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Patterns in spatial use of land-locked Atlantic salmon (*Salmo salar*) in a large lake

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ABSTRACT

Understanding the spatial use of reintroduced fish is useful for fisheries management and evaluating restoration success. Atlantic salmon (*Salmo salar*) were reintroduced into Lake Ontario in the 1990s; however, the movement ecology of these land-locked fish is unknown. Using acoustic telemetry and Floy tag mark-recaptures, we examined seasonal home range and space use of Atlantic salmon in Lake Ontario. Hatchery-raised adult Atlantic salmon were tagged with acoustic transmitters (n = 14; 8 with depth sensors) or Floy tags (n = 1915) and released. Both acoustic telemetry and Floy tag recaptures (n = 90) indicated cross lake movements, and home ranges encompassed nearly the entire lake in summer but was smaller in winter. Movements were nearshore (<2 km from shore) from spring to summer at ~20 m bathymetric depths, with movements closer to shore in the fall, and further offshore (~5.5 km from shore and 45 m bathymetric depths) in winter. Depth use was relatively shallow (<4 m) with occasional deeper dives (max = 28.5 m), and small diel vertical movements (1–5 m), moving deeper during daytime, consistent with ocean movements of Atlantic salmon. There appears to be spatial segregation among Atlantic salmon and other Lake Ontario salmonids, however, overlap likely occurs in nearshore waters during the spring. Wide-ranging movements of Atlantic salmon in binational (Canada/USA) waters reflects the importance of government agencies collaborating to ensure sustainable fisheries and the coordination of species restoration activities. This is the first study to provide detailed spatial use of Lake Ontario Atlantic salmon to assist in the management of this reintroduced species.

Introduction

Knowledge of the movement ecology of fish populations to understand habitat use, migratory pathways, life history, and population dynamics is beneficial for fisheries management and evaluating restoration success (Berger-tal and Saltz, 2014; Crossin et al., 2017). From a fisheries management perspective, knowledge of movement patterns and spatial ecology can assist in the establishment of management boundaries (Binder et al., 2017; Hayden et al., 2014; Hussey et al., 2017), spatial-temporal requirements for habitat protection (Rous et al., 2017; Simpfendorfer et al., 2010), identifying potential sources of mortality (Cooke et al., 2011; Raby et al., 2015) and stock assessment parameters (e.g. spawning site fidelity, residential vs migratory populations; Espinoza et al., 2016; Zemeckis et al., 2014). Similarly for stocked fish, understanding the post-release spatial ecology and stocking success can assist with management decisions for reasons mentioned above but also in evaluating restoration success (Berger-tal and Saltz, 2014; Klinard et al., 2020).

Understanding large-scale movements of salmonids in the Laurentian Great Lakes has aided in the management of these socially and economically important species (Crossin et al., 2017; Melstrom and Lupi, 2013). Using mark-recapture techniques such as tagging fish with coded wire tags or external Floy tags that are later recaptured by anglers has revealed long distance movements of individual Chinook salmon (*Oncorhynchus tshawytscha*) in both lakes Huron and Michigan (Adlerstein et al., 2008, 2007). However, there can be biases with mark-recapture techniques if recaptures are reliant on where angler effort exists (e.g., nearshore and/or near ports). With advances in technology, the use of acoustic telemetry has improved our knowledge of the movement ecology of salmonids in the Great Lakes (Krueger et al., 2018). Acoustic telemetry is the remote detection of tagged fish when in range of acoustic receivers in the water. The use of acoustic telemetry provides information on the location of individual fish to determine move-

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ment patterns and home ranges that mark-recapture studies may not reveal. For example, acoustic telemetry revealed spawning locations as well as distinct spatial movement patterns in populations of lake trout (*Salvelinus namaycush*) in Lake Huron (Binder et al., 2017; Riley et al., 2014) and migration pathways of lake trout in Lake Ontario (Ivanova et al., 2020). Acoustic telemetry has been proven as a suitable technique for understanding the movement ecology of mobile salmonid species in the Great Lakes.

In Lake Ontario, Atlantic salmon (*Salmo salar*) have been the subject of restoration efforts since the 1990s (OMNRF 2017). Atlantic salmon were extirpated from Lake Ontario in the 1890s from overharvesting, and habitat degradation and loss (Christie, 1974; Crawford, 2001). Since then, Lake Ontario's fish community has undergone extensive changes including the proliferation of alewife (*Alosa pseudoharengus*) in the mid-1900s in the absence of native predators, the stocking of non-native Pacific salmonids in the 1960s to reduce alewife populations (Crawford, 2001; Dettmers et al., 2012) and the introduction of dreissenid mussels (*Dreissena polymorpha* and *D. bugensis*) and round goby (*Neogobius melanostomus*) in the 1990s (Mills et al., 2003). Restoring native species to Lake Ontario, like Atlantic salmon, will involve management in the context of a dynamic fish community and forage base disparate from historical conditions. To restore self-sustaining populations, Atlantic salmon are regularly stocked at different life stages (fry or fingerling, parr, smolt) into tributaries and infrequently directly into Lake Ontario as adults. The movements of young stocked Atlantic salmon are relatively restricted within the tributaries, until smolts migrate to Lake Ontario. However, in Lake Ontario, the movement ecology and habitat use of adult land-locked Atlantic salmon is unknown, particularly in relation to other salmonids as potential competitors.

In addition to Atlantic salmon, Lake Ontario contains five other salmonids all of which are stocked (Chinook salmon, coho salmon *O. kisutch*, rainbow trout *O. mykiss*, lake trout *Salvelinus namaycush*, and brown trout *Salmo trutta*) and all of which can potentially overlap in spatial and trophic ecology. The diets of all salmonids in Lake Ontario (including Atlantic salmon) are dominated by alewife, (Brandt, 1986; Mumby et al., 2018; Rand and Stewart, 1998). Round goby are also consumed by lake trout and brown trout in greater numbers than by the other salmonids, while low proportions of rainbow smelt (*Osmerus mordax*) and sculpins (*Cottus cognatus* and *Myoxocephalus thompsonii*) are occasionally consumed by all salmonids (Mumby et al., 2018). Despite diet overlap, there is potential for spatial partitioning among salmonids. In Lake Huron, Chinook salmon are highly mobile, while lake trout occupy smaller home ranges and move < 100 km (Adlerstein et al., 2007; Binder et al., 2017). In Lake Ontario, lake trout occupy deeper depths than Chinook salmon and brown trout (Ivanova et al., 2021b; Olson et al., 1988; Raby et al., 2020), while brown trout stay closer to shore than lake trout and Chinook salmon (Nettles et al., 1987; Olson et al., 1988). Thus, there is some trophic overlap among all salmonids and discerning whether there is also a spatial overlap between Atlantic salmon and other species can determine if they occupy similar niches and potentially affect Atlantic salmon restoration success.

