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Monthly differences in the movement ecology of lake whitefish (*Coregonus clupeaformis*) in eastern Lake Ontario

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Abstract

Lake whitefish are a cold-water species that holds cultural and economic importance throughout the Great Lakes region. Anthropogenic stressors over the last 60 years (e.g., invasive species, habitat degradation, and pollution) have caused significant declines in their populations. Furthermore, there is limited knowledge on the spatial ecology and habitat use of the species in Lake Ontario. Therefore, we used acoustic telemetry to quantify horizontal and vertical habitat use by lake whitefish over a 3-year period (2021–2024) in Lake Ontario. We also evaluated seasonal changes in bottom-oriented versus suspended behaviours. Lake whitefish were heavily concentrated along the central Duck–Galloo Ridge and in 20–30 m during periods of stratification (June to September), while their distribution shifted to the south shore of Prince Edward County and 10–25 m during isothermal conditions (non-stratified; October to May) and for spawning. During the isothermal period, lake whitefish exhibited a predominantly bottom-oriented behaviour; during stratification, they exhibited both suspended and bottom-oriented behaviours. These differences in vertical and horizontal distribution may be driven by changes in thermal habitats and/or prey; however, further exploration is needed. Ongoing ecological change may influence lake whitefish distribution and behaviours, necessitating changes to monitoring and/or management that accounts for observed behaviours.

KEYWORDS

acoustic telemetry, behaviour, depth, habitat use, spatial ecology

1 | INTRODUCTION

Lake whitefish (*Coregonus clupeaformis*) are an ecologically, culturally and economically important fish species in the Laurentian Great Lakes (Ebener et al., 2021; Madenjian et al., 2002). The species serve an important ecological role as they transfer benthic energy into a mobile and harvestable resource by feeding primarily on offshore benthic production (Pothoven & Nalepa, 2006). Populations (i.e., abundance) of lake whitefish in the Great Lakes started to decline in the 1950s due to habitat degradation, overfishing and the presence of invasive parasitic sea lamprey (*Petromyzon marinus*) (Brenden et al., 2010; Ebener et al., 2021; Taylor et al., 2019). Populations stabilized by the 1980s, because of reductions in commercial harvest and the establishment of sea lamprey control programmes that reduced sea lamprey populations by 80%–90% (Smith & Tibbles, 1980). These changes resulted in historically high levels of lake whitefish in the early 1990s (Ebener et al., 2021; Owens et al., 2005). By the late 1990s and early 2000s, following the establishment and proliferation of dreissenid mussels (*Dreissena polymorpha* and *Dreissena bugensis*), populations in lakes Ontario, Huron and Michigan declined again due to reduced abundances of *Diporeia*, a benthic amphipod, that is a key prey for lake whitefish (Cook et al., 2005; Hoyle et al., 1999; Pothoven & Madenjian, 2008). *Diporeia* declines resulted in reduced growth rates, body condition and age-at-maturation, all of which remain impaired (Brenden et al., 2010; Ebener et al., 2021; Fera et al., 2015). The impact, however, of these ecosystem changes on the behaviour of lake whitefish remains poorly understood (Ebener et al., 2008, 2010).

In Lake Ontario, lake whitefish spatial ecology is inferred from historical records (Christie, 1963, 1967; Ihssen et al., 1985; Koelz, 1929), through general knowledge of the species from other Great Lakes (Ebener et al., 2010; Li et al., 2017) including oxythermal habitat preferences (10–14°C and ≥7 mg L^{-1}; Crowder & Magnuson, 1982; Bernatchez & Dodson, 1985; Reed et al., 2023), and more recently, an acoustic telemetry study focused on broad-scale movements in the Bay of Quinte and eastern Lake Ontario (Beech et al., 2024). Lake whitefish are thought to be mostly distributed in the eastern portion of Lake Ontario (east of Brighton, ON and Oswego, NY; Hoyle, 2005; OMNRF, 2023). Historical descriptions of habitat use for lake whitefish suggest that the species was concentrated east of Brighton, with the highest catches north of Main Duck Island in eastern Lake Ontario (Christie, 1963). Subsequent studies reported a more restricted distribution, including the lower Bay of Quinte and the Kingston Basin ('bay' stock) and areas surrounding the Duck Galloo Ridge ('lake' stock) (Beech et al., 2024; Christie et al., 1987; Ihssen et al., 1985). Although these broad-scale descriptions exist, fine-scale (e.g., seasonal and bathymetric) spatial ecology of lake whitefish remains poorly understood and can be informed using acoustic telemetry such as in the present study.

Lake whitefish are thought to be demersal (Kraus et al., 2023; Schaefer et al., 2022) with spring habitat occupancy believed to occur between 15 and 40 m when water temperatures are isothermal ≤16°C (Hoyle, 2015). Summer thermal habitat has been documented to occur at depths (20–50 m) below the thermocline (≤ 16°C) and could be restricted by summer hypoxia (Gorsky et al., 2012; Kraus et al., 2023). Lastly, fall and winter habitat use tends to be ≤8 m (temperatures are isothermal ≤10°C) as the species moves on to shallow rocky reefs in the fall to spawn, with winter distributions thought to be relatively near these spawning locations (Goodyear et al., 1982; Muir et al., 2025). The loss of *Diporeia* sp. (Burlakova et al., 2022; Dermott et al., 2005), however, might alter demersal behaviour of lake whitefish, as they are forced to find alternative prey [e.g., benthic (dreissenid mussels) and pelagic (*Bythotrephes longimanus*) prey] (Hoyle et al., 1999; Hoyle, 2005; Lumb et al., 2007; Emma J. Bloomfield, unpublished data). Reductions in abundance, body condition, growth rate and age-at-maturity (Ebener et al., 2021; Hoyle, 2005; Lumb et al., 2007) have been attributed to prey-driven changes in habitat occupancy (Rennie et al., 2015; Weidel et al., 2014) with recent work in the Great Lakes suggesting the species might seasonally occupy different areas than previously thought as the depth of capture (e.g., gill nets) has become shallower post-dreissenid invasion (Hoyle, 2015; Rennie et al., 2015). These novel areas could be in pelagic habitats; however, investigations into such vertical movements have not occurred. Vertical habitat use can be classified into two different types, distance below surface and distance above bottom, with distance below surface being representative of the depth of the fish from the surface usually obtained by a pressure sensor either in a biologger or in an acoustic telemetry transmitter. Although distance above bottom is derived by taking the difference between the distance below surface and the bathymetric depth at which a hydrophone is deployed. Gaining an improved understanding of the spatial ecology and vertical habitat (i.e., distance below surface and distance above bottom) use of lake whitefish will provide foundational information about how the species adjusts to current and future disturbances, including further changes in prey (e.g., benthic invertebrates) and a warming climate.

