Received: 24 February 2023 | Revised: 26 May 2023 | Accepted: 6 June 2023

DOI: 10.1002/tafs.10430

ARTICLE

Seasonal spatial ecology of Lake Trout in Lake Erie

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Abstract

Objective: Lake Trout *Salvelinus namaycush* are native coldwater apex predators that play an important role in maintaining ecosystem functionality and diversity in the Laurentian Great Lakes. Following population collapses, rehabilitation efforts were widely initiated in the Great Lakes to reestablish self-sustaining Lake Trout populations. Lake Erie may pose a challenge to these rehabilitation efforts due to limited availability of appropriate oxythermal habitat. Our goal was to investigate seasonal habitat use of adult Lake Trout in Lake Erie to inform management and rehabilitation efforts.

Methods: We used acoustic telemetry in Lake Erie, which was equiped with a lake-wide acoustic receiver grid, to quantify Lake Trout seasonal region occupancy, dispersal distances, bottom depth occupancy, space use extent, and space use overlap.

Result: We found that 32% of fish tagged in the eastern basin and all fish from the western basin dispersed more than 100 km from their tagging location, which represents a greater proportion of the population moving long distances than what has been previously documented in the Great Lakes. During stratification, Lake Trout were detected almost exclusively in the offshore eastern basin in areas where water depth exceeded 25 m. During nonstratified seasons, fish used other regions of the lake, occupying areas of highly variable depths. During fall, most fish tagged in the eastern basin occupied habitat along the southern shore of the eastern basin. Fish tagged in the western basin returned to this region in the fall of subsequent years despite occupying the offshore eastern basin during stratification and having depth occupancy, home range size, and overlap similar to that of eastern basin-tagged fish. Fish size was positively correlated with receiver depth during winter and spring, and with home range overlap during spring and summer.

Conclusion: The results of this study can begin to inform management decisions regarding stocking locations, harvest regulations, and habitat restoration to facilitate the continued rehabilitation of this important native species.

KEYWORDS

acoustic telemetry, dispersal, habitat use, home range, migration, movement ecology

INTRODUCTION

Understanding the movement ecology of fish populations is important for effective management of exploited, threatened, and invasive species (Cooke et al. 2016). Recent advancements in tracking technologies, particularly acoustic telemetry, have greatly expanded the ability of researchers and managers to incorporate movement ecology into management policies and actions (Crossin et al. 2017; McGowan et al. 2017; Hays et al. 2019; Matley et al. 2022). Information on movement patterns is particularly beneficial for management of species that cross jurisdictional boundaries during movement events. For example, Harrison et al. (2018) emphasized the need for interagency cooperation by revealing seasonal movement patterns and multi-jurisdictional residency of several marine predators, including species of tuna, sharks, pinnipeds, seabirds, and sea turtles. Numerous studies have highlighted the importance of applying movement ecology for sustainable management. For example, movement data informed decisions to prohibit harvest and protect habitat of Lemon Sharks *Negaprion brevirostris* on Florida's Atlantic coast (Kessel et al. 2014; Reyier et al. 2014; Brooks et al. 2019). In Lake Erie, successful management of Walleye *Sander vitreus*, which encounter different harvest regulations during annual migrations across state and provincial boundaries, has greatly benefited from knowledge of the species' spatial ecology (Vandergoot et al. 2019; Matley et al. 2020).

The Lake Trout *Salvelinus namaycush* is an apex predator of high management and conservation priority in North America's Laurentian Great Lakes (hereafter, "Great Lakes"; Bronte et al. 2008; Muir et al. 2013; Lake Erie Committee 2021). The Lake Trout is a coldwater species that is physiologically constrained to temperatures less than 15°C and dissolved oxygen concentrations greater than $4\,\mathrm{mgL}^{-1}$ (Evans et al. 1991), with a preference for temperatures less than 10°C and dissolved oxygen greater than $6\,\mathrm{mgL}^{-1}$ (Dillon et al. 2003). Where abundant suitable oxythermal habitat is available, prey availability influences Lake Trout movement patterns and habitat selection (Binder et al. 2021). Lake Trout typically spawn in late fall, although some spring-spawning populations exist (Bronte 1993). Large female Lake Trout produce more eggs and spawn later in the year than smaller females (Martin and Olver 1980; Casselman 1995). Spawning later often coincides with cooler water temperatures, which results in increased offspring survival (Casselman 1995) and makes large females highly important for rehabilitation efforts. Spawning site fidelity has been observed in many Lake Trout populations of both wild- and hatchery-origin fish (Krueger et al. 1986; Bronte et al. 2007; Binder et al. 2016; Pinheiro et al. 2017). Additionally, recent studies suggest that Lake Trout may exhibit fidelity to particular areas during nonspawning periods (Morbey et al. 2006; Binder et al. 2017; Riley et al. 2018). Experimental learning and memory may play a key role in repeated migration patterns of individuals (Binder et al. 2021). Long-distance dispersal (>100 km) has been noted in some Great Lakes populations (Schmalz et al. 2002; Kapuscinski et al. 2005; Riley et al. 2018; Ivanova et al. 2021) but is seemingly rare, as most studies have found that most Lake Trout disperse less than 100 km from tagging sites (Schmalz et al. 2002; Kapuscinski et al. 2005; Bronte et al. 2007; Riley et al. 2018). Movements of Lake Trout in the Great Lakes tend to follow the shoreline, rarely crossing deep, open-water areas (Pycha et al. 1965; Krueger et al. 1986; Bronte et al. 2007).

Impact statement

This study provides the first description of lakewide, year-round spatial ecology of Lake Trout in the Great Lakes. We found that Lake Trout in Lake Erie were restricted to offshore areas of the eastern basin during summer and congregated along the southern shore of the eastern basin during fall, but they dispersed widely during spring.

Although Lake Trout were historically abundant in Lake Erie, they were extirpated from the lake by the 1960s due to a combination of overfishing, predation by invasive Sea Lamprey *Petromyzon marinus*, and spawning habitat loss (Moenig 1970; Hartman 1973; Muir et al. 2013), and they are presently the focus of a binational rehabilitation effort (Lake Erie Committee 2021). Reestablishment of a self-sustaining Lake Trout population in Lake Erie's oligotrophic eastern basin has been deemed important for supporting ecosystem stability (Coldwater Task Group 2022). A healthy Lake Trout population has the potential to benefit Lake Whitefish *Coregonus clupeaformis*, which are currently at historically low abundance, and Cisco *C. artedi*, which are currently extirpated but represent a potential candidate for rehabilitation in Lake Erie (Oldenburg et al. 2007; Bronte et al. 2017; Schmitt et al. 2020; Coldwater Task Group 2022). After several decades of population declines and subsequent extirpation, a Lake Trout stocking program was initiated on Lake Erie in 1980, with the goal of reestablishing a self-sustaining population (Cornelius et al. 1995; Markham et al. 2008). Hatchery-reared yearling Lake Trout have been stocked in Lake Erie's eastern basin (i.e., New York, Pennsylvania, and Ontario jurisdictional waters) proximal to putative historic spawning reefs, and small cohorts of fish have also been stocked in the western and central basins within Ohio waters since 2012 (Lake Erie Committee 2021). Currently, the population is primarily comprised of three hatchery strains originating from

Lake Champlain (Vermont), the Finger Lakes (e.g., Seneca Lake, New York), and a small contribution from Slate Island (Lake Superior, Ontario; Coldwater Task Group 2022). While stocking efforts over the past six decades have successfully established a population of sexually mature fish, there has been little evidence of wild reproduction, in contrast to observations in the other Great Lakes (i.e., Lakes Huron, Michigan, Ontario, and Superior; Muir et al. 2013). Although some evidence of natural recruitment has been found (Fitzsimons and Williston 2000; Ludsin et al. 2004; Markham et al. 2022), the Lake Trout population is believed to be sustained almost entirely by stocked fish (Lake Erie Committee 2021; Coldwater Task Group 2022).

Restoration of Lake Erie coldwater fish species may be hindered by reduced habitat availability imposed by anthropogenic nutrient loading within the geomorphological constraints of the lake (Francis et al. 2020). Lake Erie consists of three basins: (1) the shallow (mean depth = 7.4 m), isothermal, eutrophic western basin; (2) the mesotrophic central basin (mean depth = 18.5 m), which stratifies on an annual basis with a very narrow (<2 m) hypolimnion that often becomes anoxic; and (3) the deep (mean depth = 24.4 m; maximum depth = 64 m), oligotrophic eastern basin, which stratifies on an annual basis and provides cold, highly oxygenated habitat year-round (<10°C and >4 mg L^{-1}; Figure 1A; Schertzer et al. 1987; Bolsenga and Herdendorf 1993). Historic fishery harvest and population assessment records indicate that Lake Trout and other coldwater species (e.g., Burbot *Lota lota*, Cisco, and Lake Whitefish) primarily used the eastern basin year-round, including to spawn along the shoreline during late fall (<15 m). However, a smaller population contingent of Lake Trout was