Understanding the movements and spatial ecology of Atlantic salmon in Lake Ontario will enable fisheries managers to determine habitat use and population boundaries in relation to other salmonids and evaluate restoration success while in the lake environment. In this study we used a combination of acoustic telemetry and Floy tagged and recaptured fish to assess movement patterns of adult Atlantic salmon in Lake Ontario. Our specific objectives were to better understand land-locked Lake Ontario Atlantic salmon spatial use in which we: 1) determine seasonal home ranges, 2) determine patterns in horizontal and vertical space use, 3) compare distances moved from acoustic telemetry to mark-recaptures of Floy tagged fish, and lastly 4) compare our findings to literature-based spatial use of other Lake Ontario salmonids.

Methods

Study site and acoustic receiver array

Lake Ontario is one of the five Laurentian Great Lakes in North America, and has an average depth of 86 m, maximum depth of 245 m, and a surface area of ~ 19,000 km^2. Between the study period of November 2015 and September 2020, 204 to 400 acoustic telemetry receivers (69-kHz VR2W, Innovasea, Bedford, NS, Canada) were annually deployed within Lake Ontario, as part of ongoing acoustic telemetry projects through the Great Lakes Acoustic Telemetry Observation System (GLATOS) network (Fig. 1) (Krueger et al., 2018). Receivers covering the open waters of Lake Ontario are primarily located in the western (n = 5 in 2015; 12 in 2016; 48 in 2017; 56 in 2018; 77 in 2019) and eastern regions (n = 144 in 2016; 193 in 2017; 206 in 2018; 155 in 2019), with additional receivers in the Bay of Quinte, Toronto Harbour, Hamilton Harbour, and the Niagara River. In Lake Ontario, receiver spacing varied between 1 and 15 km apart, with grid patterns used in the western and eastern regions, and a bathymetry driven design around the St. Lawrence Channel. Due to logistics, there is currently a lack of receiver coverage in the central region of Lake Ontario which will influence results and data interpretations.

Receiver moorings vary between telemetry projects but were generally composed of concrete blocks (~25 – 60 kg) as anchors connected to 28-cm trawl floats by a 3-m length of polypropylene rope. Receivers were attached midway along the rope with the hydrophone pointing upwards and suspended ~ 2 m above the lake bottom. These moorings included a ~ 30-m weighted rope running from the receiver mooring to a terminal anchor which served as a snag line for grappling when retrieving the receivers for download. Some sites used acoustic release receivers which were connected to the anchor with a 1-m rope and had the trawl float attached above the receiver on a separate 2-m rope. Communications using a hydrophone and VR-100–200 (Innovasea, Bedford, NS, Canada) would release the receiver from the anchor and the receiver would float to the surface for retrieval. Receivers were typically downloaded annually during the summer, with the last full Lake Ontario receiver array downloaded by 30 September 2020. Note that as most receivers are downloaded during the summer, full Lake Ontario coverage was only available until June 2020.

Atlantic salmon tagging and stocking

Brood-stock Atlantic salmon (Sebago and LaHave strains) used for acoustic tagging and Floy tagging were sourced from either the Ontario Ministry of Northern Development, Mines, Natural Resources and Forestry (OMNDMNRF) Normandale Fish Culture Station (Turkey Point, ON) or Harwood Fish Culture Station (Harwood, ON). A total of 37 Atlantic salmon were acoustically tagged across three periods: spring 2016 (n = 10), winter 2017 (n = 19), and spring 2019 (n = 8; Table 1). Fish were anaesthetized using a chemical solution of buffered tricaine methanesulfonate (MS-222; 200 mg/L) (2016 tagging) or electro-sedation using electric fish handling gloves (Smith-Root Inc., Vancouver, Washington, USA) (2017 and 2019 tagging) and placed in a surgery cradle where water was continuously flushed over the gills during the surgery. A ~ 20 mm incision was made on the ventral side of the fish off the midline and a V13 69-kHz transmitter (hereafter called tag; n = 22; 36 × 13 mm, 6.3 g weight in water, nominal delay 180 s; Innovasea) or V13P 69-kHz tag (n = 37; 46 × 13 mm, 6.9 g weight

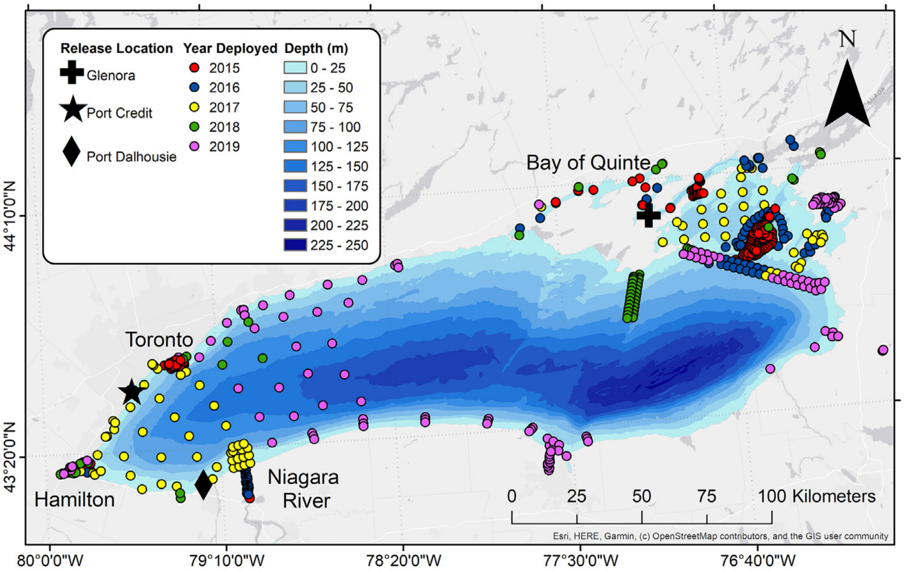

Fig. 1. Acoustically tagged Atlantic salmon (*Salmo salar*) release locations (symbols), and acoustic telemetry receiver locations by year of deployment (coloured circles) in Lake Ontario.

Table 1
Tagging details, survival, and strain information of hatchery-raised Atlantic salmon (*Salmo salar*) acoustically tagged and released into Lake Ontario over three periods. Sample sizes (n) in brackets refer to fish that were tagged and survived with depth sensor tags. Fork length (mm) is mean ± standard deviation.