In this study, we provide novel information using acoustic telemetry over a 3-year period (2021–2024) to describe monthly home range area (km^2), depth below the surface (i.e., distance below surface) and differences in bottom-oriented versus suspended behaviours (i.e., distance from the lakebed) for lake whitefish in Lake Ontario. We hypothesized that the area (km^2) of horizontal space used by lake whitefish in eastern Lake Ontario changes monthly because of seasonal changes in habitat and prey availability (Ebener et al., 2021; Reed et al., 2023). We predicted that during summer months when the lake is stratified (i.e., June through September) lake whitefish use less area and occupy offshore regions (depth > 30 m). Additionally, we hypothesized that vertical behaviours (i.e., distance below surface and distance above bottom) will change seasonally considering recent observations in diets suggest the species is feeding on pelagic prey (Lumb et al., 2007; OMNRF, 2022; Emma J. Bloomfield, unpublished data). We predict that lake whitefish will exhibit greater suspended behaviour when the lake is stratified, as their diet incorporates pelagic prey (e.g., *Bythotrephes longimanus*). By enhancing the current understanding of the spatial ecology of lake whitefish in Lake Ontario, management and conservation strategies can more accurately reflect mechanisms that govern declines in abundance, body condition, growth rates and age-at-maturity.

2 | METHODS

2.1 | Study system and acoustic telemetry array

Our study was conducted in Lake Ontario (average depth 86 m; maximum depth 244 m; surface area 18,960 km^2) with tagging efforts concentrated near Point Petre in the eastern third of the lake where current lake whitefish fisheries occur (Figure 1). Since 2021, Lake Ontario has had a continuous grid of 69 kHz receivers spaced

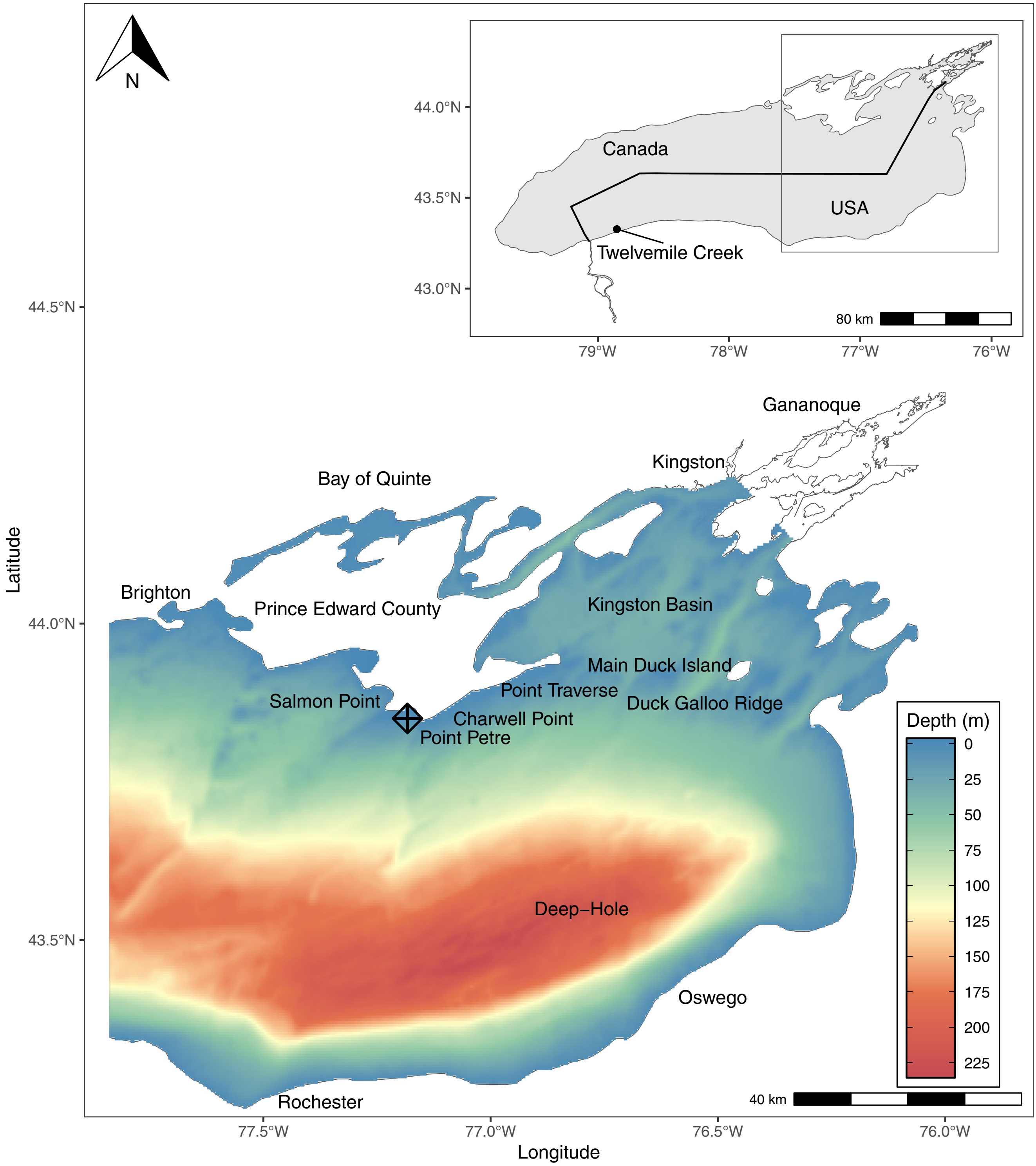

FIGURE 1 A map of eastern Lake Ontario showing major bathymetry and place names referred to in the text. The diamond represents the release location for tagged lake whitefish. The black dot in the inset map of Lake Ontario indicates the mouth of Twelvemile Creek, New York, USA, which is the furthest location from the release point that a tagged lake whitefish was detected.

~15 km apart in the offshore, with denser concentrations (~2–7.5 km) in the eastern third of the lake (Figure 2). This gridded array provides the ability to understand the behaviour of lake whitefish throughout the lake including the eastern portion. The shallower Kingston Basin of Lake Ontario is distinguished by the Duck-Galloo Ridge that consists of a series of shoals and islands that delineate this basin from the rest of Lake Ontario (Figure 1). For the region, periods of non-stratification occur from October to May with water temperature ≤ 16°C, whereas stratification occurs in June–September with the epilimnion ≥16°C (OMNRF, 2022).