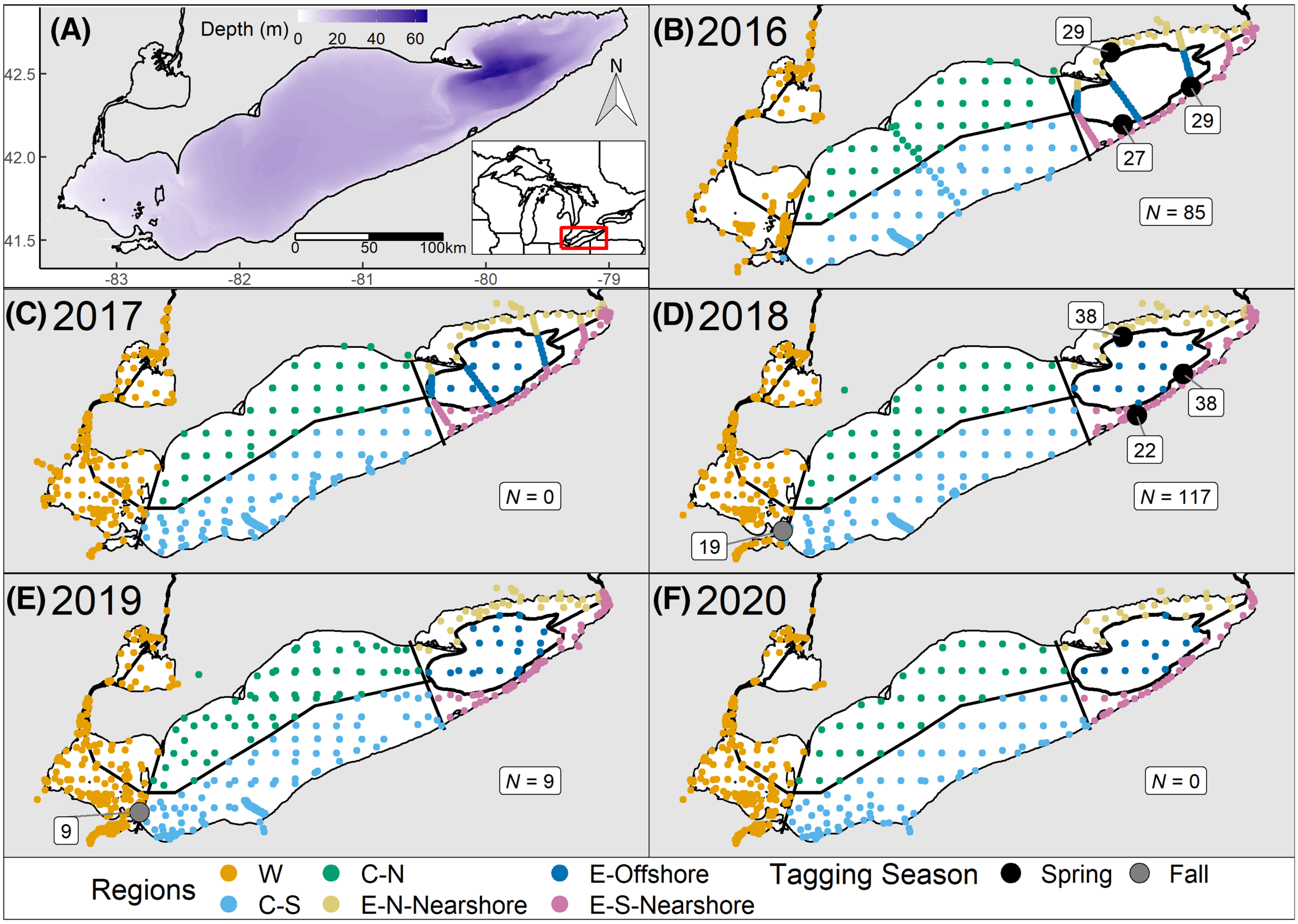

FIGURE 1 (A) Bathymetric map of the study area, Lake Erie, with inset depicting the North American Laurentian Great Lakes. (B)–(F) Lake Trout tagging locations and acoustic receiver locations are shown for individual years during the study period (2016–2020). Solid black lines indicate region divisions for consideration in residency index analyses. Small points indicate acoustic receiver locations, with color indicating the region (orange = western [W]; light blue = central south [C-S]; light green = central north [C-N]; beige = eastern north nearshore [E-N-Nearshore]; dark blue = eastern offshore [E-Offshore]; pink = eastern south nearshore [E-S-Nearshore]). Tagging release locations are represented by large black (spring tagging event) or gray (fall tagging event) circles and are labeled with the number of fish released at each location. Tagging events took place in the eastern basin in 2016 (*N* = 85) and 2018 (*N* = 98) and in the western basin in 2018 (*N* = 19) and 2019 (*N* = 9).

believed to use the western basin of Lake Erie and the Detroit River during the fall to spawn (Moenig 1970; Cornelius et al. 1995). Despite annual population assessment surveys since 1992 (Coldwater Task Group 2022), little is known about habitat use and spatiotemporal movement patterns of contemporary Lake Trout populations in Lake Erie, particularly outside the summer stratification period (Markham et al. 2008; Lake Erie Committee 2021).

The primary aim of this study was to describe the seasonal habitat use of adult Lake Trout in Lake Erie to inform management and rehabilitation. Acoustic telemetry tracking technology was used to address the following questions: (1) "How does habitat use by Lake Trout in Lake Erie vary spatially and temporally?"; (2) "Do distinct spawning season aggregations exist in the eastern and western basins of Lake Erie, and do these populations exhibit different seasonal movement patterns?"; and (3) "Is Lake Trout seasonal habitat use related to fish size?" A more complete understanding of how Lake Trout use habitat within and across jurisdictional boundaries can allow for appropriate levels of coordination in harvest regulations and habitat restoration or protection for managing the population. The movement behavior of fish during fall may suggest where stocking has been successful at creating a mature population, and this can inform future stocking efforts. Additionally, an understanding of behavior and spatial ecology is foundational to designing future studies that explicitly inform management action relating to stocking practices. Potential size-based differences in behavior could inform changes to harvest regulations or habitat protections targeted toward protecting large individuals to facilitate successful reproduction.

METHODS

Fish capture and tagging

Lake Trout for this study were collected during spring (eastern basin) and fall (western basin) between 2016 and 2019. In the eastern basin, Lake Trout were collected with overnight bottom-set gill nets (monofilament mesh, bar measure ranging from 10.2 to 25.4 cm) in May 2016 and 2018 (Lake Trout $n = 85$ and 98, respectively) in Ontario, New York, and Pennsylvania waters of Lake Erie (Table 1; Figure 1B,D). We collected Lake Trout several months outside of presumed spawning periods (October–December) to maximize the likelihood of tagging fish from a variety of potential spawning aggregations. After capture, Lake Trout were held aboard research vessels operated by state, provincial, or federal fishery agencies; the fish were kept in recirculating tanks (378–576 L) supplied with fresh lake water until the tagging process could begin. Lake Trout were immersed for 180–300 s in a eugenol solution (20 mgL^{-1} AQUI-S 20E in New York and Pennsylvania or clove oil in Ontario) until reaching stage 4 anesthesia, which is characterized by a loss of equilibrium and a loss of response to external stimuli (Summerfelt and Smith 1990). Once anesthetized, each Lake Trout was transferred to a surgical v-board in the supine position, and its gills were irrigated with fresh lake water throughout the surgical procedure. An experienced surgeon implanted the acoustic transmitter (i.e., handling, surgery, and release) in accordance with standard protocols (Cooke et al. 2012; Use of Fishes in Research Committee 2014). A 20–25-mm incision was made through the coelomic cavity with a sterilized scalpel along the ventral midline, posterior to the pectoral fins. An acoustic transmitter sterilized in betadine was inserted into the coelom, and the incision was closed with two or three interrupted sutures (Ethicon PDS-II, size 2-0 monofilament). In addition to transmitter implantation, total length was recorded and an external loop tag (Lock-on TF-4; Floy Tag and Manufacturing) was inserted through the dorsal musculature toward the posterior edge of the dorsal fin using a hollow piercing needle. Each external loop tag had a unique identification number, a contact phone number, and the printed text "REWARD $100" to encourage reporting and return of the transmitter if the fish was harvested. Prior to release, fish were held in recirculating tanks supplied with fresh lake water until they regained equilibrium and exhibited the ability to undergo sustained movement following the protocols described by Raby et al. (2012).

Lake Trout from the western basin were obtained opportunistically from a commercial fishing operation in the nearshore (<10 m) area of Catawba Island, Ohio, during October 2018 and 2019 ($n = 19$ and 9, respectively; Table 1; Figure 1D,E). After capture, Lake Trout were transported to shore and held in tanks as described above. Lake Trout tagged in the western basin were immobilized with electrical current during the surgical procedure, similar to the method described by Dembkowski et al. (2021). Briefly, electrodes were wrapped around the dorsal musculature near the pectoral (anode) and anal (cathode) fins, with current continuously supplied during the surgical procedure. Once the fish was immobilized, an acoustic transmitter was surgically implanted by following the procedure described above. After surgery, the fish was measured, tagged with an external loop tag, and placed in a recirculating tank until it was deemed ready for release as described above.

Acoustic telemetry tracking

Acoustic transmitters (InnovaSea V16-4H; 158 dB; $n = 211$) were programmed to emit a unique 69-kHz

TABLE 1 Sample size summary of Lake Trout by Lake Erie tagging basin, year, and release location (Pennsylvania [PA]; Ontario [ON]; New York [NY]; Ohio [OH]). The following are listed for each year and location (see Figure 1): the number of fish tagged and released; the number of fish with valid detections after January 1, 2017 (see Data Analysis section in Methods); the average and range of total lengths at tagging (mm); the average number of detections per individual; and the number at large in the system as of January 1 in 2018, 2019, and 2020. A fish was considered at large if it was detected on or after January 1 of a given year. Yearly totals for eastern basin-tagged fish are in italics; basin totals are in bold.

Release year	Release location	Fish tagged	Fish detected	Length (mm); mean (range)	Average detections per fish	Number at large as of Jan 1		
						2018	2019	2020
Eastern basin								
2016	PA	27	24	727 (604–855)	39,395	21	20	17
	ON	29	22	725 (665–780)	38,020	17	17	16
	NY	29	23	722 (593–850)	28,108	19	16	15
	2016 total	*85*	*69*	*724 (593–855)*	*35,194*	*57*	*53*	*48*
2018	PA	22	22	718 (510–871)	31,815	–	21	21
	ON	38	24	753 (475–875)	22,926	–	21	17
	NY	38	36	761 (652–892)	31,379	–	34	32
	2018 total	*98*	*82*	*747 (475–892)*	*29,022*	–	*76*	*70*
Eastern basin total		**183**	**151**	**737 (475–892)**	**31,842**	**57**	**129**	**118**
Western basin								
2018	OH	19	17	690 (630–758)	19,100	–	17	13
2019	OH	9	8	704 (642–762)	9897	–	–	8
Western basin total		**28**	**25**	**695 (630–762)**	**16,155**	**–**	**17**	**21**

code at random time intervals between 60 and 180 s (120-s nominal delay). Acoustic receivers (InnovaSea VR2W, VR2TX, and VR2AR; 69 kHz) were deployed throughout Lake Erie in conjunction with other acoustic telemetry studies associated with the Great Lakes Acoustic Telemetry Observation System (GLATOS; Krueger et al. 2018). Receivers were deployed as either independent stations (i.e., designed to provide presence/absence information) or clustered stations (i.e., within close proximity of another receiver to better understand fine-scale movements) throughout the lake (Figure 1; Hussey et al. 2015; Kraus et al. 2018). Receivers were deployed annually in both nearshore and offshore areas to provide broad-scale coverage for describing fish movement, although the number and location of receivers varied throughout the study period (Figure 1). Lake Trout detections started immediately after release of the first cohort in May 2016; however, movement data used for this study were left-censored (i.e., early detections were excluded from analysis) to coincide with acoustic receiver deployment and coverage corresponding with the type of analysis performed (see Data Analysis section). Based on field trials conducted in the central and eastern basins of Lake Erie prior to the current study, we assumed that the acoustic transmitters had a detection range (i.e., >50% detection probability) of approximately 750 m (C. S. Vandergoot, unpublished data).