Release group	Tagging date	Source	Release date	Release location	n tagged	Strain	Age at Release	Fork length	n survived
Spring 2016	2016–03-30	Harwood	2016–04-06	Glenora	10 (0)	LaHave	3.5	426 ± 25	5 (0)
Winter 2017	2017–12-14	Normandale	2017–12-22	Port Dalhousie	19 (17)	Sebago	2	325 ± 18	4 (3)
Spring 2019	2019–04-10	Harwood	2019–05-06	Port Credit	8 (8)	LaHave	4	459 ± 38	5 (5)

in water, nominal delay 180 s; Innovasea) equipped with pressure sensors was inserted into the body cavity. The incision was closed with 3 simple interrupted sutures (2–0 coated Vicryl Plus undyed braided suture; Ethicon, Inc.). Fish were also Floy tagged in the dorsal musculature at the posterior margin of the dorsal fin to externally identify tagged fish and fork length (FL) was measured to the nearest 1 mm. Surgeries took < 3 min and fish were transferred back to a holding tank post-surgery until stocked. Fish were monitored daily and held for a minimum of a week prior to stocking (Table 1). No mortalities occurred between tagging and the stocking event and all fish appeared healthy prior to release. Tagged fish were hand-netted into a stocking truck equipped with an aerated tank along with untagged excess brood stock for transport to release sites in Lake Ontario.

Additional releases of surplus brood stock fish from 2018 to 2020 were Floy tagged on-site and released in Lake Ontario. Eleven Floy tagging events occurred at six different release locations in which a total of 1915 fish were Floy tagged and subsequently released (Table 2). Floy tags were colour specific to release locations and contained a unique tag ID and a phone number for anglers to call in with capture information.

Data preparation

Detection data were available from March 2016 to June 2020, which were filtered to check for mortality or expelled tags, and those individuals were subsequently removed from analyses. Fish were inferred to be dead if they exhibited uncharacteristic constant depth-use profiles from the depth sensor data and stayed within the same area of the array (for those with or without depth sensors). Individuals that had detections for a short period of time (<1 month) were also removed from analyses, although mortality cannot be confirmed. Detection data was assessed for false detections, however, based on the sparseness of the array, the criteria

Table 2
Floy tagging details and sample sizes of Atlantic salmon (*Salmo salar*) Floy tagging events and recaptures in Lake Ontario, 2018–2020.

Release location	Tagging date	Source	Strain	Age at Release	Mean weight (g)	n tagged	n captured
Bronte Harbour	2018-11-28	Normandale	Sebago	3	2050	199	6
Cobourg Marina	2019-04-30	Harwood	LaHave	4	968	556	24
Grimsby	2019-11-21	Normandale	Sebago	3	1860	208	8
Grimsby	2019-11-27	Normandale	Sebago	3	1964	92	5
Port Dalhousie	2018-11-29	Normandale	Sebago	3	2050	96	5
Port Dalhousie	2019-12-11	Normandale	Sebago	4	3421	164	13
Port Dalhousie	2020-06-02	Normandale	Sebago	4.5	5710	43	4
Port Hope	2019-11-22	Harwood	Sebago	7	3500	43	0
Port Hope	2019-12-12	Harwood	LaHave	7	4050	50	0
Port Hope	2020-01-09	Harwood	LaHave	7	4150	215	10
Port of Newcastle	2019-04-30	Harwood	LaHave	4	968	249	14

for filtering false detections would remove real data and was not done (Pincock, 2012). All analyses were completed in R version 4.0.2 (R Core Team, 2020) and data preparation was conducted with the assistance from the R package *glatos* (Holbrook et al., 2020).

Each Atlantic salmon detection was assigned a location that was randomly estimated within 700 m of the receiver (i.e. within the expected detection range) which accounted for the uncertainty associated with the actual location of tagged individuals, as has been done in other studies (Ivanova et al., 2020; Klinard et al., 2020; Matley et al., 2021). Using 700 m is a realistic distance for fish to be detected, in which detection probability is still high (~80%), and random distances were determined using a detection probability curve developed from V13 range testing in Lake Ontario, in which there is a greater probability of the random position being closer to the receiver than further away (Klinard et al., 2019). For each individual, location and depth estimates were calculated using a 30-min weighted, arithmetic mean position algorithm to derive centers of activity (COAs) following the methods described in Simpfendorfer et al., (2002). A 30-min time interval was chosen which is generally suitable for a mobile species such as Atlantic salmon while also balancing the ability of an Atlantic salmon to be detected on multiple receivers while allowing the position to change. Shorter time intervals could produce a bias by amplifying the number of positions in areas with denser receiver coverage. A subset of the detection data that were only detected in Lake Ontario (excluded Bay of Quinte receivers) were used to calculate COAs to analyze lake movement and depth use (see below), as otherwise, detection data from the Bay of Quinte skewed spatial behaviour within the lake.

Seasonal designations were given to each COA, based on the detection time, and estimates of Lake Ontario's temperature dynamics and thermocline delineation from three temperature profiles collected using chains of temperature loggers deployed in eastern Lake Ontario (43.962° N, 76.586° W) from May 2017 to April 2018 (Ivanova et al., 2021a). Season was defined by spring (warming isothermal – May to July), summer (established thermocline – July to November), fall (thermocline breaking down and cooling – November to January), and winter (temperature is no longer declining and isothermal – January to May).

Floy tag recapture information collected from anglers were verified and confirmed based on records of Floy tag ID and tag colour of released fish. There were a few instances ($n = 8$) where the tag ID was unknown, yet tag colour was reported, and so it was assumed the fish was from the most recent tagging event at that release location. Recapture data was included until December 2020.

Spatial analyses

Seasonal horizontal kernel density estimates (KDE) representing the core activity space (50%) and activity space extent (95%) of individuals were calculated from the COAs for each Atlantic salmon (with > 5 COAs) using the kernelUD function in the R package *adehabitatHR* (Calenge, 2006). Seasonal KDEs were not assessed across years due to the low incidence of fish detected in multiple years, and to reduce any influence of an expanding array over the years.

The area (km^2) of each individual's seasonal home range was calculated and differences in the size of the 95% and 50% KDEs across seasons was assessed using an ANOVA with tag ID as a random effect, and differences were determined using posthoc Tukey's test. Individual seasonal 95% and 50% KDEs were plotted over top of each other as semi-transparent layers to show individual variation and general space use of the species within each season, such that the darker the home range colour, the more individuals were occupying similar areas.

