumn and winter, and in southwestern Lake Ontario in April at depth <130 m (Walsh et al., 2007), whereas they migrate to nearshore areas (<10 m) in the summer (Miller, 1986). Since the species is benthic, this probably means a distribution in the Kingston Basin when found at depth <40 m and the main basin when at greater depth. This is supported by previous studies (Dietrich et al., 2006) and more recently by trawl surveys. This implies that round goby horizontal distribution overlaps with that of lake trout during the colder months and partially during stratified periods. Raby et al. (2020) reported that the vertical/depth niche of lake trout measured using archival tags was small compared to other salmonids in Lake Ontario and suggested that lake trout probably focused their foraging in the area near the lake bottom with limited opportunistic foraging near the thermocline. Given all of the above and recent rebounding of deep-water sculpin (*Myoxocephalus thompsonii*) populations, a benthic species that was historically a major part of trout diet (DFO, 2016; Weidel et al., 2017), we suggest that different prey are available across all lake regions occupied by lake trout throughout the year and do not appear to be a critical driving force behind their distribution during stratified conditions. An incomplete understanding of seasonal prey distribution in eastern Lake Ontario prevents us from establishing this with certainty.

Lake trout had their largest mean home range core areas during the autumn, an unexpected finding for a period of spawning. However, this is also a period when individuals migrate from offshore areas of the main basin to spawning shoals closer to shore as water begins to cool and then probably to wintering grounds. Four individuals drive this large mean (two of which were statistically determined to be outliers) with much greater home range sizes than all others, including one that travelled to the western basin of Lake Ontario (ID 16869). The migration between basins occurs at the beginning of the autumn mix period, and over a short period of time (i.e. generally individuals complete the migration within a day; Ivanova et al., in preparation). Thus, the between-basin migration is not likely to have a great effect on core home range size. However, individuals visiting multiple shoals and exploring their quality and suitability for spawning may be the cause for the large home range cores during autumn—a plausible explanation given that home range estimates are based on utilisation density. Also, such behaviour is consistent with lake trout in Lake Opeongo, where fish move among multiple shoals at spawning time, visiting as many as 10 spawning shoals in a 2-week period (MacLean et al., 1981). Lake trout are known to exhibit site fidelity, but in this study, we were unable to quantify this and parse the specific movements during this period to assess a potential pre-spawning exploration. However, travel to multiple wintering grounds away from the spawning areas may be a contributor to the observed home range sizes during the autumn. Three of the four individuals with the largest home ranges had two or three home range cores, and one had a single core, although still comparatively much larger in size than other conspecifics. There were, however, four other fish that had two or more home range cores during this period but with smaller home ranges. This implies variation in the use of wintering grounds, including variation in size and/or the use of multiple wintering grounds (the latter is also supported by observed multiple core areas during isothermal conditions for 12 fish). Thus, for the autumn mix period of our study, travel to different overwintering areas seem to be contributing to the larger home range area sizes, and we suspect that inter-individual variation plays an important role.

Home range size is often positively correlated to the number of home range cores observed and while this is generally true in this study as well, it was not always so, further suggesting the existence of inter-individual variation. For example, ID 16862 had a single core during the stratified period and a home range of 91 km^2, while ID 16853 had four cores and a home range of 14.7 km^2 during the same period. Multiple home range cores are not unusual, as many species are known to move between areas based on prey patch profitability. However, this is an especially interesting finding for the stratified period, when cores are located both in the shallower Kingston Basin and in the deeper main basin. Based on data during this period, temperatures at depths *c.* 20–25 m can fluctuate greatly (by *c.* 15°C) within days, and reach temperatures considered suboptimal for lake trout (i.e. >15°C; Olson et al., 1988). This implies that shallower areas (approx. <25 m) during the stratified period are likely to be avoided by lake trout, and deeper areas would provide more suitable cooler and stable environment, although frequent short movements into these shallower areas to forage are possible. This is supported by the observations of Olson et al. (1988) and Raby et al. (2020) and their suggestion of individuals probably remaining near and below the thermocline, and may be a plausible explanation for the occurrence of cores in the two areas of the lake during this period. Thus, while it seems like some fish move from one area in the eastern basin to another possibly in response to temperature fluctuations, the majority remain distributed within the main basin. Overall, our observations of large variation in home range sizes and the number of cores imply the presence of inter-individual differences.