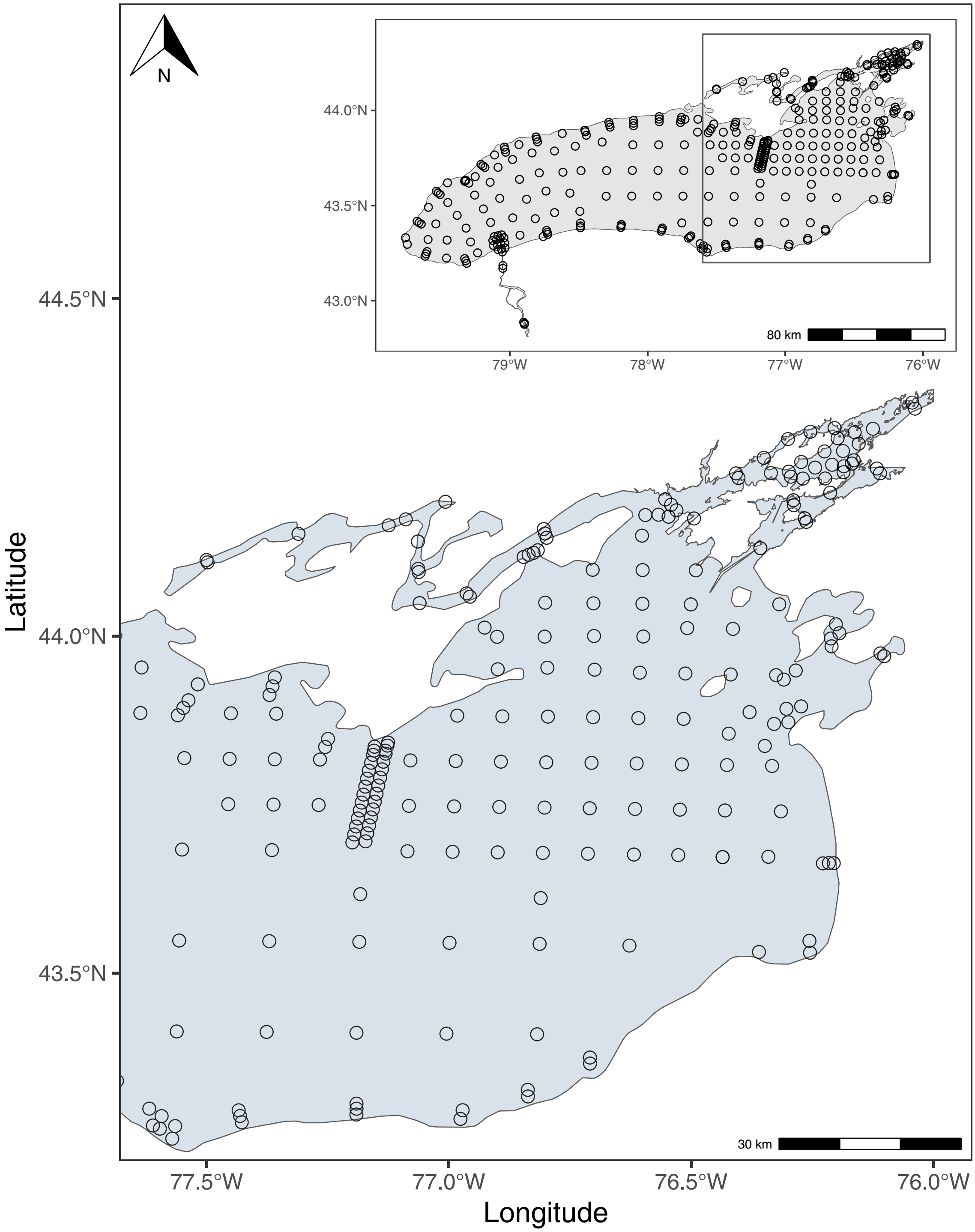

FIGURE 2 Distribution of 69 kHz acoustic telemetry receivers in eastern Lake Ontario from 2021 to 2024. The inset map contains the entire receiver array in Lake Ontario.

2.2 | Acoustic telemetry tagging

Lake whitefish were captured and implanted with acoustic transmitters (Innovasea Inc., Bedford, NS, Canada) on 9, 10 and 16 November 2021 ($n = 30$), 23 November 2022 ($n = 31$) and 20 November and 5 December 2023 ($n = 30$). Fish were captured using short-set gill nets set in the evening between 16:30 and 17:00 and lifted in the dark between 19:00 and 22:30 (3.5–5 h soak time). Nets consisted of 114-, 127-, 140- and 152-mm mesh panels (each panel 15.2 m × 2.4 m) that were attached in a sequential order to make one gang. Two gangs were attached together making a net 121.6 m in length. A total of 5–9 nets were set each night between Charwell Point and Salmon Point (Figure 1) on the south shore of Prince Edward County in shallow water (between 3 and 9 m bathymetric depth), when fish

TABLE 1 Transmitter information and biological attributes of lake whitefish tagged from 2021 to 2023 in Lake Ontario.

Year	Tag model	Tag life	Sensor range (m)	Sex	*n*	Total length (mm)	Weight (kg)
2021	V16	3395 days		F	7	494 ± 14	
				M	8	508 ± 13	
	V16P	3080 days	136	F	3	542 ± 12	
				M	11	520 ± 8	
				U	1	489	
2022	V13P	639 days	136	F	2	464 ± 1	1.19 ± 0
				M	3	470 ± 12	1.15 ± 0.02
	V16	3395 days		F	3	518 ± 26	1.67 ± 0.17
				M	7	501 ± 7	1.47 ± 0.09
	V16P	3080 days	136	F	1	482	1.48
				M	11	507 ± 7	1.51 ± 0.11
	V16TP	3650 days	168	F	3	524 ± 26	1.86 ± 0.26
				U	1	507	
2023	V13	1048 days		F	2	458 ± 2	1 ± 0.02
				M	8	493 ± 7	1.26 ± 0.07
	V13P	730 days	136	M	10	510 ± 9	1.33 ± 0.05
	V16P	2845 days	136	F	4	535 ± 15	1.81 ± 0.18
				M	6	525 ± 12	1.65 ± 0.10

Note: Values are expressed as the mean ± the standard error of the mean.

moved into this area to spawn. Fish were tagged during spawning as they were aggregated in shallower water (reduced risk of barotrauma) making them easier to catch. Fish were transported to shore in aerated live wells, then held in a 6 m diameter inflatable swimming pool for a maximum of 1 h prior to and following surgery. Total length (mm) and weight (0.1 g) were recorded, and sex was determined when possible.