Description of seasons

To evaluate temporal differences in Lake Trout movement patterns, four seasons were defined based on modeled annual water temperature patterns. Season breaks were informed by modeled surface and bottom temperature estimates from a fixed position located in the middle of the eastern basin (42.5359193, −79.78226437) using the Great Lakes Operational Forecasting System (Chu et al. 2011). Seasons were defined as (1) spring: the period extending from when bottom temperatures increased past 2°C to when surface and bottom temperatures differed by more than 15°C (average = April 18–June 21; range = 51–87 days); (2) summer (i.e., stratification): the period extending from when surface and bottom temperatures differed by more than 15°C to when surface and bottom temperatures differed by less than 5°C (average = June 21–October 10; range = 104–119 days); (3) fall: the period extending from when surface and bottom temperatures differed by less than 5°C to when bottom temperatures decreased below 4°C (average = October 10–January 1; range = 80–100 days); and (4) winter: the period during which bottom temperatures remained between 4°C and 2°C (average = January 1–April 18; range = 74–125 days).

Data analysis

A common issue with acoustic telemetry detection data is the occurrence of false detections, which can arise from numerous factors (e.g., acoustic signal collision or misinterpretation) and potentially lead to biased results (Simpfendorfer et al. 2015). To remove false detections from the data set, we used the false_detections function from the R package glatos (Holbrook et al. 2022). Specifically, potential false detections were removed if the time separating subsequent detections at a single receiver exceeded 3600 s (30× the nominal delay of the tags; Pincock 2012). Lake Trout detection data were also filtered to identify and remove fish that were presumed to be dead. Fish were assumed dead if they were detected on a single receiver for longer than 3 months without being detected on another receiver during that period. When a fish was assumed to have died near a receiver ($n = 13$), all detections after the first detection at that receiver were removed from the data set to reduce the bias associated with including data observed from a dead fish (Klinard and Matley 2020). Fish were also assumed dead if they (1) were never observed on a receiver after release or (2) were not detected on any receiver for over 6 months and were not reported as being harvested. Filtering criteria were selected based on individual detection histories indicating that no fish was confirmed to be alive (i.e., mobile, detected on more than one receiver) after being detected on only one receiver continuously for more than 3 months or after going undetected for more than 6 months. During the study, 38 tagged fish were considered dead after being missing for more than 6 months. Fish that were defined as dead within 30 days posttagging ($n = 14$) were considered mortalities associated with the collection, handling, or tagging process, and all detections from these fish were removed from the analysis. Lastly, detection data were restricted to the period from January 1, 2017, to December 31, 2020, due to incomplete receiver coverage prior to 2017 (Figure 1B). After filtering, 176 fish (83% of the 211 fish released) with valid detections remained in the data set (Table 1). Of those fish, 44 died during the study period, 5 of which were reported as harvested by anglers. After a fish was released, the acoustic transmitter could cease working (transmitter failure) or could be expelled from the coelom of the fish; however, tag expulsion was not observed and is unlikely to have affected the results or conclusions from this study.

Detection data were analyzed using a regional residency index (RI), dispersal distance, return rate, home range, and receiver depth occupancy. Detections on receivers that were deployed between January 1, 2017, and December 31, 2020, were used to estimate RI, dispersal, and receiver depth occupancy, as these analyses rely on presence/absence information observed over broad geographic scales (Figure 1). Home range estimates (i.e., space use area estimates) were based on detections observed between January 1, 2018, and December 31, 2020, after the receiver grid array was deployed throughout the eastern basin (Figure 1; compare 2017 [panel C] versus 2018 [panel D] in the eastern basin).

Seasonal basin occupancy

The regional RI, defined as the number of days on which a fish was detected at a group of receivers of interest divided by the total number of days on which the fish was detected (Kessel et al. 2016), was used to quantify seasonal spatial presence or absence. Regions of interest were defined based on basin (western, central, or eastern), national waters (north or south of the Canada–U.S. boundary for the central and eastern basins), and depth (offshore [≥25 m] versus nearshore [<25 m] in the eastern basin). The combination of these factors produced six distinct regions: western basin, central basin north, central basin south, eastern basin north nearshore, eastern basin south nearshore, and eastern basin offshore (Figure 1). Regions were used to provide general, broad-scale occupancy trends while accounting for yearly changes in the receiver array.

Long-distance dispersal

Dispersal distance was used to quantify the distance traveled by all individuals. The dispersal distance of a detection was calculated as the straight-line distance between the release site and the location of the receiver using the distm function from the R package geosphere (Hijmans 2022). The maximum dispersal distance of each fish was summarized to quantify long-distance dispersal.

Western basin migrations

Site fidelity to the area where fish were tagged was evaluated for Lake Trout that were tagged during the fall in the western basin. Since all fish tagged in the western basin that were detected ($n = 25$) dispersed to the eastern basin after the spawning period, site fidelity was defined as detection within 50 km of the tagging site during fall seasons subsequent to tagging. During each fall in which a fish completed the migration to the western basin, migration time was calculated as the difference between the last detection in the eastern basin and the first detection within 50 km of the tagging site. Duration of stay was defined as the difference between the first and last detections within 50 km of the tagging site. Return migration time was defined as the difference between the last detection within 50 km of the tagging site and the first detection at a receiver in the eastern basin.

Depth occupancy

Since telemetry transmitters were not equipped with depth sensors, water depth at the receiver on which a fish was detected (i.e., bathymetric depth occupancy) was used as a proxy for fish depth. The actual depth that fish occupied within the water column was unknown. Seasonal bathymetric depth occupancy (hereafter, "depth occupancy"; m) estimates were calculated for fish that were detected at least 4 days in a season with a minimum of three observations per day to ensure that estimates would not be biased by few observations from few individuals.

Space use extent and space use overlap

Seasonal home ranges constructed for each tagged Lake Trout were used to quantify horizontal (i.e., two-dimensional by latitude and longitude) space use extent and space use overlap. To account for potential biases associated with time periods having a high number of detections in a short timeframe or in areas with fine-scale receiver coverage, centers of activity, which approximate animal locations within 30-min time intervals (Simpfendorfer et al. 2002; COA function from the R package VTrack; Campbell et al. 2012), were used as inputs rather than raw detection data. Individual seasonal home ranges were calculated from centers of activity using the kernel utilization distribution (KUD) at the 95% level with the kernelUD function from the R package adehabitatHR (Calenge 2006). The utilization distribution overlap index (UDOI; Fieberg and Kochanny 2005) was used to calculate seasonal space use sharing of individuals via the kerneloverlaphr function from adehabitatHR (Calenge 2006). The UDOI considers the overlap as well as the utilization distribution of two individuals to create a metric that is between 0 and 1 for uniformly distributed and less than complete (i.e., <100%) overlap; however, the metric can be greater than 1 if space use has a high degree of overlap in more heavily used areas. Seasonal overlap estimates were obtained for a fish by averaging pairwise overlap values between that individual and all others. To construct meaningful seasonal home range estimations, we required fish to have at least 10 centers of activity per season with detections ranging at least 5 days to be included in home range analyses.

Models

To compare seasonal differences in behavior, linear mixed models were fitted to detection data from fish tagged in the eastern basin during 2017–2020 for depth occupancy and during 2018–2020 for home range size and overlap using the lmer function from the R package lme4 (Bates et al. 2015). For assessing depth occupancy, season (categorical), year (categorical), and the season × year interaction were considered as fixed effects, and individual fish (categorical) was treated as a random effect. Bottom depth analyses included data from an average of 100 eastern basin-tagged fish per season (range = 49–136) per year. To assess home range size ($\log_e$ transformed), detection period (i.e., the period between the first and last detections in a given season; continuous) and the number of centers of activity (continuous) were also included as fixed factors to account for sensitivity in home range analyses to differences in detection histories. Similarly, to assess home range overlap, average detection period (continuous) and the combined number of centers of activity (continuous) were calculated for each pairwise comparison and then averaged by individual when individual overlap was calculated. For seasonal comparison of the home range overlap of fish tagged in the eastern basin, individual averaged overlap was calculated using only pairwise comparisons with other eastern basin-tagged fish. Home range size and overlap analyses included data from an average of 117 eastern basin-tagged fish per season (range = 52–137) per year.

To evaluate potential differences in behavior between fish tagged in the eastern and western basins, linear mixed models were fitted to detection data from 2019 and 2020, as the first cohort of western basin-tagged fish was tagged in late 2018. Individual fish was treated as a random effect, and season, year, tag basin (categorical), and associated interactions were considered fixed effects for assessing depth occupancy. Basin comparison bottom depth analyses included data from an average of 113 eastern basin-tagged fish per season (range = 92–122) and 18 western basin-tagged fish per season (range = 14–23) per year. Detection period and the number of centers of activity were additional fixed effects in assessing home range size ($\log_e$ transformed) and home range overlap, as described for the eastern basin model. For the tagging basin comparison of home range overlap, individual averaged overlap for fish tagged in both basins was calculated using pairwise comparisons with all fish. Centers of activity and detection period were *Z*-score standardized for all models in which they were included as fixed effects. Basin comparison home range size and overlap analyses included data from an average of 119 eastern basin-tagged fish per season (range = 114–127) and 19 western basin-tagged fish per season (range = 16–23) per year.

Length

To assess potential behavioral differences across the length range of sampled adult Lake Trout, linear models or linear mixed models were fitted to data only from eastern basin-tagged fish due to the small sample and narrow range of lengths from the western basin sample. Since age samples were not collected, estimation of individual-based growth was not applicable; therefore, length at tagging was used, and we considered only observations occurring within the first year after a fish was released. To evaluate depth occupancy, a linear mixed model was fitted with season, length at tagging, and the interaction as fixed factors and with tagging year as a random factor. The length-based depth occupancy analysis included data from an average of 141 fish per season (range = 126–154). Only fish tagged in 2018 were considered for length-based home range analyses, as the receiver grid was not complete until after fish tagged in 2016 had been at large (i.e., time in the system after tagging) for over a year. To evaluate home range size ($\log_e$ transformed) and home range overlap, a linear model was fitted, considering season, length at tagging, the season × length interaction, centers of activity, and detection period as fixed effects. The length-based home range size and overlap analyses included data from an average of 77 fish per season (range = 75–81).