A single lake trout (out of 24) made a cross-lake movement from the eastern to the western basin of Lake Ontario (ID 16869), providing further evidence of inter-individual variation. Also, this is evidence that the eastern and western populations are not entirely spatially segregated. Given the lack of coverage for the majority of the main basin, we are unable to estimate how far other individuals may venture into this region during isothermal conditions. However, 16 (of 24) individuals were continuously detected around the Kingston Basin during that isothermal period, suggesting that this extensive movement behaviour is probably not common for lake trout. The drivers behind and significance of this cross-lake movement are not clear at present. A mark–recapture study done in Lake Michigan found that lake trout remained within a 80-km radius (Schmalz et al., 2002). However, Rybicki (1990) showed that other lake trout in Lake Michigan made cross-lake movements of 120 km. The distance travelled by our lake trout from Duck-Galloo Ridge to the mouth of the Niagara River was >200 km, which is greater than the distances reported by the above-mentioned studies. It should be noted that this one individual in our study, apart from this cross-lake movement, had behaviour similar to the majority of the tagged individuals with stratified home range exclusively in the main basin. Thus, while we observed variation in the spatial distribution among some lake trout during stratification, we believe that others may exhibit inter-individual variation in regard to exploratory behaviour.

On a broader scale, inter-individual variation is an important consideration for rehabilitation or reintroduction of species, because it provides the population with potential to use multiple habitats, aid in reestablishment efforts through adaptability, and perhaps even increase the impact of their function in the ecosystem. In this study, the home range sizes between seasons were not statistically different, suggesting that observed inter-individual variation in home range location was a preference rather than a population level response to local conditions. The potential of fish using multiple habitats is seen in our study with fish occupying both deeper and shallower basins to various extents throughout all seasons, suggesting wide use of available and/or more profitable resources. Another major implication of such variation is related to the function a species has in the ecosystem. Lake trout, in particular, is considered key to the cycling of energy between offshore and nearshore zones (Ives et al., 2019; Ryder & Kerr, 1990). Considering our results, we could deduce that energy cycling is temporally correlated to the movement of the species from offshore (main basin) to nearshore (Kingston Basin) and vice versa. Thus, seasonal distribution variation between individuals may indicate that some play a larger and/or slightly different role from others. For example, while most individuals link the nearshore and offshore in the spring, some individuals provide a link during summer stratification, and others may do so during isothermal conditions. Thus, our results underline the key role of inter-individual variation in species reintroduction efforts, and this being a crucial component when focus is on improving ecosystem function.

5 | CONCLUSIONS

The existence of inter-individual variation in the distribution and movement behaviour of populations, as observed here for lake trout, has important implications for predicting the effects of increasing water temperatures driven by climate change on species distributions and their bioenergetics, the fit and potential function of reintroduced animals in the ecosystem, as well as, better understanding of overall lake ecosystem function. This study also accentuates the importance of selecting for behavioural variation among stocked individuals as a key consideration for other species rehabilitations in ecosystems with a variety of habitats. Given the above, our results inform not only on the Lake Ontario and lake trout ecology but would also be useful for informing decision-making across all Laurentian Great Lakes, other freshwater ecosystems, and other species undergoing rehabilitation or reintroduction.

Future studies should consider incorporating environmental data into study designs, depth- and/or temperature-sensing acoustic tags, and metrics to assess competition with other species. Identification of strain of tagged fish would allow for detailed interpretation of plasticity in observed behaviours and whether there is evidence of an adaptive or genetic basis. Taken together, this information would provide major clues as to the drivers of the behaviours and selection of habitat, and identify constraints to species rehabilitation both currently and under potential climate change scenarios.

ACKNOWLEDGMENTS

The use of experimental animals complied with the Canadian animal welfare laws, guidelines and policies as approved by the University of Windsor Animal Care Committee (AUPP 18_11) and the OMNRF (Animal Use Protocol #135). A.T.F. and T.B.J. conceived and designed the study, contributed to manuscript writing and editing; S.V.I. helped design the study, performed the analysis, wrote the manuscript; B.M. helped with and coordinated field work and contributed to the conception of the study and manuscript editing. The authors would like to extend thanks to NYSDEC (Captain Alan Fairbanks, Jana Lantry, Michael Connerton, Nick Massa, Gaylor Massia), OMNRF (Al MacIntosh, Jeff Buckley), and USGS (Stacey Furgal) for assistance in netting and tagging the fish, and the OMNRF, DFO and USFWS vessel crews for servicing and downloading the acoustic arrays. Financial support was received through the Canada-Ontario Agreement on Great Lakes Water Quality and Ecosystem Health to T.B.J., ATF CRC grant, and scholarships to S.V.I. from University of Windsor and NSERC.