Surgeries followed standard procedures (Beech et al., 2024; Cooke et al., 2012). Fish were electro-sedated using electric fish handling gloves (Smith-Root, Vancouver, WA, USA) while in a mesh cradle with a continuous flow of fresh lake water over their gills. Lidocaine (6–10 mg kg^{-1}) was subcutaneously injected at the incision site. A transmitter was inserted into the peritoneal cavity through a small midline incision between the pelvic and pectoral fins and closed with two to three sutures (3–0 Vicryl sutures, Ethicon, NJ, USA). The transmitter type, number of fish tagged, mean length and mean weight for each year are reported in Table 1 with transmitter specifications reported in Table S1. Fish were externally marked with a self-locking loop tag (Floy Tag & Manufacturing Inc., Seattle, WA, USA) through the dorsal muscle posterior to the dorsal fin to alert commercial harvesters to the internal tag. Surgeries and external marking were typically completed in less than 3 min. Fish were returned to the pool for approximately 10 min of observation prior to being released from shore in the vicinity of capture. Tagging procedures followed and were approved by the OMNR Fisheries Animal Care Committee for permit number 171 on 1 November 2021. Acoustic detections were retrieved during the fall of each year from the Lake Ontario Great Lakes Acoustic Telemetry Observation System (GLATOS) centralized database.

2.3 | Data and statistical analysis

Acoustic detection data recorded between November 2021 and October 2024 were used in this analysis. Data manipulation, analyses and figures were produced in R version 4.4.1 with statistical significance being set to 0.05 and the data reported as the mean ± the standard error of the mean. Acoustic telemetry detection data were cleaned by removing detections from transmitter identifiers (IDs) that were not affiliated with the tagging efforts described above (Lake Ontario lake whitefish project) and using a minimum lag filter (i.e., time between detections) that was applied to each transmitter ID at each receiver (Pincock, 2012). Data were further inspected visually using abacus plots (Klinard & Matley, 2020) to identify suspected fish mortality or tag expulsion. Transmitter IDs with continuous detections at a single station and/or at a consistent depth were removed. Fish that were detected for less than 30 days and not reported as harvested were assumed to be tagging-related mortalities and were removed from the analysis (Izzo et al., 2024). Lastly, the first week of detections for all retained fish was removed considering tagging effects (Matley et al., 2024).

To understand monthly horizontal spatial use for lake whitefish in eastern Lake Ontario, the filtered acoustic telemetry detections were grouped by ID and 20 minute intervals to create a centres-of-activity (COA) dataset that included the number of detections, number of stations and the mean latitude and longitude. This dataset was further analysed by calculating the kernel utilization densities (KUD) estimates using the package {amt}; for each month an individual was detected with density levels set to 50%, 80% and 95% (Signer et al., 2019).

These 50% KUDs have been described as the core home range of an animal, the 80% as the majority home range of an animal and the 95% as the maximum home range of an animal (Ivanova et al., 2021). To understand the home range and spatial extent of the tagged population, KUDs were calculated by aggregating all individual detections for all fish, each month, with density levels set to 50%, 80% and 95%. Kernel densities were calculated when an individual had a minimum number of five or more locations in a month. The area of each density level was determined for each individual and month detected, and a generalized linear mixed-effects model (GLMM) using the package {glmmTMB} with a Gamma error distribution and link function set to log was used to determine if there were monthly changes in horizontal spatial use (Brooks et al., 2017). Models were made for each density level, considering that comparing the areas between levels does not make sense. Each model had a response variable of the area used and a predictor of month with the ID of each fish and the year as random effects.

To understand monthly differences in the distance below surface of the fish (i.e., vertical spatial use), we determined the mean depth occupied for each hour of each day for each fish that were implanted with transmitters equipped with depth sensors. A generalized additive mixed-effect model (GAMM) with a Gamma error distribution and link function set to log was used determine whether the distance below surface of the fish (i.e., response) differs by day-of-year (i.e., predictor), whereas a GLMM with a Gamma error distribution and link function set to log was used to determine whether distance below surface of the fish (i.e., response) differs among months (i.e., predictor). The model structure for the GAMM consisted of the daily mean distance below surface of the fish as the response with day-of-year as a smoother using cyclical cubic regression spline (cc) that had 30 knots and crossed random effects of individual fish and year. The structure of the GLMM had mean hourly distance below surface of the fish as the response with month as a predictor and crossed random effects of year and individual fish.

We also determined fish distance off the lake bottom to explore differences in monthly bottom-oriented versus suspended behaviour. We used the filtered detection data described in the first paragraph of this section and not COA positions for this analysis. First, we randomly sampled 250 bathymetric points within the 50% detection range (Klinard et al., 2019) surrounding each acoustic receiver station depending on each transmitter type (V13 or V16) for each detection. Generated depths that were shallower than the reported transmitter depths were removed because the fish could not physically occupy these locations. From these samples, we calculated the mean depth surrounding each receiver for each fish detection. We determined the distance the fish was from the bottom by subtracting the depth of the fish (from the depth sensor in the acoustic transmitter) from the mean depth that the receiver covered. If the distance from the bottom was greater than 5 m the fish was considered suspended off bottom and if the distance from the bottom was less than 5 m the fish was considered bottom-oriented. Hourly estimated distance from bottom was calculated for each day (1–365) for each individual. Changes in mean hourly distances from bottom (i.e., response) were assessed on a daily (i.e., smoother) and monthly (i.e., predictor) basis using a GAMM with a Tweedie error distribution and link function set to square root and GLMM with a Gamma error distribution and the link function set to log. The model structure for the GAMM consisted of the daily mean distance from bottom as the response with day-of-year as a smoother using cc spline that had 60 knots and crossed random effects of individual fish and year. The structure of the GLMM had mean hourly distances off bottom as the response with month as a predictor and crossed random effects of year and individual fish.

For GLMMs, model fit was assessed by evaluating the residuals and using the package {DHARMa} to assess whether the model was appropriate for the data (Hartig, 2022), whereas GAMM model fits were assessed using the package {gratia} (Simpson, 2024). Post-hoc comparisons of monthly differences in KUD areas, distance above bottom and distance below surface of the fish were conducted using Tukey's post hoc test with Šidák correction using the package {emmeans} (Lenth, 2024).

3 | RESULTS

3.1 | Detection summary

The raw movement data consisted of 91 individuals that were tagged in late November to early December of each year for 3 years (2021–2023; $n = 30$–31 each year). After the data were filtered, 81 fish were assessed for this study with 59% ($n = 48$) having a transmitter equipped with pressure sensors providing the depth of the fish in metres (range = 1.5–82.5 m). Our analysis consisted of 537,875 detections of 81 fish on 113 of 153 (71%) possible receivers in eastern Lake Ontario. Each lake whitefish averaged 6640 ± 1118 detections on 13 ± 1 receivers and had an average detection duration of 233.1 ± 27.8 days. Fish were not detected along the north shore of Lake Ontario west of Brighton ($n = 159$ receivers covering 46.2% of the lake area), but five individuals (5.5% of tagged fish) were detected on the south shore west of Oswego, with the furthest detection from the tagging location near the confluence of Twelvemile Creek at Wilson, New York, USA. These movements represent 0.05%–12.10% of the total detections of the five fish and occurred between December and April, with two of the five fish returning to the Kingston Basin by May.