For all models, the model fit was evaluated by observing model residuals. Residuals for all models describing home range area fit poorly, with strong skews, suggesting the need for a $\log_e$ transformation of the response. Predictions from home range area models were back-transformed, accounting for the log transformation bias. The full model for each response variable considered all potentially relevant effects, and all possible model subsets were considered as alternatives. Akaike's information criterion corrected for finite sample sizes (AIC_c) was used to evaluate the various candidate models via the dredge function from the R package MuMIn (Bartoń 2020). Candidate models with an AIC_c difference (ΔAIC_c) less than 2 were considered to have some evidentiary support for being the best performing model. If there were multiple models with values of ΔAIC_c less than 2, model predictions were averaged using the modavgPred function from the R package AICcmodavg (Mazerolle 2020). If no other models had ΔAIC_c less than 2, then only the best performing model was considered. Model effect sizes and uncertainty were calculated with the ggpredict function from the R package ggeffects (Lüdecke 2018). All statistical analyses were performed in R version 4.2.2 (R Core Team 2022).

RESULTS

Seasonal basin occupancy

Broad-scale habitat occupancy of Lake Trout in Lake Erie varied seasonally. Fish that were tagged in the eastern basin had the highest RI (i.e., [days detected in region/total days detected] ×100), on average, in the eastern offshore region during most seasons (winter: mean RI = 62%; spring: mean RI = 73%; summer: mean RI = 94%; Figure 2E), with the exception of fall (mean RI = 29%; Figure 2E). Nearly all eastern basin-tagged fish (99%) occupied the eastern offshore region more than any other region during summer (Table 2), including 83% that occupied this region on more than 90% of days during summer stratification. The proportion of time spent in the eastern offshore region varied widely on an individual level when the water column was isothermal (Figure 2E). During fall, eastern basin-tagged fish had the highest occupancy in the eastern south nearshore region (mean RI = 65%; Figure 2F), and 75% of fish occupied this region more than any other region in the fall (Table 2). During winter and spring, individual variation in region occupancy was high, with highest average population occupancy observed in the eastern offshore region (winter: mean RI = 62%; spring: mean RI = 73%), followed by the eastern south nearshore (winter: mean RI = 25%; spring: mean RI = 17%), eastern north nearshore (winter: mean RI = 4%; spring: mean RI = 10%), and central south (winter: mean RI = 10%; spring: mean RI = 3%) regions (Figure 2C–E). Eastern basin-tagged Lake Trout used the central north region infrequently (mean RI < 1% in every season), and none were detected in the western basin during the study (Figure 2A,B).

Lake Trout that were tagged in Ontario, Pennsylvania, and New York waters (i.e., eastern basin) of Lake Erie exhibited similar spatiotemporal habitat use patterns. Residency indices for fish tagged in Ontario waters were lower in the eastern north nearshore region compared to the other regions (e.g., offshore and south nearshore regions) in the eastern basin across seasons, a result similar to that

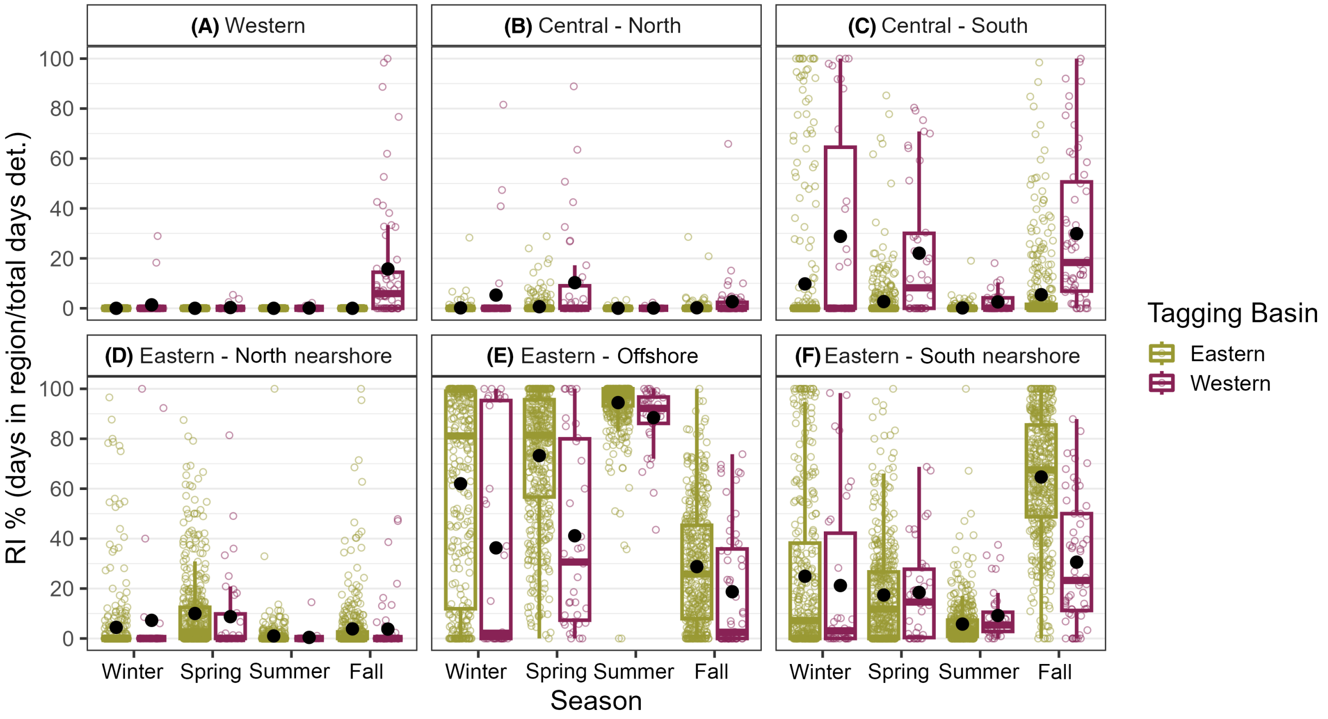

FIGURE 2 Seasonal residency index (RI, %; [number of days detected in the region/total number of days detected] × 100) by region—(A) western, (B) central north, (C) central south, (D) eastern north nearshore, (E) eastern offshore, and (F) eastern south nearshore—for Lake Trout tagged in the eastern or western basin of Lake Erie. Each open circle represents one fish in 1 year. The underlying box plots contain the box ranging from the first to third quartile, the solid horizontal line representing the median, the solid black circle representing the mean, and whiskers extending up to 1.5 times the interquartile range. See Figure 1 for region divisions.

TABLE 2 Percentage of Lake Trout tagged in the eastern or western basin of Lake Erie that occupied a region (see Figure 1 for region divisions) for the majority of days during each season (see Methods for season definitions). "Number" indicates the number of fish having adequate data (detections on >4 days in a season) to be included. Years were considered independently, so each fish is often considered more than once. For the rare instance in which a fish had a tie for the most occupied region, both regions were counted for that fish, resulting in the potential for a row to sum to slightly more than 100%.

Season	Western (%)	Central north (%)	Central south (%)	Eastern north nearshore (%)	Eastern south nearshore (%)	Eastern offshore (%)	Number
Eastern basin							
Winter	0	0	11	4	21	65	457
Spring	0	0	1	8	11	82	505
Summer	0	0	0	0	1	99	519
Fall	0	0	3	2	79	17	500
Western basin							
Winter	0	6	27	4	21	42	52
Spring	0	13	24	11	13	42	38
Summer	0	0	0	0	0	100	36
Fall	13	2	27	2	35	23	60

for fish tagged along the south shore in New York and Pennsylvania (Figure 3D–F). Pennsylvania-tagged fish had slightly higher occupancy in the eastern south nearshore region compared to New York- and Ontario-tagged fish during winter (mean RI = 34% versus 21% and 20%, respectively) and spring (mean RI = 26% versus 14% and 12%, respectively; Figure 3F). Conversely, Pennsylvania-tagged fish had lower occupancy in the eastern offshore region compared to New York- and Ontario-tagged fish during winter (mean RI = 52% versus 68% and 66%, respectively) and spring (mean RI = 64% versus 77% and 79%, respectively; Figure 3E), although all three groups

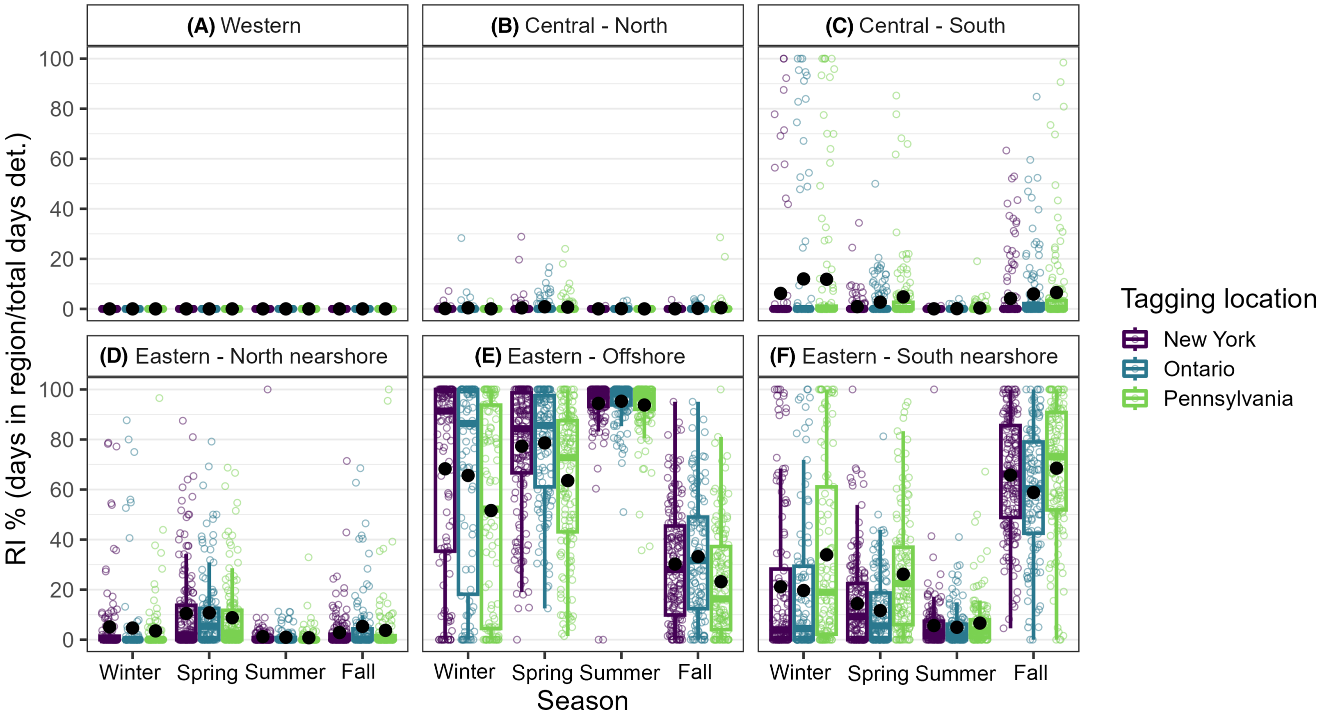

FIGURE 3 Seasonal residency index (RI, %; [number of days detected in the region/total number of days detected] × 100) by region—(A) western, (B) central north, (C) central south, (D) eastern north nearshore, (E) eastern offshore, and (F) eastern south nearshore—for Lake Trout tagged in New York, Ontario, or Pennsylvania waters of Lake Erie. Each open circle represents one fish in 1 year. The underlying box plots contain the box ranging from the first to third quartile, the solid horizontal line representing the median, the solid black circle representing the mean, and whiskers extending up to 1.5 times the interquartile range. See Figure 1 for region divisions.

had a high degree of individual variability during these seasons (Figure 3). Most (range = 79–87%) of the eastern basin-tagged fish occupied the eastern offshore region for more than 90% of the summer period (Table 2). Regardless of tagging location, during fall, eastern basin-tagged fish spent the most time in the eastern south nearshore region (RI range = 59–69%), followed by the eastern offshore region (RI range = 23–33%). Since fish that were tagged from Ontario, Pennsylvania, and New York occupied similar habitats throughout the year, all fish tagged in the eastern basin were combined for further analysis.