CONFLICT OF INTEREST

The authors state that no conflict of interest exists, such as relationship or interest that may be perceived as influencing their objectivity. All work undertaken is in conformity with any and all legal requirements, including animal welfare, and to the Journal's policy.

DATA AVAILABILITY STATEMENT

Data from this project has not been made available or shared due to it still undergoing analyses for other projects.

ORCID

Silviya V. Ivanova https://orcid.org/0000-0003-2886-8533

Aaron T. Fisk https://orcid.org/0000-0002-4208-4068

REFERENCES

Adlerstein, S. A., Rutherford, E. S., Claramunt, R. M., Clapp, D. F., & Clevenger, J. A. (2008). Seasonal movements of Chinook salmon in Lake Michigan based on tag recoveries from recreational fisheries and catch rates in gill-net assessments. *Transactions of the American Fisheries Society*, *137*(3), 736–750. https://doi.org/10.1577/T07-122.1

Begon, M., Townsend, C. R., & Harper, J. L. (2006). *Ecology – From individuals to ecosystems* (4th ed.). Blackwell Publishing.

Bergstedt, R. A., & O'Gorman, R. (1989). Distribution of alewives in southeastern Lake Ontario in autumn and winter: A clue to winter mortalities. *Transactions of the American Fisheries Society*, *118*, 687–692. https://doi.org/10.1577/1548-8659(1989)118<0687

Calenge, C. (2006). The package adehabitat for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modeling*, *197*, 516–519.

Carlson, A. R., & Siefert, R. E. (1974). Effects of reduced oxygen on the embryos and larvae of lake trout (*Salvelinus namaycush*) and largemouth bass (*Micropterus salmoides*). *Journal of the Fisheries Research Board of Canada*, *31*(4), 1393–1396. https://doi.org/10.1139/f74-165

Casselman, J. M., & Lewis, C. A. (1996). Habitat requirements of northern pike (*Esox lucius*). *Canadian Journal of Fisheries and Aquatic Sciences*, *53*(Suppl. 1), 161–174.

Christie, W. J. (1972). Lake Ontario: Effects of exploitation, introductions, and eutrophication on the salmonid community. *Journal Fisheries Research Board of Canada*, *29*, 913–929.

Cline, T. J., Bennington, V., & Kitchell, J. F. (2013). Climate change expands the spatial extent and duration of preferred thermal habitat for Lake Superior fishes. *PLoS One*, *8*(4), e62279. https://doi.org/10.1371/journal.pone.0062279

Colborne, S. F., Rush, S. A., Paterson, G., Johnson, T. B., Lantry, B. F., & Fisk, A. T. (2016). Estimates of lake trout (*Salvelinus namaycush*) diet in Lake Ontario using two and three isotope mixing models. *Journal of Great Lakes Research*, *42*, 695–702. https://doi.org/10.1016/j.jglr.2016.03.010

Colby, P. J. (1973). Response of the alewives, *Alosa pseudoharengus*, environmental change. In E. Chavin (Ed.), *Responses of fish to environmental changes* (pp. 163–198). Thomas Springfield.

Collingsworth, P. D., Bunnell, D. B., Murray, M. W., Kao, Y. C., Feiner, Z. S., Claramunt, R. M., … Ludsin, S. A. (2017). Climate change as a long-term stressor for the fisheries of the Laurentian Great Lakes of North America. *Reviews in Fish Biology and Fisheries*, *27*(2), 363–391. https://doi.org/10.1007/s11160-017-9480-3

DFO (2016). *Species at risk act management plan for the deepwater sculpin (*Myoxocephalus thompsonii*) in Canada (Great Lakes-Western St. Lawrence populations) deepwater sculpin [proposed]*.