Movement and depth analyses

The maximum distance an acoustic tagged fish moved from the release location was determined from the raw detection data, and spatial and temporal plots of detections were assessed to determine whether fish crossed from the western to the eastern region, or vice versa. Similarly, the distance and duration from the release event to the capture event of Floy tagged fish were determined. In case certain tagging events had disproportionate recaptures of fish nearby at the time of release (due to increased angler activity compared to other events), we verified that there was no bias in the distance from release or number of days until recapture across Floy tagging events, (ANOVA – distance: $F_{8,81} = 0.248$, $p = 0.980$; duration: $F_{8,81} = 1.278$, $p = 0.266$). Thus data from all recaptures were grouped together and summarized.

We also determined if there were any seasonal and/ or diurnal patterns in horizontal space use (bathymetric depth and distance from shore) and depth use with acoustic tagged fish in the main lake area based on the 30-min COA positions after excluding any Bay of Quinte detections as the narrow and twisting geography of the Bay would confound the analysis. Using 30-min COAs reduces the occurrence of temporal autocorrelation and helps standardize the number of detections between individuals (e.g., a sedentary fish near a receiver could have up to 60 detections in 30 min as opposed to a mobile fish that swam by and was detected once). Bathymetric depth and nearest distance to shore were determined for each COA position. COA positions were overlayed with the Lake Ontario bathymetry raster collected by NOAA National Geophysical Data Center to obtain bathymetric depth. The distance from the COA positions to the nearest mainland shoreline was obtained using the Lake Ontario shoreline polygon modified from the bathymetry raster in which islands had been removed. Distances could not be determined when incorporating islands, which were primarily associated with the eastern region, and was not perceived to greatly influence results. Some COA positions were not designated a bathymetric depth (likely from being too close to shore) and were removed for that analysis. Depth values were the mean 30-min depths from the COA calculations determined from each Atlantic salmon tagged with depth sensors ($n = 8$).

We used linear mixed models to assess seasonal and diel patterns in bathymetric depth, distance to shore, and depth use with the *nlme* package in R (Pinheiro et al., 2020). For each model, response variables were log transformed to meet the assumptions of normality and heteroscedasticity. Fixed predictor variables for each model were season, time of day, season × time of day, and year, and tag ID was included as a random effect. Due to an imbalance in sample sizes, we only assessed spring and winter seasons for depth use. Time of day was categorical with four 6-hr intervals: late night 00–06 hr; morning 06–12 hr; midday 12–18 hr; early night 18–24 hr. These times roughly distinguish between day and night, as dawn and dusk are approximately at 06:00 and 20:00. Thus, 00–06 and 18–24 were considered night, and 06–12 and 12–18 intervals were considered day. Year was added as a categorical covariate to help control for the changing array, in which receiver coverage expanded and covered deeper locations over the years. Only 2018 and 2019 years of data were available for fish with depth sensors and depth use estimates. A posthoc Tukey's test determined which season, time periods and years differed when they were significantly influenced by bathymetric depth, distances from shore, or depth use.

All analyses were conducted in R and significance was assessed at $\alpha = 0.05$. Unless stated otherwise, values are reported in mean ± standard error (SE). Assumptions of normality and heterogeneity were visually assessed using qqplot and fitted vs residual plots.

Results

Of the 37 acoustically tagged Atlantic salmon, 6 (16%) were never detected, 10 (27%) were considered dead, 7 (19%) had less than one month of data, and 14 (38%) were alive with good quality data, 8 of which had depth sensors, and used in subsequent analyses (Electronic Supplementary Material (ESM) Table S1). Seasonally, the 95% KDE of activity space indicated that Atlantic salmon are generally using all areas of Lake Ontario, particularly in summer, and more restricted activity space in winter (Fig. 2). Differences in the extent of overlap of individuals was related to the season of a stocking event and the number of individuals representing a season (fall had the fewest individuals (n = 3) contributing to the KDE), otherwise the KDE covered both the east and west arrays in all seasons (albeit the lack of receiver coverage in the central region). The size of individual fish 95% KDEs ranged from 0.7 to 18 851 km^2 and varied between seasons (χ^2_3 = 11.420, p = 0.009) with fish having a smaller estimated home range during winter (557 ± 302 km^2) than in summer (9673 ± 3478 km^2; Table 3). The 50% KDE also showed seasonal variation; Atlantic salmon used the east and west arrays in all seasons but were more restricted and further offshore in the winter (Fig. 2). However, across all seasons only the size of 50% KDEs in winter (133 ± 100 km^2) was significantly smaller than summer (4014 ± 1923 km^2; χ^2_3 = 11.240, p = 0.010; Table 3). The number of individuals detected at each receiver followed similar seasonal trends as the KDEs (ESM Fig. S1).

The mean maximum distance that acoustic tagged Atlantic salmon moved from their release location was 168.4 ± 27.2 km with a range of 13.3 to 262.0 km. More than half of the salmon were detected in both the western and eastern regions of Lake Ontario (64%, n = 9 of 14), and 43% (n = 6 of 14) moved back and forth between the western and eastern region at least once, as is reflected in the KDEs.

With the Floy tagging data, there were 90 recaptures from 11 tagging events for a mean recapture rate of 4.58 ± 0.30% (total recapture rate of 4.70%; Table 2). The mean distance from the release location to the capture location of Floy tagged fish was 68.44 ± 8.73 km with a range of 0.1 to 296.4 km within Lake Ontario. One recapture occurred along the St. Lawrence River at Lake St. Francis which was 475.4 km from release location. Floy tagged fish spent on average 135 ± 13 days in the lake until capture (range: 2–557 days). Spatially, the capture locations occurred around the entire perimeter of Lake Ontario, except northeast Lake Ontario and more captures occurred closer to the release locations (Fig. 3). Of the 90 recaptures, 13 occurred in rivers primarily during winter (Dec – April; n = 10) but also in the fall (October; n = 2) and into spring (May; n = 1). The 13 Floy tagged Atlantic salmon were captured in 8 different rivers spanning the lake: 18 Mile Creek, Black River, Bowmanville Creek, Bronte Creek, Keg Creek, Ganaraska River, Oak Orchard Creek, and Oswego River (Fig. 3).

Atlantic salmon were detected between 0 and 25.8 km from shore. Distance from shore varied by season and time of day but did not interact (season: χ^2_3 = 1107.209, p < 0.001; time of day: χ^2_3 = 34.273, p < 0.001; interaction: χ^2_9 = 11.780, p = 0.226) and also varied by year (χ^2_3 = 624.238, p < 0.001), with aR^2 of 0.69. Atlantic salmon were closest to shore in the fall (0.3 ± 0.1 km), followed by summer (0.5 ± 0.2 km), spring (1.2 ± 0.5 km), and winter (5.5 ± 2.4 km; Fig. 4A) when controlling for time of day and year. The distance-to-shore trends could be spatially seen based on the KDEs and number of fish detected at receivers (Fig. 2; ESM Fig. S1). Receivers further from shore had more Atlantic salmon detected in winter, only nearshore receivers detected salmon in fall, and offshore and nearshore receivers detected salmon in spring and summer (ESM Fig. S1). Atlantic salmon also moved slightly further from shore during the afternoon hours (12–18 hrs; 1.2 ± 0.5 km; Fig. 4B) when controlling for season and year. The COA positions were furthest from shore in 2019 (4.2 ± 1.9 km) than other years (2016 and 2017: 0.7 ± 0.3 km; 2018: 0.5 ± 0.2 km) when controlling for season and time of day, partially matching the array expansion further from shore over the years.