Lake Trout that were tagged in the western basin had regional occupancy patterns similar to those of eastern basin-tagged fish for most of the year (i.e., winter, spring, and summer), but considerable differences in movement patterns and occupancy during the fall were evident. Similar to eastern basin-tagged fish, western basin-tagged fish had high eastern offshore occupancy on average during summer (mean RI = 88%; Figure 2E), and all fish occupied the eastern offshore region more than any other region during summer (Table 2). During winter and spring, there was high individual variation among western basin-tagged fish. By evaluating the most occupied region for each fish during each season, we found that at least 10% of western basin-tagged fish occupied five different regions (all except the western region) most regularly during spring and at least 10% of fish occupied four different regions during fall (Table 2). Compared to eastern basin-tagged fish, the western basin-tagged fish tended to have higher occupancy in the central south region (Figure 2C) but lower occupancy in the eastern offshore region (Figure 2E) throughout the year, particularly during winter and spring. On average, western basin-tagged fish spent 33% of their time during the fall in the eastern south nearshore region compared to 65% for eastern basin-tagged fish (Figure 2F). Lake Trout that were tagged in the western basin tended to reside along the southern shoreline of Lake Erie during the fall, as occupancy was highest in the eastern south nearshore region (31%), followed by the central south (30%), eastern offshore (19%), and western (16%) regions (Figure 2).

Long-distance dispersal

Lake Trout in Lake Erie frequently dispersed long distances from their tagging locations. Forty-two percent of all tagged Lake Trout were detected a maximum distance of more than 100 km from their tagging location, with a median maximum dispersal distance of 94.6 km (mean = 126.6 km; range = 1.7–349.7 km). Fish that were tagged in the eastern basin had a median maximum dispersal of 91.4 km (mean = 95.2 km; range = 1.7–235.6 km) from their tagging location, and 32% dispersed over 100 km. All fish tagged in the western basin dispersed more than 100 km, with a median maximum dispersal of 314.2 km (mean = 316.0 km; range = 296.7–349.7 km).

Western basin migrations

Lake Trout that were tagged in the western basin during fall exhibited directed movements toward the central and eastern basins soon after release. All fish that were tagged in the western basin dispersed to the eastern basin within 2 months of tagging, and most dispersed within a matter of days or weeks, except for one individual that did not travel to the eastern basin until approximately 5 months posttagging. Fish returned to the area within 50 km of the tagging site during fall at a rate of 71% (25 of 35). Fish that were tagged in 2018 had a higher tendency to migrate than those tagged in 2019. For Lake Trout tagged in 2018, 93% (14 of 15) migrated back to the western basin at least once, with an overall return rate of 78% (21 of 27) over both years, while 50% (4 of 8) of the fish tagged in 2019 migrated back to the western basin the following year. These directed western migrations were typically rapid (median = 5.1 days; range = 3.0–18.6 days), and individuals generally spent little time in the area (median = 10.2 days); however, the duration of stays was highly variable, and one individual spent several months in the western basin each year (range = <1.0–88.4 days). Migration back to the eastern basin was slightly longer than the directed western migration (median = 6.5 days; range = 3.4–41.1 days). Additionally, outside of fall, several individuals that were tagged in the western basin appeared to make rapid migrations from the eastern basin to the western basin or the western central basin during late spring, before returning to the eastern basin during early summer.

Depth occupancy

Using receiver depth as a proxy for bottom depth, the best performing model (i.e., lowest AIC$_c$) describing the depth occupancy of eastern basin-tagged fish included season, year, and the season × year interaction as fixed effects and individual fish as the random effect (Table S1 [available in the Supplement in the online version of this article]). In each year, eastern basin-tagged fish occupied areas with deepest waters during summer (range = 38–43 m) and shallowest waters during the fall (range = 14–20 m; Figure 4A). Although considerable interannual variation was evident (Figure 5A), on average eastern basin-tagged Lake Trout occupied similar depths during the winter (32 m; range = 26–36 m) and spring (34 m; range = 29–38 m; Figure 4A). Nearshore (<15 m) movement following thermal destratification in the fall (October/November) was sudden and consistent among years (Figure 5A). After the nearshore movement during the fall (presumably to spawn), eastern basin-tagged Lake Trout tended to reside

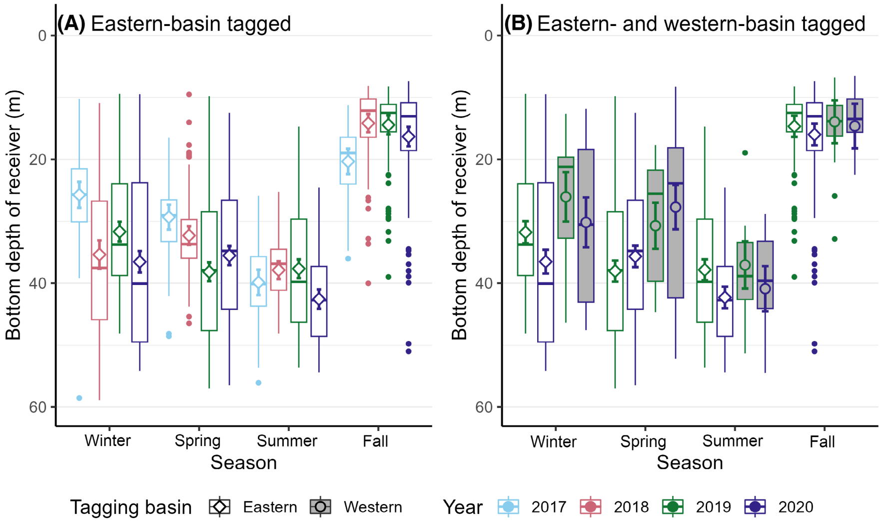

FIGURE 4 Average seasonal bottom depth of receivers at which Lake Trout were detected (A) by year (2017–2020) for eastern basin-tagged fish and (B) by year (2019–2020) and by tagging basin for fish tagged in the eastern and western basins of Lake Erie. Box plots show raw data, with the box ranging from the first to third quartile, the solid horizontal line representing the median, whiskers extending 1.5 times the interquartile range, and outliers shown as small points. Large shapes (diamonds or circles) indicate model predictions, with error bars depicting the 95% confidence intervals of the predictions. Colors of box plots and model predictions correspond to years (light blue = 2017; pink = 2018; green = 2019; purple = 2020), and shading of the box plot and shape and shading of the large icon correspond to tagging basin (diamond with white box = eastern; circle with gray box = western).

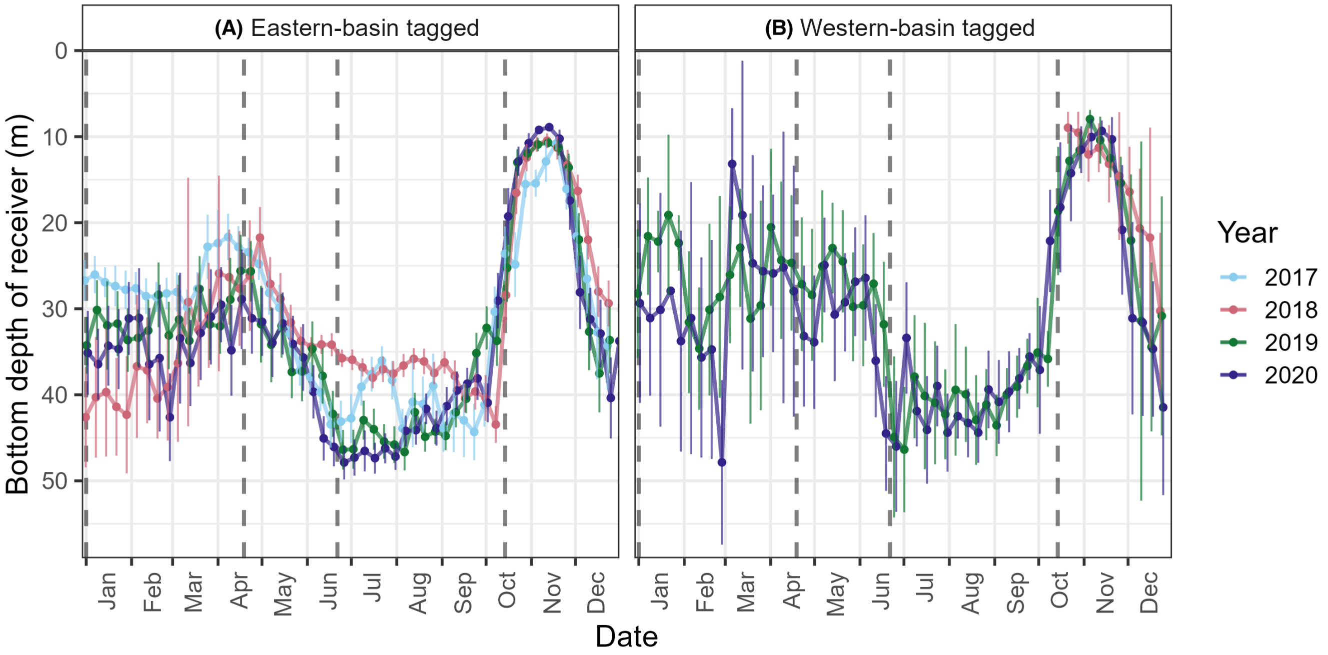

FIGURE 5 Weekly average bottom depth of receivers (m) at which Lake Trout were detected by year for fish tagged in the (A) eastern basin and (B) western basin of Lake Erie. Each weekly average considers the average of the average depth of the receivers from all fish having at least 2 days with at least three observations in a week. Error bars represent 95% confidence intervals of the weekly population average. Vertical dashed lines indicate average season breaks.