Dietrich, J. P., Morrison, B. J., & Hoyle, J. A. (2006). Alternative ecological pathways in the eastern Lake Ontario food web—round goby in the diet of lake trout. *Journal of Great Lakes Research*, *32*(2), 395–400. https://doi.org/10.3394/0380-1330(2006)32[395:AEPITE]2.0.CO;2

Evans, D. O. (2007). Effects of hypoxia on scope-for-activity and power capacity of lake trout (*Salvelinus namaycush*). *Canadian Journal of Fisheries and Aquatic Sciences*, *64*(2), 345–361. https://doi.org/10.1139/f07-007

Fieberg, J., & Kochanny, C. O. (2005). Quantifying home-range overlap: The importance of the utilization distribution. *Journal of Wildlife Management*, *69*(4), 1346. https://doi.org/10.2193/0022-541X(2005)69

Findlay, R., Gennari, E., Cantor, M., & Tittensor, D. P. (2016). How solitary are white sharks: Social interactions or just spatial proximity? *Behavioral Ecology and Sociobiology*, *70*(10), 1735–1744. https://doi.org/10.1007/s00265-016-2179-y

Fitzsimons, J. D. (1995). Assessment of lake trout spawning habitat and egg deposition and survival in Lake Ontario. *Journal of Great Lakes Research*, *21*(Suppl. 1), 337–347. https://doi.org/10.1016/S0380-1330(95)71108-X

Fitzsimons, J. D., Brown, S. B., Honeyfield, D. C., & Hnath, J. G. (1999). A review of early mortality syndrome (EMS) in Great Lakes salmonids: Relationship with thiamine deficiency. *Ambio*, *28*(1), 9–15.

Garside, E. T. (1959). Some effects of oxygen in relation to temperature on the development of lake trout embryos. *Canadian Journal of Zoology*, *37*(5), 689–698. https://doi.org/10.1139/z59-069

Goodyear, C. S., Edsall, T. A., Ormsby Dempsey, D. M., Moss, G. D., & Polanski, P. E. (1982). Atlas of the spawning and nursery areas of Great Lakes fishes. In *US Fish and Wildlife Service, FWS/OBS-82/52*.

Guzzo, M. M., Blanchfield, P. J., Chapelsky, A. J., & Cott, P. A. (2016). Resource partitioning among top-level piscivores in a sub-Arctic lake during thermal stratification. *Journal of Great Lakes Research*, *42*(2), 276–285. https://doi.org/10.1016/j.jglr.2015.05.014

Hansen, M. J. (1999). Lake trout in the Great Lakes: Basinwide stock collapse and binational restoration. In W. W. Taylor, & C. P. Ferreri (Eds.), *Great Lakes fisheries policy and management: A binational perspective* (pp. 417–454). Michigan State University Press.

Hiruki, L. M., Schwartz, M. K., & Boveng, P. L. (1999). Hunting and social behaviour of leopard seals (*Hydrurga leptonyx*) at Seal Island, South Shetland Islands, Antarctica. *Journal of Zoology*, *249*(1), 97–109. https://doi.org/10.1017/S0952836999009097

Holden, J. P. (2019). *Status of Lake Trout in Ontario Waters of Lake Ontario*. Ontario Ministry of Natural Resources and Forestry, Lake Ontario Management Unit, Picton, Ontario, Canada. Lake Ontario Assessment Report LOA 19.03. https://doi.org/10.13140/RG.2.2.12824.01288

Hoyle, J. A., Holden, J. P., & Yuille, M. J. (2017). Diet and relative weight in migratory walleye (*Sander vitreus*) of the Bay of Quinte and eastern Lake Ontario, 1992–2015. *Journal of Great Lakes Research*, *43*(5), 846–853. https://doi.org/10.1016/j.jglr.2017.01.013

Hunter, E., Metcalfe, J. D., & Reynolds, J. D. (2003). Migration route and spawning area fidelity by North Sea plaice. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *270*(1529), 2097–2103. https://doi.org/10.1098/rspb.2003.2473

Hurlbert, S. H. (1978). The measurement of niche overlap and some relatives. *Ecology*, *59*, 67–77. https://doi.org/10.2307/1936632

Ives, J. T., McMeans, B. C., McCann, K. S., Fisk, A. T., Johnson, T. B., Bunnell, D. B., … Muir, A. M. (2019). Food-web structure and ecosystem function in the Laurentian Great Lakes—Toward a conceptual model. *Freshwater Biology*, *64*(1), 1–23. https://doi.org/10.1111/fwb.13203

Jagielo, T., Hoffmann, A., Tagart, J., & Zimmermann, M. (2003). Demersal groundfish densities in trawlable and untrawlable habitats off Washington: Implications for the estimation of habitat bias in trawl surveys. *Fishery Bulletin*, *101*(3), 545–565.