The bathymetric depth that Atlantic salmon were detected ranged between 0.3 and 153.1 m depth. Bathymetric depth interacted with season and time of day (season: χ^2_3 = 585.060, p < 0.001; time of day: χ^2_3 = 7.921, p = 0.048; interaction: χ^2_9 = 28.086, p < 0.001) and had a year effect (χ^2_3 = 390.548, p < 0.001) with a R^2 of 0.60. Similar to distance from shore, overall Atlantic salmon were at the shallowest bathymetric depths during fall (5.2 ± 1.2 m), followed by spring and summer (22.0 ± 4.6 m and 19.6 ± 4.2 m, respectively), and winter (45.5 ± 9.6 m; Fig. 5) when controlling for time of day and year. The time of day did not vary within the spring, summer, and winter, however, in the fall, fish were detected at shallower bathymetric depths in the morning and early night (06-12hrs: 3.4 ± 0.9 m; 18-24hrs: 3.3 ± 1.0 m; Fig. 5) when controlling for year. Bathymetric depth of COA positions were shallowest in 2018 (6.9 ± 1.5 m), followed by 2019 (17.9 ± 4.1 m), 2016 (26.5 ± 6.3 m yet statistically similar to 2019 and 2017), and deepest in 2017 (31.1 ± 7.2 m) when

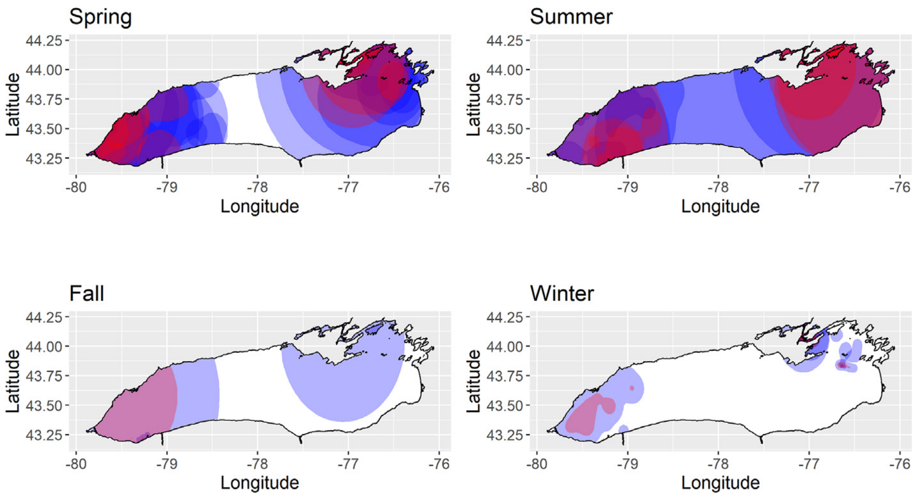

Fig. 2. Estimated seasonal core home ranges (50% kernel density estimation in red) and activity space (95% kernel density estimation in blue) for individual Atlantic salmon (*Salmo salar*) in A) spring (n = 12), B) summer (n = 6), C) fall (n = 3), and D) winter (n = 9) in Lake Ontario. Darker colour indicates areas of high use by multiple individuals.

Table 3
The mean (±SE), min and max 50% and 95% kernel density estimates (KDEs) (km^2) of individual acoustically tagged Atlantic salmon (*Salmo salar*) in Lake Ontario.

		Individual AKDE size					
		50%			95%		
Season	**n**	Mean ± SE	Min	Max	Mean ± SE	Min	Max
Spring	12	1307 ± 520	5.8	5727	5169 ± 1557	59	15,109
Summer	6	4014 ± 1923	23	11,433	9673 ± 3478	76	18,851
Fall	3	1080 ± 1078	0.1	3236	4033 ± 4001	0.7	12,036
Winter	9	133 ± 100	1.7	928	557 ± 302	10	2884

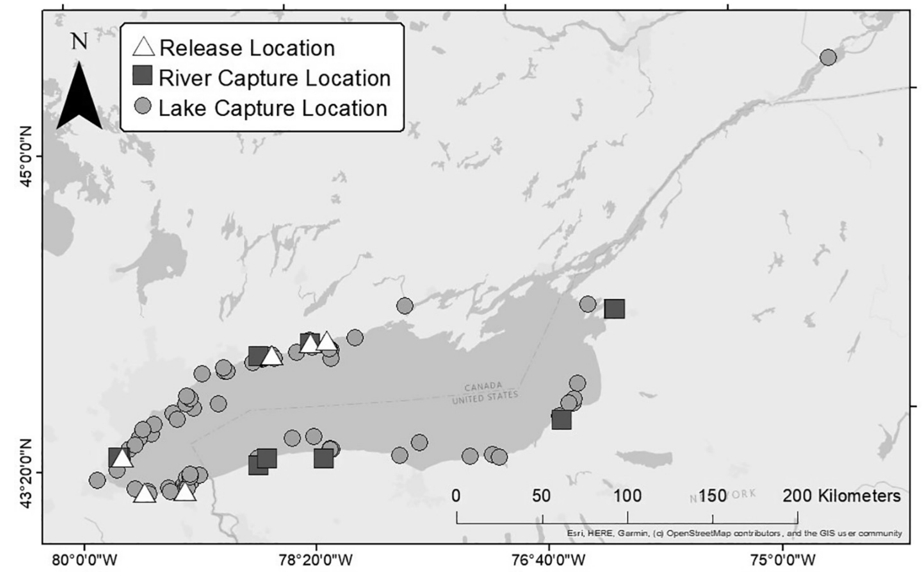

Fig. 3. Release and capture locations of Floy tagged Atlantic salmon (*Salmo salar*) in Lake Ontario, 2018–2020. Capture locations are designated as either river or lake.