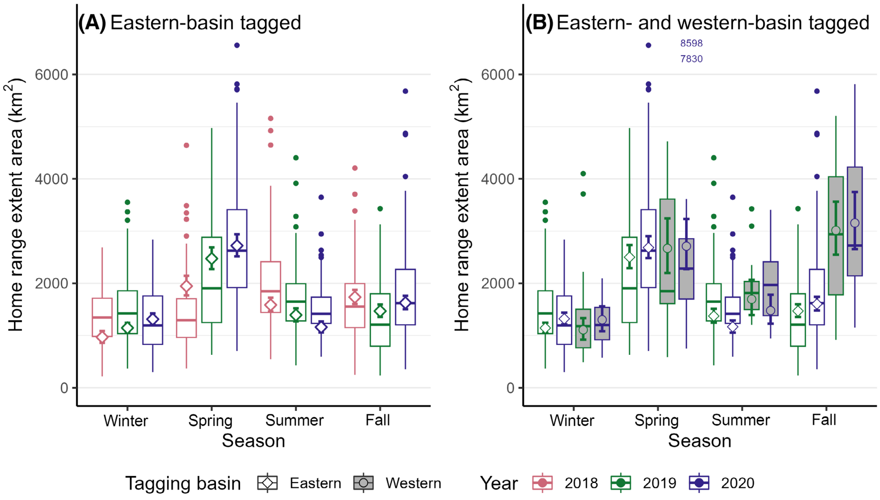

FIGURE 6 Average seasonal 95% kernel utilization distribution (KUD) home range area (km^2) presented (A) by year (2018–2020) for eastern basin-tagged Lake Trout and (B) by year (2019–2020) and by tagging basin for fish tagged in the eastern and western basins of Lake Erie. Box plots show raw data, with the box ranging from the first to third quartile, the solid horizontal line representing the median, whiskers extending 1.5 times the interquartile range, and outliers shown as small points. In panel B, two outliers extended beyond the bound of the graph and are shown numerically. Large shapes (diamonds or circles) indicate model predictions, with error bars depicting the 95% confidence intervals of the predictions. Colors of box plots and model predictions correspond to years (pink = 2018; green = 2019; purple = 2020), and shading of the box plot and shape and shading of the large icon correspond to tagging basin (diamond with white box = eastern; circle with gray box = western).

in areas of deeper water (>25 m) between December and March, headed back toward shore (20–35 m) during April, and then moved back offshore (>30 m) in May and as summer progressed and the eastern basin thermally stratified (Figure 5A).

Western basin- and eastern basin-tagged Lake Trout occupied similar depths throughout the year; however, seasonal differences were evident. Of the candidate models evaluated, there was support for two models (models 1 and 2). Both models included season, year, tagging basin, the season × year interaction, and the season × tagging basin interaction as fixed effects and individual fish as a random effect; model 2 additionally included the year × tagging basin interaction as a fixed effect (Table S2). Weighted averaging of the two supported models suggested little effect of an interaction between year and basin, leading to very similar trends within each year. Western basin-tagged fish occupied shallower areas than eastern basin-tagged fish during winter (western: 26 m, 95% confidence interval [CI] = 22.1–30.1 m; eastern: 32 m, 95% CI = 30.0–33.6 m) and spring (western: 31 m, 95% CI = 27.0–34.4 m; eastern: 38 m, 95% CI = 36.3–39.8 m) in 2019 (Figure 4B). Western basin- and eastern basin-tagged fish had very similar depth occupancy during the summer (western: 37 m, 95% CI = 33.3–40.9 m; eastern: 38 m, 95% CI = 36.1–39.6 m), and fall (western: 14 m, 95% CI = 10.5–17.4 m; eastern: 15 m, 95% CI = 13.0–16.4 m) of 2019 (Figure 4B). Similar to eastern basin-tagged fish, Lake Trout that were tagged in the western basin moved into shallow water (<15 m) after thermal destratification during October and November and then moved into variable mid-depth areas during January–May (Figure 5B).

Space use extent

During the study period, space use extent, as measured based on home range estimates from KUDs at the 95% level, varied seasonally for Lake Trout in Lake Erie, with some interannual variability. Of the models evaluated, a model with season, year, the season × year interaction, centers of activity, and detection period as fixed effects and individual fish as a random effect was the best performing model based on AIC_c (Table S3). Eastern basin-tagged fish consistently had the largest horizontal space use extent during spring, although space use during this season was variable across years, with smaller space use during the spring of 2018 (1947.6 km^2; 95% CI = 1768.9–2144.5 km^2) compared to 2019 (2473.7 km^2; 95% CI = 2273.9–2691.0 km^2) and 2020 (2720.7 km^2; 95% CI = 2517.5–2940.3 km^2; Figure 6A). Contrary to predictions, seasonal space use extent was smallest during summer only in 2020 (1160.7 km^2; 95% CI = 1058.9–1272.1 km^2), whereas space use in 2018 and 2019 was smallest during winter (2018: 969.0 km^2, 95% CI = 861.7–1089.7 km^2; 2019: 1147.2 km^2, 95% CI = 1057.8–1244.1 km^2; Figure 6A).

Similar home range extent patterns existed for eastern basin- and western basin-tagged fish based on model estimates from three candidate models with significant plausibility. Fixed effects for the first model included season, year, tagging basin, the season × year interaction, and the season × tagging basin interaction, with individual fish as a random effect; the second model additionally included the year × tagging basin interaction as a fixed effect, and the third model included the season × year × tagging basin interaction in addition to all fixed effects from the second model (Table S4). Fish that were tagged in the western basin had a space use extent size similar to that of eastern basin-tagged fish during winter 2019 (western: 1109.0 km^2, 95% CI = 921.3–1335.0 km^2; eastern: 1144.9 km^2, 95% CI = 1052.6–1245.4 km^2) and spring 2019 (western: 2669.0 km^2, 95% CI = 2197.2–3241.9 km^2; eastern: 2500.8 km^2, 95% CI = 2290.0–2731.0 km^2) and insignificantly larger space use during summer 2019 (western: 1695.7 km^2, 95% CI = 1392.4–2065.0 km^2; eastern: 1374.5 km^2, 95% CI = 1246.9–1515.0 km^2; Figure 6B). However, during fall, the space use extent for western basin-tagged fish (3085.1 km^2) was nearly twice as large as that of eastern basin-tagged fish (1538.1 km^2) on average (Figure 6B). There was little effect of year on the difference between tagging basins (average seasonal difference between tagging basins in 2020 versus 2019 = −31.9 km^2; range = −141.6 to 16.8 km^2).

Individual space use overlap

Space use overlap among individual eastern basin-tagged Lake Trout, as calculated using UDOI, varied seasonally but exhibited interannual consistency. A model with season, year, the season × year interaction, centers of activity, and detection period as fixed effects and individual fish as a random effect was the most plausible among the candidate models evaluating space use overlap (Table S5). Seasonal space use overlap within eastern basin-tagged individuals was highest and consistent across years during summer (average = 0.56; range = 0.54–0.60) and fall (average = 0.56; range = 0.54–0.58; Figure 7A). There was more than twice as much variability (i.e., based on the interquartile range) in home range overlap estimates for eastern basin-tagged fish during the fall compared to the other seasons (Figure 7A). Eastern basin-tagged fish showed the lowest seasonal overlap during winter (average = 0.24; range = 0.21–0.25), followed by spring. Spring was the only season with notable interannual variability, as overlap in spring 2018 (0.45; 95% CI = 0.38–0.51) was higher than that in spring 2019 (0.28; 95% CI = 0.24–0.33) and 2020 (0.35; 95% CI = 0.31–0.38; Figure 7A).

Western basin-tagged Lake Trout exhibited trends in seasonal home range overlap similar to those of eastern basin-tagged fish, although one notable difference was evident. Home range overlap was compared with a model in which season, year, tagging basin, the tagging basin × season interaction, centers of activity, and detection period were fixed effects and individual fish was treated as the random effect (Table S6). Similar to

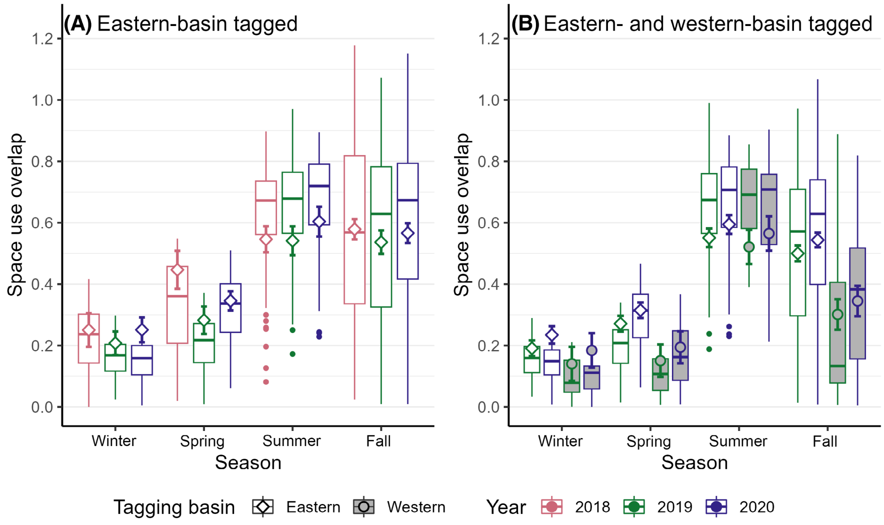

FIGURE 7 Seasonal space use overlap (A) by year (2018–2020) for eastern basin-tagged Lake Trout compared to other eastern basin-tagged Lake Trout and (B) by year (2019–2020) and by tagging basin for eastern basin- and western basin-tagged Lake Trout compared to all other Lake Trout. Box plots show raw data, with the box ranging from the first to third quartile, the solid horizontal line representing the median, whiskers extending 1.5 times the interquartile range, and outliers shown as small points. Large shapes (diamonds or circles) indicate model predictions, with error bars depicting the 95% confidence intervals of the predictions. Colors of box plots and model predictions correspond to years (pink = 2018; green = 2019; purple = 2020), and shading of the box plot and shape and shading of the large icon correspond to tagging basin (diamond with white box = eastern; circle with gray box = western).