3.2 | Kernel densities

We observed monthly differences in the location occupied and area used by lake whitefish, with changes in the 50% (GLMM; $\chi^2_{1,11} = 67.58$, ≤ 0.001), 80% (GLMM; $\chi^2_{1,11} = 63.89$, $p \leq 0.001$) and 95% (GLMM; $\chi^2_{1,11} = 63.89$, $p \leq 0.001$) KUDs among months (Table 2). From January through April, lake whitefish tended to use the southwest shore of Prince Edward County, the Kingston basin, Chaumont Bay and central Duck Galloo Ridge (Figure 3). During May horizontal space use shifted east, becoming more focused on the Duck Galloo Ridge. Movement became further constrained to the central Duck Galloo Ridge in June through September. In October,

TABLE 2 The surface area of eastern Lake Ontario (8884.3 km^2; east of Brighton, ON, CAN and Rochester, NY, USA; west of Gananoque, ON, CAN) used for each month by lake whitefish for the 50%, 80% and 95% kernel utilization densities (KUD).

Month	Area used (km^2; 50%)	Area used (km^2; 80%)	Area used (km^2; 95%)	Percentage of available area used (50%)	Percentage of available area used (80%)	Percentage of available area used (95%)
Jan	155 ± 14^{ab}	438 ± 43^{a}	890 ± 93 ^{a}	1.74 ± 0.15	4.93 ± 0.49	10.02 ± 1.04
Feb	135 ± 22^{ab}	356 ± 51^{a}	666 ± 80^{a}	1.53 ± 0.25	4.00 ± 0.57	7.49 ± 0.90
Mar	132 ± 14^{a}	361 ± 35^{a}	713 ± 65^{a}	1.49 ± 0.15	4.06 ± 0.39	8.02 ± 0.73
Apr	135 ± 9^{a}	370 ± 26^{a}	738 ± 54^{a}	1.51 ± 0.10	4.16 ± 0.29	8.31 ± 0.60
May	137 ± 9^{a}	369 ± 24^{a}	735 ± 47^{a}	1.54 ± 0.11	4.16 ± 0.27	8.27 ± 0.53
Jun	138 ± 18^{a}	369 ± 44^{a}	728 ± 75^{a}	1.56 ± 0.21	4.15 ± 0.49	8.19 ± 0.84
Jul	170 ± 34^{ab}	451 ± 87^{ab}	902 ± 173^{ab}	1.91 ± 0.38	5.08 ± 0.98	10.15 ± 1.94
Aug	144 ± 22^{ab}	405 ± 63^{ab}	795 ± 129^{ab}	1.62 ± 0.24	4.55 ± 0.71	8.95 ± 1.45
Sep	189 ± 27^{ab}	523 ± 75^{ab}	1031 ± 141^{ab}	2.13 ± 0.30	5.89 ± 0.84	11.60 ± 1.59
Oct	241 ± 56^{ab}	637 ± 160^{ab}	1250 ± 305^{ab}	2.71 ± 0.63	7.17 ± 1.81	14.07 ± 3.43
Nov	184 ± 16^{ab}	504 ± 46^{ab}	955 ± 85^{ab}	2.07 ± 0.18	5.67 ± 0.51	10.74 ± 0.95
Dec	217 ± 13^{b}	624 ± 35^{b}	1271 ± 67^{b}	2.44 ± 0.15	7.02 ± 0.40	14.31 ± 0.76

Note: Letters denote statistical differences between months within a KUD category with alpha set at 0.05. Values are expressed as the mean ± the standard error of the mean.