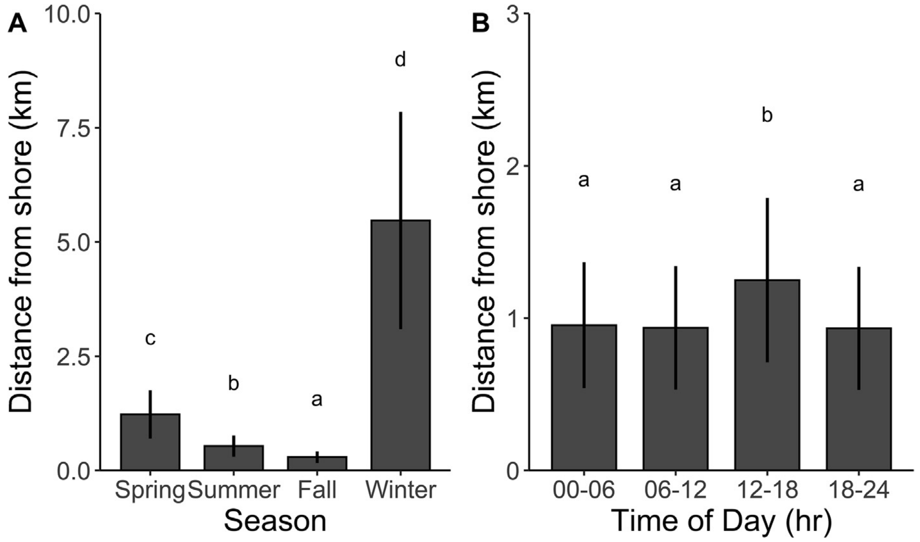

Fig. 4. Mean (±SE) distance from shore (km) that acoustically tagged Atlantic salmon (*Salmo salar*) were detected across A) seasons and B) time of day in Lake Ontario, 2016–2019.

controlling for season and time of day. The year variation did not match the array expansion into deeper waters and being able to detect fish at deeper depths over years.

The 30-min average depth use of Atlantic salmon in Lake Ontario ranged between 0.02 and 28.5 m among the 8 individuals with depth sensor tags, in which the majority of depth detections were shallow (<4m) across seasons, with occasional dives in the spring of up to 13 m and the deepest dives occurring during the winter (Fig. 6A). Models indicated that depth use was best predicted by an interaction with season (spring and winter only due to available data) and time of day (time of day: $\chi^2_3 = 188.397$, $p < 0.001$; season: $\chi^2_1 = 12.773$, $p < 0.001$; interaction: $\chi^2_3 = 31.632$, $p < 0.001$) and did not vary by year ($\chi^2_1 = 1.945$, $p = 0.163$), with a R^2 of 0.43. Atlantic salmon were deeper during

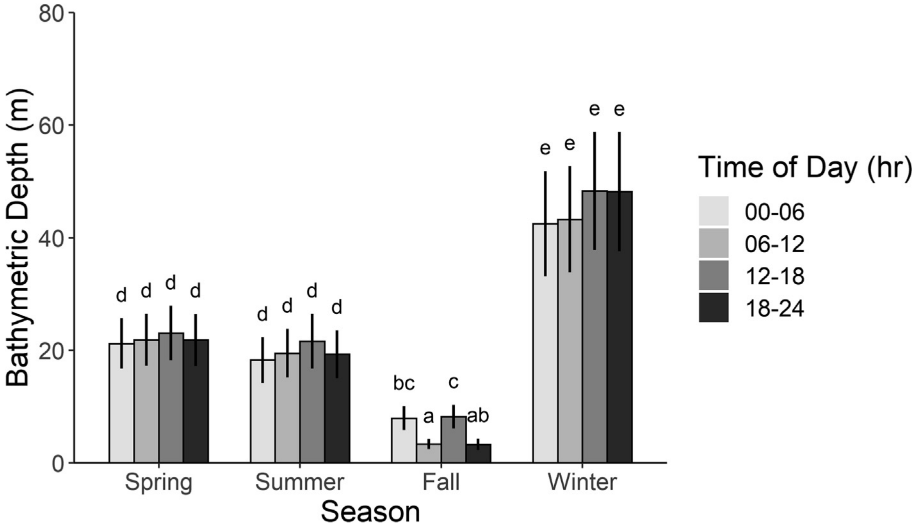

Fig. 5. Mean (±SE) bathymetric depths (m) that acoustically tagged Atlantic salmon (*Salmo salar*) were detected by season and time of day in Lake Ontario, 2016–2019.

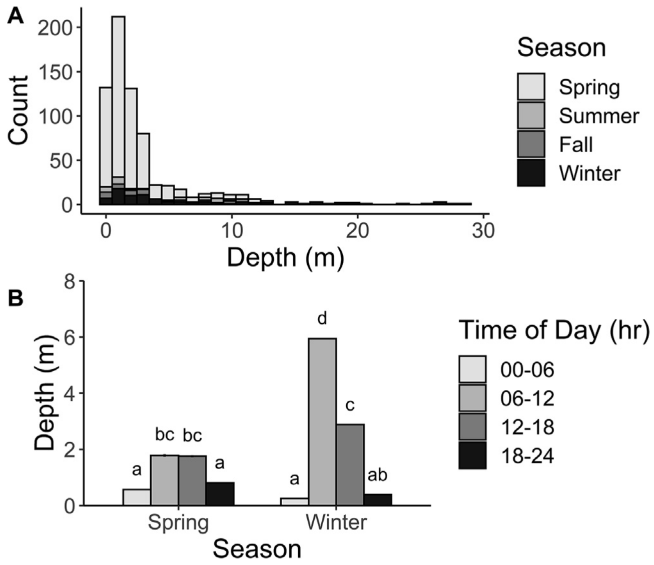

Fig. 6. Depth use of acoustically tagged Atlantic salmon (*Salmo salar*) in Lake Ontario by A) histogram of depths by season and B) linear mixed model results of the mean ± standard error seasonal and time of day depth use trends. Note: summer and fall were not included in the model due to sample imbalances.

daytime hours (06-12hrs and 12-18hrs: 1.8 ± 0.04 m) in the spring when controlling for year (Fig. 6B). In winter, Atlantic salmon showed a similar trend of being deeper during daytime hours (06-12hrs: 5.9 ± 0.02 m, and 12-18hrs: 2.9 ± 0.005 m) when controlling for year. Atlantic salmon were deeper at dawn (06–12 hrs) in winter than they were during spring (Fig. 6B).