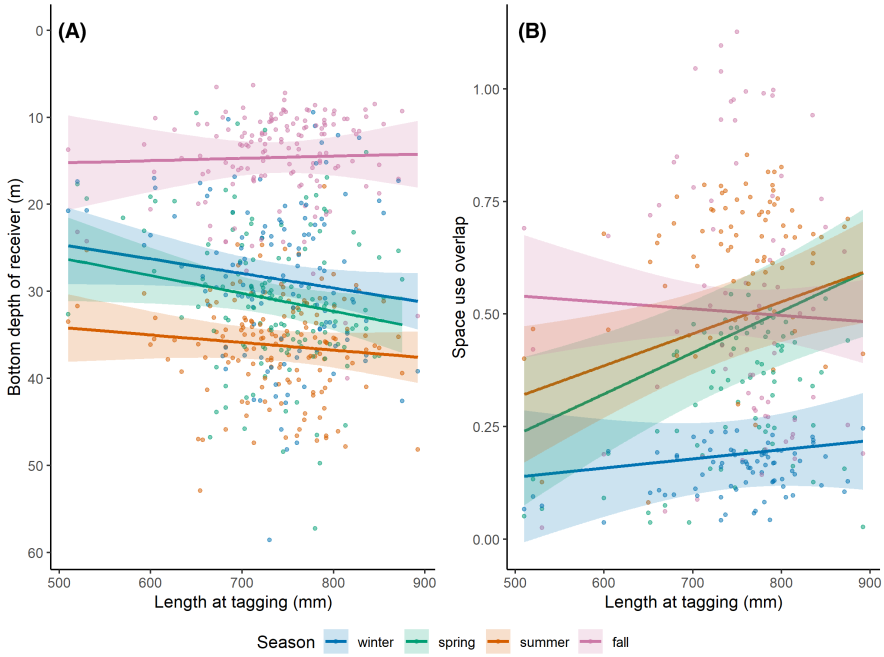

FIGURE 8 (A) Seasonal average bottom depth (m) of receivers at which Lake Trout were detected and (B) space use overlap by Lake Trout relative to fish total length at tagging (mm). Seasons were defined based on water temperature (see Methods); thus, the timing of season breaks varied among years. On average, winter was January 1–April 18, spring was April 18–June 21, summer was June 21–October 10, and fall was October 10–January 1. Model predictions are given by solid lines, with shaded areas depicting 95% confidence intervals.

patterns observed for eastern basin-tagged fish, home range overlap for western basin-tagged fish was highest during the summer and fall and lowest during winter and spring (Figure 7B). Western basin-tagged fish exhibited significantly lower space use overlap than eastern basin-tagged fish during spring (western: 0.15, 95% CI = 0.10–0.20; eastern: 0.27, 95% CI = 0.25–0.30) and fall (western: 0.30, 95% CI = 0.25–0.35; eastern:

0.50, 95% CI = 0.47–0.53) of 2019 (Figure 7B). Although lower, space use overlap for western basin-tagged fish was similar to that for eastern basin-tagged fish during the winter (western: 0.14, 95% CI = 0.09–0.20; eastern: 0.20, 95% CI = 0.17–0.22) and summer (western: 0.52, 95% CI = 0.47–0.58; eastern: 0.55, 95% CI = 0.52–0.58) in 2019 (Figure 7B).

Length

Seasonally, the depth of water occupied and the space use overlap for Lake Trout tagged in the eastern basin of Lake Erie were related to fish size (i.e., total length at tagging), whereas space use extent size was not related to fish size. Fish depth (using receiver depth as a proxy for fish depth) was best described by two candidate models considering length, season, and the length × season interaction as fixed effects and tagging year as a random effect (Table S7). Larger fish tended to be detected in deeper water (i.e., on average) than smaller fish during winter (0.017 m depth per mm increase in length [hereafter, "m depth mm^{-1}"]; 95% CI = −0.001 to 0.34 m depth mm^{-1}; 6.38 m over the range of observed lengths, 510–892 mm) and spring (0.021 m depth mm^{-1}; 95% CI = 0.001–0.040 m depth mm^{-1}; 7.85 m over the length range; Figure 8A). During summer (0.009 m depth mm^{-1}; 95% CI = −0.007 to 0.024 m depth mm^{-1}; 3.34 m over the length range) and fall (−0.003 m depth mm^{-1}; 95% CI = −0.025 to 0.020 m depth mm^{-1}; −0.97 m over the length range), length had no meaningful effect on the depth occupied (Figure 8A).

To evaluate a potential effect of length on space use extent, log-transformed home range size was modeled considering various fixed parameters. Of the models evaluated, two models that included season, centers of activity, and detection period (with the second model additionally including length) had the most support (Table S8). There was no meaningful relationship between fish length and space use extent (0.0001 km^2 per mm increase in length; 95% CI = −0.0004 to 0.0006).

To evaluate a potential effect of length on space use overlap between an individual Lake Trout and the rest of the sampled population, the best model considered the fixed effects of season, length, the season × length interaction, centers of activity, and detection period (Table S9). Larger fish had higher space use overlap with other individuals during spring (effect of length = 0.0009 per mm increase in length [hereafter, "mm^{-1}"]; 95% CI = 0.0003–0.0014 mm^{-1}; 0.35 over the range of observed lengths, 510–892 mm) and summer (0.0007 mm^{-1}; 95% CI = 0.0002–0.0012 mm^{-1}; 0.27 over the length range; Figure 8B) than smaller individuals. However, length had no meaningful effect on space use overlap during winter (0.0002 mm^{-1}; 95% CI = −0.0003 to 0.0007 mm^{-1}; 0.08 over the length range) or fall (−0.0001 mm^{-1}; 95% CI = −0.0007 to 0.0004 mm^{-1}; −0.06 over the length range; Figure 8B).

DISCUSSION

This study is the first in the Great Lakes to examine Lake Trout movements year-round in a system with intensive, whole-lake coverage of acoustic receivers (i.e., grid with receivers spaced ≤15 km). During summer, as expected, Lake Trout in Lake Erie typically occupied deep areas in the offshore eastern basin, had relatively small space use extent sizes, and exhibited a large degree of space use overlap. After the breakdown of thermal stratification, Lake Trout tagged in the eastern basin made rapid, directed movements to shallower water. During fall, eastern basin-tagged Lake Trout primarily occupied the south nearshore eastern region, occupied the shallowest depths of the year, had small space use extents, and displayed relatively large home range overlap. Lake Trout had highly variable regional and depth occupancy throughout the eastern and central basins during winter and spring and low space use overlap. Lake Trout that were tagged in the western basin returned to this region in the fall of subsequent years despite occupying the offshore eastern basin almost exclusively during stratification. Western basin-tagged fish had similar depth occupancy, home range size, and overlap compared to eastern basin-tagged fish except during fall. Lake Trout length at tagging was positively correlated with receiver depth during winter and spring and with space use overlap during spring and summer.

Lake Trout in Lake Erie were observed frequently traveling large distances. Although we expected that Lake Trout tagged in the shallow western basin would disperse long distances to find suitable thermal habitat during summer stratification, surprisingly, nearly one-third of fish tagged in the deep eastern basin dispersed over 100 km. Long-distance dispersals of eastern basin-tagged fish were largely a consequence of movement during the spring season. These long-distance dispersals were made by a much greater proportion of fish than has been reported in other studies within the Great Lakes (Eschmeyer et al. 1953; Schmalz et al. 2002; Riley et al. 2018; Ivanova et al. 2021); however, this is likely a consequence of differences in methodology. Unintentional biases in methodology can lead to incorrect conclusions, particularly when studying movement (e.g., Gowan et al. 1994). Measures of Lake Trout dispersal from several previous Great Lake studies used mark–recapture methods (Eschmeyer et al. 1953; Schmalz et al. 2002), where dispersal was inferred as the distance between tagging and recapture locations, or acoustic telemetry that relied on sparse receiver coverage (Riley et al. 2018; Ivanova et al. 2021). For example, in Lake Superior, 9% of fish were recaptured more than 160 km from the tagging site (Eschmeyer et al. 1953). In Lake Michigan, 90% of fish were recaptured within 69 km (Schmalz et al. 2002) of their initial tagging location. During a telemetry study of multiple populations in Lake Huron, 3–9% of fish were detected at a maximum distance of over 100 km from their release location (Riley et al. 2018). Lastly, in Lake Ontario, 1 of 24 individuals (4%) was detected over 200 km from its release site (Ivanova et al. 2021). Dispersal measures from previous Great Lakes studies likely represent minimum estimates of dispersal distances, as it is likely that the study organisms traveled much further distances and simply were not detected. Considering that Lake Erie is the smallest of the Great Lakes, it is conceivable that Lake Trout would undergo long-distance dispersal and movements at similar—if not higher—rates in the other lakes compared to Lake Erie. However, we also cannot rule out the possibility that conditions in Lake Erie contribute to Lake Trout moving greater distances in this lake than in the other Great Lakes. For example, it is possible that a mismatch exists between the area that provides suitable summer oxythermal habitat (i.e., the offshore eastern basin) and the areas that provide optimal forage opportunities. Suboptimal oxythermal habitat during stratification in the western basin likely drives the movement of fish tagged in the western basin. However, it seems unlikely that oxythermal habitat quality alone drives the long-distance movement of fish tagged in the eastern basin, as these fish have access to preferred oxythermal summer habitat in relatively close proximity to stocking areas and historic spawning habitat (Coldwater Task Group 2022).

As hypothesized, tagged Lake Trout were primarily located in the offshore (>25-m water depth) region of the eastern basin during summer stratification. Therefore, the most intense intraspecific competition for habitat has the potential to occur during stratification, compared to nonstratified seasons when fish have access to a larger area of suitable habitat. While being physiologically restricted during stratification, Lake Trout displayed some interannual differences in behavior. Notably, the fish were located in areas with deeper depths in 2020 than in 2018 and 2019; likewise, the extent of space use was largest during 2018 and smallest during 2020. These patterns correlate with interannual differences found in August diets. In 2020, Rainbow Smelt *Osmerus mordax*, a pelagic prey species that typically serves as the primary prey item of Lake Trout, occurred in 94% of nonempty Lake Trout stomachs, whereas Round Goby *Neogobius melanostomus*, a benthivorous species, only occurred in 4% of nonempty stomachs (Coldwater Task Group 2022). Conversely, in 2018 and 2019, the occurrence of Rainbow Smelt in nonempty stomachs ranged from 57% to 61%, whereas the occurrence of Round Goby ranged from 37% to 58% (Coldwater Task Group 2022). This suggests that interannual differences in space use may be influenced by the availability and distribution of alternate prey species.