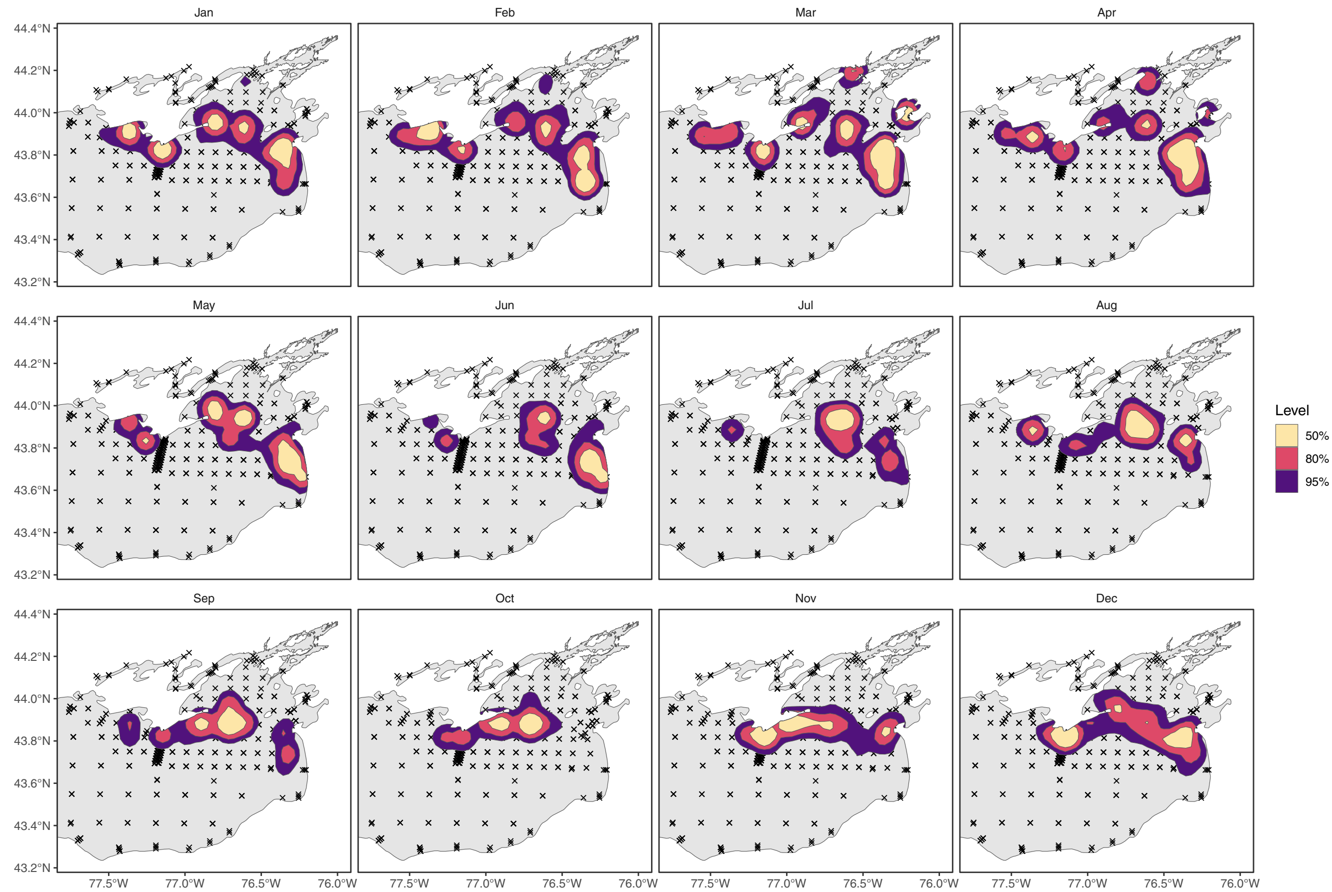

FIGURE 3 Monthly kernel utilization densities (KUD) for the tagged population (aggregation of individual KUDs) of lake whitefish (*Coregonus clupeaformis*) in eastern Lake Ontario. Each × represents the location of an acoustic telemetry receiver that a tagged lake whitefish could have been detected on. The orange fill represents the 50% KUD, the red fill represents the 80% KUD and the purple fill represents the 95% KUD.

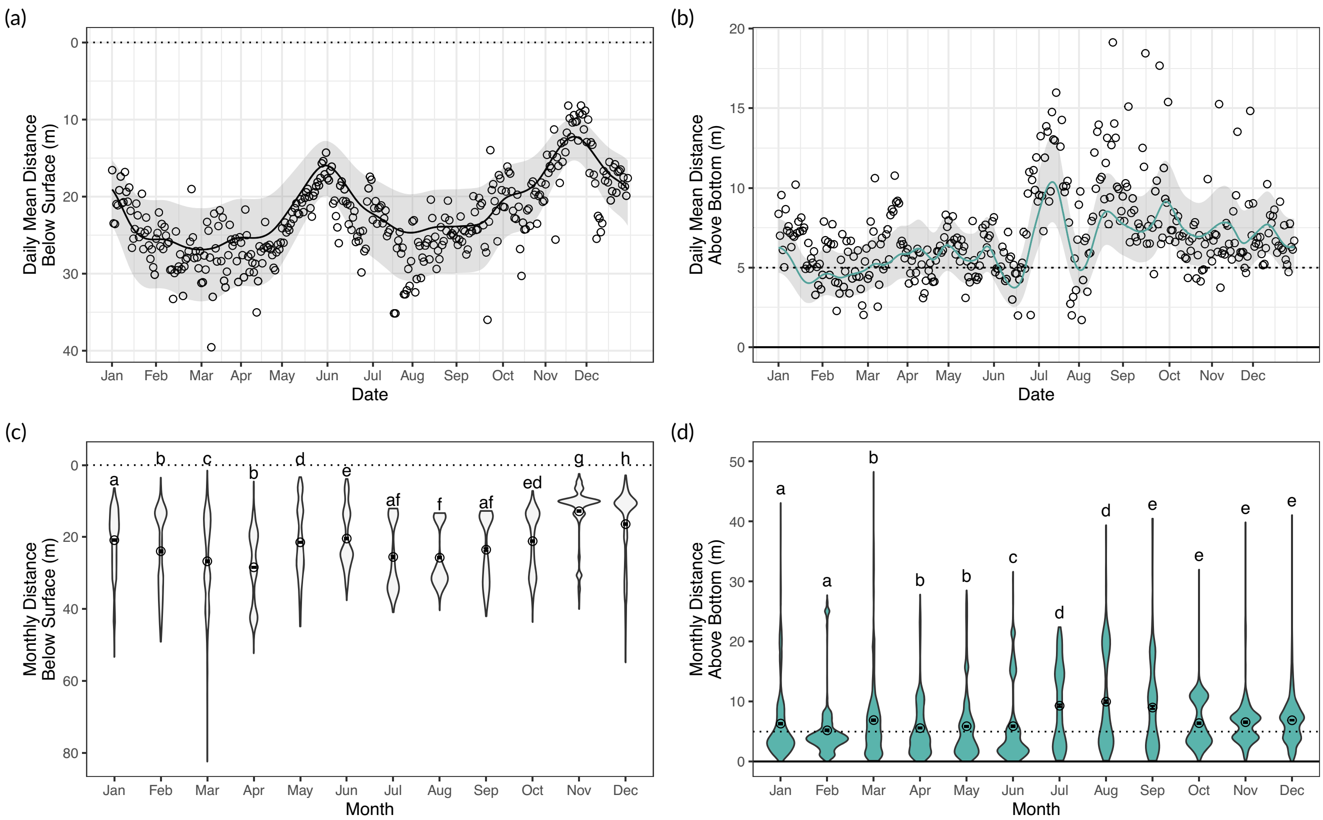

FIGURE 4 Daily and monthly fish distance below surface (a, c, respectfully) and distance above bottom (b, d, respectfully) for lake whitefish (*Coregonus clupeaformis*) in eastern Lake Ontario. Grey shading indicates the 95% confidence intervals for generalized additive mixed-effects models, whereas open-circles are the daily mean for each measurement. Differences in letters represent statistical significance with alpha set to 0.05. Points and error bars in (c, d) represent the mean ± the standard error of the mean. The dotted line in (a, c) represents the surface, whereas in (b, d) it represents 5 m off the bottom of the lakebed.

lake whitefish started returning to the south shore of Prince Edward County more than the Duck Galloo Ridge. Habitat use in November was concentrated along the southwest shore of Prince Edward County but did extend to the Duck Galloo Ridge. The use of these areas (west of Point Traverse) became more prominent after spawning (late November to early December) as fish started to use the outer portion of the eastern area of Lake Ontario. The 50% area used by lake whitefish was significantly lower in June than in December (Table 2). The 80% area used was significantly lower in April, May and June when compared to December and the 95% area used was significantly lower in February, April, May and June, than December (Table 2). Overall, the 50% area used (core home range) by lake whitefish ranged from 1.49% to 2.71% (mean) of eastern Lake Ontario while the extent of fish movement ranged from 7.49% to 14.31% of the eastern portion of Lake Ontario (Table 2).