Discussion

Understanding the movement and home ranges of Atlantic salmon in Lake Ontario expands our limited knowledge of land-locked Atlantic salmon ecology while providing information that can assist in the restoration efforts of this native species and salmonid fisheries management in general. Using acoustic telemetry and Floy tag recaptures we were able to monitor land-locked Atlantic salmon movements in a large lake. Survival of stocked adult Atlantic salmon with quality data was low (38%). Atlantic salmon were wide-ranging and moved between the eastern and western regions of Lake Ontario. There were seasonal differences in home ranges, in which summer home ranges were estimated to be larger than winter and encompassed most of the lake. The lowest sample sizes for home range analyses occurred in the fall which could be partially attributed to returning to rivers and not being detected. Where receivers were present, Atlantic salmon primarily used the nearshore (<2 km from shoreline and 25 m bathymetric depths) but moved further offshore in winter (5.5 km from shoreline and 45 m bathymetric depth). Small diel vertical movements occurred, moving 1–5 m deeper during the day but generally Atlantic salmon stayed in shallow depths (<4m) in the water column with occasional deeper dives (max of 28.5 m).

Adult Atlantic salmon had a relatively low post-stocking survival which may be influenced by additional stressors related to hatchery conditions and transportation (Brown and Day, 2002; Cowx, 1994). The continuous monitoring of acoustic telemetry and the added benefit of depth data could verify a stocking mortality of 34%, while 30% of fish survived and had good quality detection data. Atlantic salmon smolts from other acoustic telemetry tagging studies have incurred high mortality post-stocking, not related to the actual tagging event (Holbrook et al., 2011; Huusko et al., 2018; Larocque et al., 2020; Thorstad et al., 2012). Stocking of larger fish is correlated with decreased post-release mortality (Brown and Day, 2002), however, Atlantic salmon may be a particularly sensitive species to additional stressors based on these high levels of mortality post-stocking, especially after spawning in the fall (e.g., winter 2017 acoustic tagging event). Tagging was not perceived to influence mortality in this study, as no mortalities occurred between tagging and the stocking event. It is likely that handling and transportation stressors may have attributed to the post-release mortality. Coho salmon (*Oncorhynchus kisutch*) have shown increased corticosteroids, a measure of stress, and mortality from transportation (Specker and Schreck, 1980). Although hatcheries try to optimize conditions to reduce stress and mortality, revisiting and monitoring stress levels during the stocking process and ensuring adequate prey sources upon stocking may lead to methods to improve post-release survival in sensitive species.

The combination of acoustic telemetry and Floy tag recaptures provides both fine- and large-scaled details of fish movements. Acoustic telemetry receivers collected data year-round, in areas further offshore than where anglers generally fish. With the expansion of the acoustic receiver array in Lake Ontario over the years, there was greater offshore depth coverage to verify that the habitat use of Atlantic salmon was not a function of receiver placement (e.g., conclude nearshore use of fish based on receivers only placed in the nearshore). Although we accounted for this year factor in our analyses, increased receiver coverage throughout the entire lake would be optimal, particularly to understand pathways for crossing the lake and to increase home range accuracy, but extremely logistically challenging. Regardless, the year-round coverage from acoustic telemetry revealed seasonal movements and depth use that would otherwise not be observed, particularly overwinter in which occupation of deeper bathymetric depths further from shore were observed. Conversely, Floy tagging fish had a 40x larger sample size and showed a similar lake-wide movement trend to telemetry results based on angler recaptures (albeit biased to the nearshore and in the vicinity of harbours where angler effort is higher). The large sample sizes that can be obtained from Floy tagging is beneficial to be able to determine larger-scale movements as seen here, and given enough recaptures could potentially determine the location and timing of river entry for spawning more easily than acoustic telemetry in such a large lake. For instance, Atlantic salmon were found in eight rivers that could be related to spawning movements. However, the effectiveness of Floy tag recaptures depends on the angling effort which is spatially and temporally biased. Interestingly, one Floy tagged fish was recaptured in the St. Lawrence River. Based on this one Floy tag recapture and lack of acoustic tagged fish being detected entering the St. Lawrence River, the amount of straying towards the St. Lawrence River and potentially the ocean was extremely low, verifying that newly-introduced Lake Ontario Atlantic salmon are primarily land-locked, as historical populations appeared to be (Guiry et al., 2020, 2016). Using both methods together increased our confidence that Atlantic salmon have a large home range and individuals were quite variable in their movements.

The movement ecology of Atlantic salmon in land-locked lakes bears similarities to anadromous populations migrating in the ocean. Anadromous Atlantic salmon are highly mobile performing large forays in the ocean before migrating back to the rivers to spawn (Jonsson and Jonsson, 2011). A few studies have determined the ocean movements of Atlantic salmon using pop-off satellite archival tags and/or data storage tags (Chittenden et al., 2013; Hedger et al., 2017; Lacroix, 2013; Reddin et al., 2011; Strøm et al., 2018, 2017). Salmon from both the Miramichi River and Bay of Fundy, Canada followed the coastline during the oceanic migration to feeding grounds towards the Labrador Sea, however, the movement patterns appear to be quite variable among individuals (Lacroix, 2013; Strøm et al., 2018, 2017). In our study, we found that Atlantic salmon moved long-distances and used the nearshore, although we do not know the exact pathway and whether they followed the coastline as in the ocean. In the ocean, Atlantic salmon spend most of their time in the upper water column (<10 m) presumably feeding on fish, diving infrequently to deeper depths of up to 1000 m (Hedger et al., 2013; Lacroix, 2013; Reddin et al., 2011; Strøm et al., 2018, 2017). Lake Ontario Atlantic salmon were also found to use primarily shallow depths (<10 m) which is likely attributed to feeding on pelagic alewife (Mumby et al., 2018). Deeper dives in the ocean have been suggestive of benthic feeding, which may be occurring periodically in Lake Ontario as well as a benthic round goby was found in a Lake Ontario Atlantic salmon stomach (Larocque, unpublished data) and was estimated to contribute ~ 10% of the diet using stable isotope analyses (Larocque et al. *in review*). Seasonal and diel differences in depth use have also occurred in the ocean, in which Atlantic salmon were deeper during the daytime, as seen in our study, and during late winter/early spring (Hedger et al., 2017; Reddin et al., 2011; Strøm et al., 2018, 2017). Seasonal depth use followed the mixed layer or stratification of the thermocline (Hedger et al., 2017; Strøm et al., 2018). Lake Ontario Atlantic salmon could be using the same strategy, however, more depth data across all seasons would better discern this. Only spring and winter data were available for analyses, and this could be why major depth differences were not observed. The similarities in the roaming behaviour and depth use of Atlantic salmon in the ocean compared to large lakes could assist in determining foraging activities/methods and other aspects of their movement ecology.