We tagged Lake Trout in the eastern basin during spring in an attempt to tag a heterogeneous mix of fish originating from different spawning aggregations in the eastern basin. However, nearly all eastern basin-tagged fish spent most of their time during fall in the eastern south nearshore region, suggesting that these fish could be spawning or staging to spawn in this region of the lake. Although 37% of fish tagged in the eastern basin were tagged in Ontario waters during the spring, only three eastern basin-tagged fish (2%) spent the majority of their time during fall along the north shore of the eastern basin. The tendency of eastern basin-tagged fish to occupy the eastern south nearshore region during fall suggests that many of these fish were likely stocked in this region, as Lake Trout are known to return to natal rearing or stocking locations (reviewed by Binder et al. 2021; Marsden et al. 2021), even over long distances (Binder et al. 2017; Riley et al. 2018). Although some studies have found that the timing of spawning migrations is variable among years (Binder et al. 2016; Marsden et al. 2016), Lake Trout in the current study exhibited relatively consistent interannual nearshore movements. The aim of this study was to provide a general overview of the spatial and temporal movements of Lake Trout in Lake Erie, but it would be worthwhile for future Lake Trout movement studies in Lake Erie to focus more specifically on spawning behavior. For example, research regarding the timing of movement onto spawning sites, precise spawning locations, fine-scale searching behavior, and the extent of sex and strain differences in movement behaviors could be valuable for informing stocking locations, stocking strains, and priority areas for habitat restoration.

During isothermal seasons, Lake Trout are not subject to temperature and oxygen constraints; consequently, it was unknown how fish would use available habitat in Lake Erie. Binder et al. (2021) hypothesized that prey availability and abundance would direct habitat selection and space use if Lake Trout were not constrained physiologically. Unfortunately, it is unclear how forage fish abundance in Lake Erie influences Lake Trout movement, as forage information comes from a variety of sources that are not spatially or temporally standardized and diet surveys are only conducted during summer (Forage Task Group 2022). Blanchfield et al. (2009) found that ice cover during winter influenced habitat use in an inland lake (Experimental Lakes Area in northwestern Ontario), whereas in Lake Erie this does not appear to be a driving force, as fish did not seem to behave differently in years with little ice cover (maximum ice coverage = 35% in 2017 and 16% in 2020) compared to years with a high degree of ice cover (maximum ice coverage = 95% in 2018 and 94% in 2019; National Oceanic and Atmospheric Administration 2022). Although no trends in bottom depth of the receiver or space use extent were correlated with trends in ice cover, it is unknown whether or how swimming depth within the water column was affected by ice cover.

During spring, region occupancy and depth occupancy were highly variable among individuals and years. It is difficult to identify what may be contributing to annual differences in winter and spring behavior. In 2017 and 2019, fish were detected in areas of deeper water in spring than winter; in 2018, fish occupied areas of shallower water in spring; and in 2020, depth occupancy was similar between spring and winter. Additionally, it should be emphasized that depth occupancy measured here represents only the water depth in the area where a fish was detected but not its vertical location within the water column. A related experimental deployment of a small number of pressure-sensitive tags in Lake Trout in Lake Erie suggested that fish tended to be suspended in the water column during the spring months, whereas they were near the bottom during the remainder of the year (T. R. Funnell and C. S. Vandergoot, unpublished data). A more thorough understanding of vertical habitat use by Lake Trout in addition to horizontal space use could be a priority for future studies. Space use extent sizes were largest during spring for eastern basin-tagged Lake Trout, suggesting that fish are most active and mobile over long distances during this season. Movements in spring are expected to be driven largely by prey availability. Although we might expect that prey were most available or concentrated in the spring of 2018 compared to 2019 and 2020 because space use extent was smallest and overlap was largest during 2018, this may have been driven by the influx of newly tagged individuals that were released together at one of three stocking locations rather than being caused by yearly behavioral differences. Ultimately, during nonstratified seasons, Lake Trout showed the tendency to roam and disperse considerable distances after facing thermal constraints during stratification.

Overall, Lake Trout that were tagged in the western basin exhibited movement patterns and habitat use similar to those of eastern basin-tagged fish, with a few notable exceptions. Like the eastern basin-tagged Lake Trout, western basin-tagged fish were restricted to the offshore eastern basin during stratification as expected due to physiological constraints—specifically that cold, well-oxygenated water was only present in the eastern basin. These two tagging groups differed in that (1) western basin-tagged fish occupied the central southern region more than eastern basin-tagged fish during nonstratified periods (i.e., fall, spring, and winter) and (2) western basin-tagged fish had larger home ranges and lower home range overlap than eastern basin-tagged fish during most seasons. Fish that were tagged in the western basin during the fall showed strong fidelity to the region in which they were tagged, as 78% of western basin-tagged fish migrated over 260 km each way to return to that area during subsequent fall seasons. Considering the fidelity of Lake Trout to their stocking locations (Binder et al. 2021) and the distance traveled, fish that were tagged in the western basin were very likely to have been stocked in the western basin. The ability of these fish to return to hypothesized stocking locations despite the generally suboptimal conditions and substantial cost of migration to the western basin provides further evidence that stocking in suitable spawning locations is of extreme importance for the restoration of this species (Krueger et al. 1995; Muir et al. 2013; Riley et al. 2019). The migrations made by western basin-tagged fish were often rapid to and from the hypothesized spawning location, and fish often spent little time in the area. Tendency to migrate did not seem to be dependent on year; among the 12 individuals that were observed for two spawning seasons, three fish did not migrate in 2019 and three others did not migrate in 2020. It is unknown whether these fish attempted to spawn elsewhere, such as with the eastern basin aggregation, or skipped spawning. Other Great Lakes Lake Trout have been found to skip spawning (Sitar et al. 2014), and this strategy would be plausible given the high cost associated with the long-distance migration. Although it is unknown how Lake Trout home to rearing or stocking locations, a range of mechanisms has been proposed, including imprinted and conspecific olfactory cues, sound, bathymetry, hydrodynamics, solar cues, geomagnetic orientation, or learning and memory (Binder et al. 2021). Additionally, the tendency for fish tagged in the western basin to be more likely to use the southern part of the central basin and less likely to utilize the eastern north nearshore region during non-spawning, nonstratified periods could be attributable to a familiarity with and prior exposure to the central basin during spawning migrations.

Increased space use sharing by larger Lake Trout during spring and summer suggests the potential for a higher degree of intraspecific competition as compared to smaller individuals, and this result could be driven by large Lake Trout occupying more preferred habitat. Seasonal differences in space use overlap differed for large and small Lake Trout. Large Lake Trout experienced the highest overlap during summer, whereas for smaller fish, overlap was highest during fall. While these trends are statistically meaningful, they should be interpreted with caution, as lengths were taken from length at tagging during the spring. Length assignments will be most accurate during spring, soon after measurement, but subsequent variation in growth rates could lead to variable divergence of true size from initial measures, particularly during the fall and winter after potentially rapid summer growth. However, we assume that relative sizes were unbiased—that is, the smallest fish in the sample remained smallest, although we acknowledge that small fish were more likely to grow faster over the first year posttagging.

Large female Lake Trout are of considerable importance for the successful rehabilitation of the species because larger females produce more eggs and spawn later in the year than smaller fish (Martin and Olver 1980; Casselman 1995). Delayed spawning is likely to be of increased importance in Lake Erie, considering its southern location, shallow bathymetry, and corresponding warm temperatures as compared to other lakes within the geographic range of Lake Trout. However, the average age of females is lower in Lake Erie than in other systems (Rogers et al. 2019), possibly due to increased Sea Lamprey predation on older, larger fish (Swink 1991; Schneider et al. 1996; Stapanian and Madenjian 2007). Across the range of lengths studied, we found no differences in behavior during fall at the seasonal scale. Future studies could consider sex, growth over time, and strain to build on our understanding of how groups within the population could be behaving differently. Studies focused on differential temperature occupancy, fine-scale timing and location of spawning, and Sea Lamprey interactions could be beneficial to best inform rehabilitation and management through potential mechanisms such as alteration of stocking strains or locations.

The tendency for Lake Trout to use areas of Lake Erie outside of the offshore eastern basin during nonstratified periods provides support for ecosystem management and restoration efforts to be broadly focused on the basinwide or lakewide level. The frequent long-distance movements of Lake Trout, often resulting in occupancy of several different jurisdictional waters across the United States and Canada, emphasize the benefits of interagency cooperation in managing this species. Future studies focused directly on occupancy within and movement between jurisdictional boundaries, which were beyond the scope of this study, could further inform management actions. Interagency cooperation in managing Lake Erie is facilitated through the Lake Erie Coldwater Task Group of the Lake Erie Committee, guided by the Joint Strategic Plan for Management of Great Lakes Fisheries, but other systems could benefit from cooperative management of species that regularly move between different jurisdictional waters. Lake Trout tagged in the eastern basin, regardless of tagging jurisdiction, were detected most frequently in the southern shore of the eastern basin during the suspected spawning period, suggesting that habitat restoration efforts in this region would be beneficial for lakewide Lake Trout rehabilitation efforts. Additionally, restoration of offshore spawning reefs of historic importance could be beneficial in promoting spawning at cooler water temperatures; however, more investigation into the potential for offshore reefs in Lake Erie is needed. This study provides the first holistic description of lakewide, year-round behavior of adult Lake Trout in the Great Lakes. Results described here provide foundational knowledge for building an understanding of this ecologically and culturally important native species and can support future research to aid Lake Trout rehabilitation efforts in Lake Erie and elsewhere.

ACKNOWLEDGMENTS

This work was partially funded by the Great Lakes Fishery Commission (Grant 2013_BIN_44024) through Great Lakes Restoration Initiative appropriations (Grant GL-00E23010) and by the Great Lakes Fish and Wildlife Restoration Act (F15AP00996). We thank field crews from the U.S. Geological Survey, New York State Department of Environmental Conservation, Pennsylvania Fish and Boat Commission, Ontario Ministry of Natural Resources and Forestry, and Ohio Department of Natural Resources for their work in maintaining receiver deployments and collecting and tagging fish. We thank Kelly Robinson and Brian Roth for providing helpful comments on an early draft of the manuscript. This is Contribution 115 of GLATOS and Contribution 2023–07 of the Quantitative Fisheries Center at Michigan State University. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

CONFLICTS OF INTEREST STATEMENT

There is no conflict of interest declared in this article.

DATA AVAILABILITY STATEMENT

All data are available upon request.

ETHICS STATEMENT

Handling of fish was carried out in accordance with American Fisheries Society *Guidelines for the care and use of fishes* (Use of Fishes in Research Committee 2014).

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