3.3 | Distance below surface and distance above bottom

Fish did not use depths >82.5 m, with 99% of detections on receivers <60 m deep, even though receivers are distributed across all available depths (5–240 m). Daily distance below surface of the fish (GAMM day-of-year smoother; edf = 18.74, ref. df = 28, $F = 1492.3$, $p \leq 0.001$; explained 63.5%; $R^2 = 0.696$; Figure 4a) differed among days with longer trends extending among months. Daily depth increased from January through April (20–30 m), then decreased rapidly between May and the start of June (15–20 m). Daily distance below surface for lake whitefish decreased rapidly from mid-June through late-September (20–30 m), then gradually decreased to an annual minimum in late November coincident with spawning. Monthly summaries of distance below surface for lake whitefish reinforced the general depth trends (GLMM; $\chi^2_{1,11} = 6767.3$, $p \leq 0.001$; Figure 4c) but also reveal changes in the range of depths occupied. The average distance below surface that lake whitefish used gradually increased from January (20.9 ± 0.2; 6.5–53.4 m) through April (28.4 ± 0.2; 4.6–52.4 m). Average distance below surface remained around 25–30 m from May through September, although the minimum depth increased (12.0–13.0 m) and the range of depths used (12.0–41.0 m) was less in July through September compared to May and June. After September, average distance below surface used decreased, with the shallowest average distance below surface occurring in November (12.8 ± 0.2; 2.4–40.0 m) and December (16.4 ± 0.2; 2.8–54.9 m), presumably as the species moved into shallower areas to spawn. The range of depths occupied also increased from September through December (2.4–55.0 m).

Daily distance above bottom for lake whitefish differed among days (GAMM day-of-year smoother; edf = 28.12, ref. df = 58.00, $F = 62.60$ $p \leq 0.001$; deviance explained 41.2%; $R^2 = 0.391$; Figure 4b), with both greater variation and greater distance of bottom from July through October compared to the period from January through June. We did investigate distance above bottom by each hour in a day (i.e., 0–23 h) among months and did not see differences. Similar trends were seen when data were analysed more broadly by month (GLMM; $\chi^2_{1,11} = 1057.7$, $p \leq 0.001$; Figure 4d). From January through June, lake whitefish were more bottom-oriented with the mean distance above bottom varying between 5.3 ± 0.1 m (i.e., February; 0.1–71.3 m) and 7.0 ± 0.2 m (i.e., March; 0.2–55.7 m). By early July, lake whitefish exhibit greater distances off bottom with majority being >5 m (Figure 4b). From July through December, fish often demonstrated bimodal bottom-oriented and suspended behaviour, with fish showing the strongest suspended behaviour in August (9.9 ± 0.2 m) and September (9.1 ± 0.3 m). In October, fish exhibited distances off bottom that were more similar to winter and spring distances (6.4 ± 0.2 m; Figure 4b), whereas November (7.8 ± 0.2 m) and December (7.5 ± 0.1 m) were again reflective of suspended behaviour. From January through June, 59.5% or more of detections were classified as bottom-oriented compared to suspended, although fish in March only exhibited bottom-oriented behaviour 45.8% of the time. From July through September fish exhibited suspended behaviours for >52.2% of detections, before becoming more bimodal (50.8% bottom-oriented and 49.2% suspended detections) in October, and more prominently suspended (> 65%) in November and December.

4 | DISCUSSION

Our study provides novel information about horizontal and vertical space use (i.e., distance below surface and distance above bottom) of lake whitefish in Lake Ontario. This study is only the second telemetry study on lake whitefish in Lake Ontario and provides new observations using an expanded receiver array, a greater number of fish tagged, a longer study duration and a novel analysis of bottom-oriented and suspended behaviours. During non-stratified cooler months (i.e., Oct–May; water temperature ≤ 16°C), lake whitefish were distributed along the south and west shores of Prince Edward County and along the Duck Galloo Ridge, whereas during warmer months (i.e., June–September; periods of stratification with the epilimnion ≥16°C) fish distribution was more concentrated on the Duck-Galloo Ridge. Home range core and extent (i.e., 50 and 95%) changed more during seasonal transition periods (e.g., September–October) than among individual months within a season (e.g., March–April). Core home ranges were small regardless of month when compared to the overall extent of eastern Lake Ontario, with fish using approximately 14% or less of eastern Lake Ontario. Fish did not use much of the Kingston Basin with the areas used having not been previously documented (i.e., winter movement between Amherst and Simcoe Island) and were not observed using the Bay of Quinte. Furthermore, if fish moved between north (Prince Edward County) and south (New York State) shores of Lake Ontario, they did not move directly across the lake and instead they moved along the Duck-Galloo Ridge with bathymetric depth restricted between 10 and 50 m. There were a few individuals ($n = 5$; 5.5% of tagged individuals) that made more extensive movements along the south shore (i.e., Oswego, NY, USA to Wilson, NY, USA). These movements, however, were infrequent and likely demonstrate straying individuals and not population trends in movement and behaviour for lake whitefish from the north shore of eastern Lake Ontario. An ongoing species spatial delineation project suggests the majority of lake whitefish occupy northeastern Lake Ontario, with no known spawning stocks along the south or western shorelines (Josh Egan, USGS, personal communication). Overall, our findings demonstrate that lake whitefish use a restricted range of depths with horizontal space use representing <14% of eastern Lake Ontario throughout the year.

Our observations of seasonal horizontal and vertical movement were slightly different and more comprehensive for lake stock lake whitefish than a previous study that focused on general horizontal movement for bay and lake stocks in eastern Lake Ontario (Beech et al., 2024). Our study benefited from a more extensive receiver network and larger number of tagged fish, that revealed more frequent use of the Duck-Galloo Ridge and greater temporal use of the southern shore of Prince Edward County. We also confirmed a much more restrictive range of depths used by lake whitefish that included no evidence of fish traversing deep water when moving between north and south shorelines. Furthermore, we provide novel information about bottom-oriented and suspended behaviours of lake whitefish that were previously unknown. These differences in observations between our study and Beech et al. (2024) could be attributed to differences in tagging cohorts and sample size, yearly changes in thermal habitats and/or prey abundances that can drive movement and the improved detection coverage caused by the addition of receivers throughout Lake Ontario to completely grid the lake. Considering we did not tag fish from the Bay of Quinte we cannot compare nor postulate about the behaviour of this stock. Furthermore, neither our (spawned on the south shore of Prince Edward Count; lake stock) nor lake stock lake whitefish from Beech et al. (2024) enter the Bay of Quinte, confirming historical observations (Christie, 1963, 1967; Ihssen et al., 1985; Koelz, 1929). This more comprehensive description of lake whitefish behaviour and spatial occupancy can support evidence-based management decisions including stock management and harvest limits, including continuous management of lake whitefish as two discrete stocks (i.e., lake and bay stocks) in Lake Ontario.