Atlantic salmon start moving into rivers to spawn between early summer and fall and timing is highly variable throughout their range (Hansen and Jonsson, 1991; Scott and Crossman, 1998). In Canada, Atlantic salmon spawn between October and November but varies by latitude (Scott and Crossman, 1998). The movement of Atlantic salmon closer to shore and at shallower bathymetric depths in the fall may indicate movement into rivers for spawning, as has been seen with anadromous populations (Davidsen et al., 2013). Fall was also the season with the fewest individuals detected which could mean some individuals had already moved into the rivers by this time. Regardless, it is suggestive with the movements closer to shore from spring through fall that Atlantic salmon may be preparing to move into the rivers. Over the time of the study, there was not adequate receiver coverage at river mouths to determine if fish are homing to a river or when they enter, which could confirm the fall movements closer to shore are related to spawning. Since 2018, fish counters with cameras have been installed on two rivers (Credit River, ON and Ganaraska River, ON) to monitor Atlantic salmon returns to answer questions pertaining to migration timing and abundance, and in 2018, fishway cameras indicated five Atlantic salmon moving upstream in September and October on the Credit River (OMNRF, 2019). However, Atlantic salmon upstream movement may vary temporally by tributary, and there are many tributaries that are not monitored in Lake Ontario where Atlantic salmon were found historically (Parsons, 1973). Floy tagging recaptures within eight rivers confirmed some river returns and potential spawning locations, and while the timing of river entry is still unknown, most river captures occurred in the winter, suggesting a fall migration into rivers. An alternative hypothesis to the fish movements observed is that these fish stocked as adults in the main lake may not stage near river mouths as they have no natal river on which to home. Thus, Atlantic salmon movements closer to shore in preparation of migrating into rivers are merely anecdotal unless more information can be collected to support or refute these hypotheses.

Spatial overlap could occur seasonally between some Lake Ontario salmonids and Atlantic salmon. In Lake Ontario, brown trout tend to stay nearshore (<2 km) year-round and spend the spring and summer near the thermocline (mean (±SD) depths of 14.6 ± 6.7 m) at warmer temperatures (13.4 ± 3.7 °C; Nettles et al., 1987; Olson et al., 1988b). Atlantic salmon may overlap in the nearshore area but at shallower depths with brown trout from spring to fall, however, brown trout populations were more localized in their movements (Nettles et al., 1987) unlike Atlantic salmon which may differentiate spatial use between the two species. Notably, most Atlantic salmon are incidentally angled when fishers are targeting brown trout in the spring, indicating spatial overlap during this season (C. Lake and E. Lantiegne, pers. comm.). Atlantic salmon may also have some spatial overlap with coho salmon and rainbow trout (*Oncorhynchus mykiss*). In the spring, coho salmon and rainbow trout were angled close to the surface in the nearshore of Lake Ontario (Aultman and Haynes, 1993), using similar depths as Atlantic salmon in our study. However, coho salmon movements are unknown in lake environments and whether coho salmon and Atlantic salmon have distinct distributions to reduce overlap in other seasons is unknown. Rainbow trout seem to only spatially overlap with Atlantic salmon in the spring. In Lake Ontario, rainbow trout move from the nearshore at shallow depths in the spring to further offshore (40 to 65 bathymetric m) and deeper (11–16 m) in the summer and fall (Stewart and Bowlby, 2009) which does not overlap with the nearshore, shallow depth use of Atlantic salmon in the summer and fall.

Spatial use of the Lake Ontario water column by Atlantic salmon appeared to differ from that of lake trout and Chinook salmon. Lake trout stay below the thermocline (25.4 ± 8.9 m) at cooler temperatures (10.1 ± 2.8 °C) (Olson et al., 1988) but can appear nearshore during the spring before moving to deeper waters as temperatures rise in the summer (Lane et al., 1996; Raby et al., 2020). Thus, lake trout occupy deeper waters than Atlantic salmon in Lake Ontario, and do not appear to spatially overlap. Lake trout also have localized movements (<100 km; Binder et al., 2017; Ivanova et al., *in revision*) that may further segregate spatial use of the two species. Chinook salmon appear to move nearshore in the spring and further from shore as waters warm in the summer, while occupying depths near the thermocline (18.3 ± 7.3 m) at warmer temperatures (14.4 ± 2.9 °C) (Olson et al., 1988; Raby et al., 2020; Stewart and Bowlby, 2009). During the fall, Chinook salmon can move closer to shore (25–35 bathymetric m) and occupy shallower depths (9–12 m) consistent with river mouth staging, and similar to Atlantic salmon (Stewart and Bowlby, 2009). Chinook salmon are also wide-ranging and move large distances(Adlerstein et al., 2008, 2007; Ivanova et al., 2021b). Atlantic salmon may overlap spatially in the horizontal plane with Chinook salmon, especially given their long-distance movements, however, there is segregation in depth use. Raby et al. (2020) found that Chinook salmon with pop-off data storage tags occupied deeper depths in the summer (21.3 ± 1.7 m) than spring (14.4 ± 2.5 m), which is deeper than Atlantic salmon during the spring in our study. Also Chinook salmon underwent extensive deep dives during the winter (>160 m) with a max depth of 218 m observed (Raby et al., 2017), while Atlantic salmon stayed relatively shallow (max depth of 28.5 m). Based on our data, there is limited spatial overlap between Atlantic salmon and other salmonids in Lake Ontario, occurring primarily during the spring with some species. However, verifying the spatial use with acoustic telemetry across all species may provide details that previous studies were not able to capture. Also, increased receiver array coverage, Atlantic salmon sample sizes and detections across seasons (particularly for depth use) would further expand our understanding of Atlantic salmon spatial use and overlap among Lake Ontario salmonids.

Understanding the movement ecology of Atlantic salmon will influence management decisions, stock assessment and restoration efforts. The highly mobile, wide ranging movements of Atlantic salmon in binational (Canada/USA) waters reflects the importance of government agencies working together to ensure sustainable fisheries and species restoration. Monitoring the movements and survival of stocked adult Atlantic salmon indicated that stocking strategies need to reduce stressors to improve survival, albeit few adults tend to be stocked relative to younger life stages. The diet similarities among Lake Ontario salmonids could potentially result in competition between species if resources were low in abundance. However, there appears to be spatial segregation either horizontally or vertically among species such that they are feeding at different depths in the water column and/or bathymetric depths and distance from shore compared to Atlantic salmon. Salmonids are most likely to spatially overlap in nearshore waters during the spring, and monitoring of salmonids may be best focused in those areas at this time. Further studies to determine the timing and location of river entry for spawning will also aid fisheries management and monitoring restoration success of Atlantic salmon in Lake Ontario. Using a combination of acoustic telemetry and Floy tag recaptures, this is the first study on the detailed spatial use and movements of Lake Ontario Atlantic salmon providing insight on the movement ecology of land-locked populations.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jglr.2021.12.002.

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