Kawaguchi, T., & Desrochers, A. (2018). A time-lagged effect of conspecific density on habitat selection by snowshoe hare. *PLoS One*, *13*(1), e0190643. https://doi.org/10.1371/journal.pone.0190643

Kessel, S. T., Hussey, N. E., Crawford, R. E., Yurkowski, D. J., O'Neill, C., & Fisk, A. T. (2015). Distinct patterns of Arctic cod (*Boreogadus saida*) presence and absence in a shallow high Arctic embayment, revealed across open-water and ice-covered periods through acoustic telemetry. *Polar Biology*, *39*(6), 1057–1068. https://doi.org/10.1007/s00300-015-1723-y

King, J. R., Shuter, B. J., & Zimmerman, A. P. (1999). Empirical links between thermal habitat, fish growth, and climate change. *Transactions of the American Fisheries Society*, *128*(4), 656–665. https://doi.org/10.1577/1548-8659(1999)128<0656:elbthf>2.0.co;2

Klinard N. V., Halfyard E. A., Matley J. K., Fisk A. T., Johnson T. B. (2019). The influence of dynamic environmental interactions on detection efficiency of acoustic transmitters in a large, deep, freshwater lake. *Animal Biotelemetry*, *7*(1), 1–17. https://doi.org/10.1186/s40317-019-0179-1

Landsman, S. J., Nguyen, V. M., Gutowsky, L. F. G., Gobin, J., Cook, K. V., Binder, T. R., … Cooke, S. J. (2011). Fish movement and migration studies in the Laurentian Great Lakes: Research trends and knowledge gaps. *Journal of Great Lakes Research*, *37*(2), 365–379. https://doi.org/10.1016/j.jglr.2011.03.003

Lantry, B. F., Lantry, J. R., & Connerton, M. J. (2018). Lake trout rehabilitation in Lake Ontario, 2017. In *NYSDEC Lake Ontario Annual Report, Bureau of Fisheries, Lake Ontario Unit and St. Lawrence River Unit to the to the Great Lake Fishery Commission's Lake Ontario Committee*. New York State Department of Environmental Conservation.

Luo, M. K., Madenjian, C. P., Diana, J. S., Kornis, M. S., & Bronte, C. R. (2019). Shifting diets of lake trout in northeastern Lake Michigan. *North American Journal of Fisheries Management*, *39*(4), 793–806. https://doi.org/10.1002/nafm.10318

MacLean, J. A., Evans, D. O., Martin, N. V., & DesJardine, R. L. (1981). Survival, growth, spawning distribution, and movements of introduced and native lake trout (*Salvelinus namaycush*) in two inland Ontario Lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, *38*, 1685–1700. https://doi.org/10.1139/f81-217

Magnuson, J., Crowder, L., & Madvick, P. (1979). Temperature as an ecological resource. *American Zoologist*, *19*, 331–343.

Magnuson, J., Meisner, J. D., & Hill, D. K. (1990). Potential changes in the thermal habitat of Great Lakes fish after global climate warming. *Transactions of the American Fisheries Society*, *119*, 254–264. https://doi.org/10.1577/1548-8659(1990)119<0254

Miller, P. J. (1986). Gobiidae. In P. J. P. Whitehead, M. L. Bauchot, J. C. Hureau, J. Nielsen, & E. Tortonese (Eds.), *Fishes of the north-eastern Atlantic and the Mediterranean* (Vol. *III*, pp. 1019–1095). UNESCO.

Morbey, Y., Addison, P., Shuter, B. J., & Vascotto, K. (2006). Within-population heterogeneity of habitat use by lake trout *Salvelinus namaycush*. *Journal of Fish Biology*, *69*(6), 1675–1696. https://doi.org/10.1111/j.1095-8649.2006.01236.x

Mumby, J. A., Larocque, S. M., Johnson, T. B., Stewart, T. J., Fitzsimons, J. D., … Fisk, A. T. (2018). Diet and trophic niche space and overlap of Lake Ontario salmonid species using stable isotopes and stomach contents. *Journal of Great Lakes Research*, *44*(6), 1383–1392. https://doi.org/10.1016/j.jglr.2018.08.009

Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., & Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(49), 19052–19059. https://doi.org/10.1073/pnas.0800375105

Negus, M. T., Schreiner, D. R., Halpern, T. N., Schram, S. T., Seider, M. J., & Pratt, D. M. (2008). Bioenergetics evaluation of the fish community in the western arm of lake superior in 2004. *North American Journal of Fisheries Management*, *28*(6), 1649–1667. https://doi.org/10.1577/M07-176.1

O'Gorman, R., Mills, E. L., & DeGisi, J. (1991). Use of zooplankton to assess the movement and distribution of alewife (*Alosa pseudoharengus*) in south-central Lake Ontario in spring. *Canadian Journal of Fisheries & Aquatic Sciences*, *48*, 2250–2257.

Olson, R. A., Winter, J. D., Nettles, D. C., & Haynes, J. M. (1988). Resource partitioning in summer by salmonids in south-central Lake Ontario. *Transactions of the American Fisheries Society*, *117*(6), 552–559.

Plumb, J. M., & Blanchfield, P. J. (2009). Performance of temperature and dissolved oxygen criteria to predict habitat use by lake trout (*Salvelinus namaycush*). *Canadian Journal of Fisheries & Aquatic Sciences*, *66*, 2011–2023. https://doi.org/10.1139/F09-129

Raby, G. D., Johnson, T. B., Kessel, S. T., Stewart, T. J., & Fisk, A. T. (2017). A field test of the use of pop-off data storage tags in freshwater fishes. *Journal of Fish Biology*, *91*(6), 1623–1641. https://doi.org/10.1111/jfb.13476

Raby, G. D., Johnson, T. B., Kessel, S. T., Stewart, T. J., & Fisk, A. T. (2020). Pop-off data storage tags reveal niche partitioning between native and non-native predators in a novel ecosystem. *Journal of Applied Ecology*, *57*(1), 181–191. https://doi.org/10.1111/1365-2664.13522

Riley, S. C., Roseman, E. F., Nichols, S. J., O'Brien, T. P., Kiley, C. S., & Schaeffer, J. S. (2008). Deepwater demersal fish community collapse in Lake Huron. *Transactions of the American Fisheries Society*, *137*(6), 1879–1890. https://doi.org/10.1577/t07-141.1

Rush, S. A., Paterson, G., Johnson, T. B., Drouillard, K. G., Haffner, G. D., Hebert, C. E., … Fisk, A. T. (2012). Long-term impacts of invasive species on a native top predator in a large lake system. *Freshwater Biology*, *57*(11), 2342–2355. https://doi.org/10.1111/fwb.12014

Rybicki, R. W. (1990). *Growth, survival, and straying of three lake trout strains stocked in the refuge of northern Lake Michigan*. Michigan Department of Natural Resources, Fisheries Research Report No. 1977.

Ryder, P. A., & Edwards, C. J. (Eds.) (1985). *A conceptual approach for the application of biological indicators of ecosystem quality in the Great Lakes Basin*. Report to the Great Lakes Science Advisory Board, International Joint Commission.

Ryder, R. A., & Kerr, S. R. (1990). Harmonic communities in aquatic ecosystems: A management perspective. In L. T. Van Densen, B. Teinmetz, & R. H. Hughes (Eds.), *Management of freshwater fisheries. Proceedings of the EIFAC symposium, Göteborg, Sweden, May 31–June 3, 1988* (pp. 594–623). Wageningen, Netherlands: Pudoc.

Schmalz, P. J., Hansen, M. J., Holey, M. E., McKee, P. C., & Toneys, M. L. (2002). Lake trout movements in northwestern Lake Michigan. *North American Journal of Fisheries Management*, *22*(3), 737–749. https://doi.org/10.1577/1548-8675(2002)022<0737:LTMINL>2.0.CO;2

Schneider, C. P., Kolenosky, D. P., & Goldthwaite, D. B. (1983). *A joint plan for the rehabilitation of lake trout in Lake Ontario*. GLFC.

Sellers, T. J., Parker, B. R., Schindler, D. W., & Tonn, W. M. (1998). Pelagic distribution of lake trout (*Salvelinus namaycush*) in small Canadian Shield lakes with respect to temperature, dissolved oxygen, and light. *Canadian Journal of Fisheries and Aquatic Sciences*, *55*(1), 170–179. https://doi.org/10.1139/f97-232

Shuter, B. J., & Lester, N. P. (2004). Climate change and sustainable lake trout exploitation: Predictions from a regional life history model. In J. Gunn, R. Steedman, & R. Ryder (Eds.), *Boreal shield watersheds: Lake trout ecosystems in a changing environment* (pp. 281–291). Lewis/CRC Press.