The distance below surface and distance above bottom for lake whitefish provides previously unknown insight into vertical behavioural patterns for the species in Lake Ontario. Fish occupied deeper water during periods of seasonal stratification (i.e., June–September) than non-stratified periods (i.e., October–May) that could be a result of the species seeking preferred thermal habitats (10–14°C) that are energetically beneficial (Crowder & Magnuson, 1982; Dabrowski, 1985; Gorsky et al., 2012). Lake Ontario tends to have dissolved oxygen levels >7 mg L^{-1} (OMNRF, 2023); therefore, hypoxia is an unlikely factor influencing these distributions (Kraus et al., 2023), with temperature and/or prey being a more likely driver of these changes in depth use (Guiden et al., 2019; Hansen, 2021; Pörtner & Peck, 2010). These abiotic and biotic factors, however, have not been fully investigated and are a knowledge gap in understanding the spatial ecology of lake whitefish. Future research needs to combine our observations of changes in distance below surface and distance above bottom with direct measurements of changes in thermal habitats, prey distributions and/or diets to verify these hypotheses.

Distance above bottom consisted of bimodal distributions during the summer and fall, indicating fish were exhibiting both bottom-oriented and suspended behaviours, whereas in winter and spring bottom-oriented behaviours dominated. Lake whitefish are described as a demersal species occupying cooler, offshore habitats (Kraus et al., 2023; Schaefer et al., 2022), with previous understanding of vertical habitat use based on sampling that was strongly biased to benthic habitats (bottom set gears) (Fera et al., 2017; OMNRF, 2022; Rennie et al., 2015). Further, historical diet studies show strong reliance on benthic *Diporeia* sp. (>70 m; Burlakova et al., 2018) indicating lake whitefish likely inhabited deeper waters and/or spent significant time on or near the bottom (Dermott et al., 2005; Herbst et al., 2013; Nalepa et al., 2005). Our bimodal observations during warmer months may reflect a shift to using shallower waters (i.e., distance above bottom) after the collapse of *Diporeia* sp. and/or a feeding strategy that incorporate both bottom-oriented and suspended behaviours. Recent studies have shown changes in the depth of capture (i.e., bathymetric depth; trawls and gill nets) of lake whitefish in the Great Lakes, with depth initially increasing with the introduction of dreissenids, then drastically decreasing in the mid-2000s (Riley & Adams, 2010; Rennie et al., 2015; Fera et al., 2017). These trends potentially illustrate a wider trend that lake whitefish are adjusting feeding strategies to account for the loss of nutrient-rich benthic prey. These hypotheses, however, need to be further explored considering the limited number of prey studies and our study being the first study to classify movement data into bottom-oriented or suspended lake whitefish. Current population metrics (i.e., abundance, condition, maturation and growth rates) are based off of late-summer and fall monitoring programmes that rely on benthic gear (OMNRF, 2022). These methods may fail to capture shifts in habitat use and behaviour. Monitoring programmes should consider how these potentially novel or emerging behaviours may impact their assessment of lake whitefish stocks.

Overall, our observations of lake whitefish in Lake Ontario are comparable to movement studies of the species in other Great Lakes. These observations include the prevalence of along-shoreline movements (e.g., Lake Huron; Li et al., 2017), hypolimnetic occupancy during stratified conditions (Gorsky et al., 2012; Kraus et al., 2023; Reed et al., 2023) and high seasonal location fidelity (e.g., repeated yearly movement to same locations; Reed et al., 2023; Izzo et al., 2024). Noticeably, lake stock lake whitefish in Lake Ontario move comparatively shorter distances compared to populations in lakes Huron, Michigan and Superior (Ihssen et al., 1981; Isermann et al., 2020; Li et al., 2017). This reduced range of movement may be attributed to closer proximity to habitat and food resources in Lake Ontario compared to other Great Lakes (Hoyle, 2015). A more restricted range of movement may make the Lake Ontario lake whitefish more vulnerable to exploitation and/or habitat changes that could compromise management objectives and thus fisheries management should continue to closely monitor harvest and abundance.

Our observed horizontal and vertical distributions may not be consistent with previously documented habitat use as the species may be altering behaviour in response to the loss of essential prey (e.g., *Diporeia*) that influences energy allocation (Christie et al., 1987; Ihssen et al., 1981; Rennie et al., 2009). Changes in prey availability and habitat occupancy can profoundly influence energy allocation for a species because sub-optimal prey may be less nutritious and/or more energy may be needed to locate (e.g., horizontal and/or vertical movement) and ingest novel prey (Pothoven & Madenjian, 2013; Pothoven & Nalepa, 2006). Higher foraging costs and/or less energy-rich prey can result in less energy for somatic and gonadal production, because energy allocation becomes focused on survival and food acquisition (Canosa & Bertucci, 2020). Recent population health indicators (i.e., condition, age-at-maturity, growth rates and abundance) have declined for lake whitefish in Lake Ontario (Lumb et al., 2007; OMNRF, 2022) and throughout the Laurentian Great Lakes (Ebener et al., 2021). These changes have been attributed to the lack of optimal benthic prey and/or thermal habitats (Lumb & Johnson, 2012; Taylor et al., 2024; Tellier et al., 2023). Although our study provides insights into lake whitefish behaviour, future studies should explore the drivers (e.g., combining diets and/or stable isotopes with telemetry) that contributed to observed localized spatial distributions and suspended behaviours (Izzo et al., 2024; Kraus et al., 2024).

Lake whitefish hold cultural and commercial value in Lake Ontario (Casselman et al., 1996; Ebener et al., 2008). Localized spatial occupancy (i.e., habitat compression) and possibly increases in movements in search of prey (i.e., increased energy expenditures) may result in lake whitefish being easily exploited (Bailey et al., 2022; Dunlop et al., 2018; Kraus et al., 2024). This could result in increases in catch-per-unit-effort related to activity and not abundance. Furthermore, targeted effort (e.g., harvest or assessment) in specific areas (lake whitefish utilize <14% of the eastern portion Lake Ontario) could inflate abundance estimates biasing the overall understanding of lake whitefish stocks in eastern Lake Ontario. Monitoring and evidence-based management decisions are essential to ensure the sustainability of the species in the lake (Isermann et al., 2020). Fisheries assessment and monitoring efforts could be better informed based on spatial and depth distribution observed in the present study, improving information on population status (e.g., abundances, condition and maturation and growth rates) and the mechanisms that influence the population (e.g., benthic processes).

AUTHOR CONTRIBUTIONS

Study design was conceived by Timothy B. Johnson, Brent W. Metcalfe and Emma J. Bloomfield. Statistical analyses and figure curation were completed by Benjamin L. Hlina and Rylie L. Robinson. Benjamin L. Hlina drafted the first version of the manuscript with all authors contributing to revisions.

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CONFLICT OF INTEREST STATEMENT

All authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code related to this study are available at the following links: https://doi.org/10.5281/zenodo.15595457.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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