Simpfendorfer, C. A., Heupel, M. R., & Hueter, R. E. (2002). Estimation of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movements. *Canadian Journal of Fisheries and Aquatic Sciences*, *32*, 23–32. https://doi.org/10.1139/F01-191

Smith, S. H. (1968). Species succession and fishery exploitation in the Great Lakes. *Journal of the Fisheries Research Board of Canada*, *25*, 667–693.

Stewart, D. J., Weininger, D., Rottiers, D. V., & Edsall, T. A. (1983). An energetics model for lake trout, *Salvelinus namaycush*: Application to the Lake Michigan population. *Canadian Journal of Fisheries and Aquatic Sciences*, *40*(6), 681–698. https://doi.org/10.1139/f83-091

Stewart, T., Todd, A., & LaPan, S. (2017). *Fish community objectives for Lake Ontario*. Retrieved from www.glfc.org/pubs/FisheryMgmtDocs/Fmd17-01.pdf

Thibodeau, M. L., & Kelso, J. R. M. (1990). An evaluation of putative lake trout (*Salvelinus namaycush*) spawning sites in the Great Lakes. *Canadian technical report of fisheries and aquatic sciences*, *1793*.

Thorson, J. T., Fonner, R., Haltuch, M. A., Ono, K., & Winker, H. (2017). Accounting for spatiotemporal variation and fisher targeting when estimating abundance from multispecies fishery data. *Canadian Journal of Fisheries & Aquatic Sciences*, *74*, 1794–1807. https://doi.org/10.1139/cjfas-2015-0598

Vander Zanden, M. J., Casselman, J. M., & Rasmussen, J. B. (1999). Stable isotope evidence for food web consequences of species invasions in lakes. *Nature*, *401*, 464–467. https://doi.org/10.1038/46762

Walker, N. D., Maxwell, D. L., Le Quesne, W. J. F., & Jennings, S. (2017). Estimating efficiency of survey and commercial trawl gears from comparisons of catch-ratios. *ICES Journal of Marine Science*, *74*(5), 1448–1457. https://doi.org/10.1093/icesjms/fsw250

Walsh, M. G., Dittman, D. E., & O'Gorman, R. (2007). Occurrence and food habits of the round goby in the profundal zone of southwestern Lake Ontario. *Journal of Great Lakes Research*, *33*(1), 83–92. https://doi.org/10.3394/0380-1330(2007)33

Walsh, S. J. (1996). Efficiency of bottom sampling trawls in deriving survey abundance indices. *Science Council Studies*, *28*, 9–24.

Weidel, B. C., Walsh, M. G., Connerton, M. J., & Holden, J. (2017). *Trawl-based assessment of Lake Ontario pelagic prey fishes including alewife and rainbow smelt*. NYSDEC.

White, E., Mihoff, M., Jones, B., Bajona, L., & Halfyard, E. (2014). *White-Mihoff false filtering tool*.

Wilson, E. (1905). On the whales, seals and birds of Ross Sea and South Victoria Land. In R. Scott (Ed.), *The voyage of the 'discovery'* (vol. *II*, pp. 469–494). Charles Scribner's Sons.

Yuille, M. J., Fisk, A. T., Stewart, T., & Johnson, T. B. (2015). Evaluation of Lake Ontario salmonid niche space overlap using stable isotopes. *Journal of Great Lakes Research*, *41*(3), 934–940. https://doi.org/10.1016/j.jglr.2015.05.011

Zhong, Y., Notaro, M., & Vavrus, S. J. (2019). Spatially variable warming of the Laurentian Great Lakes: An interaction of bathymetry and climate. *Climate Dynamics*, *52*(9–10), 5833–5848. https://doi.org/10.1007/s00382-018-4481-z

How to cite this article: Ivanova SV, Johnson TB, Metcalfe B, Fisk AT. Spatial distribution of lake trout (*Salvelinus namaycush*) across seasonal thermal cycles in a large lake. *Freshwater Biology*. 2020;00:1–13. https://doi.org/10.1111/fwb.13665