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RESEARCH ARTICLE

Spatial ecology of non-native common carp (*Cyprinus carpio*) in Lake Ontario with implications for management

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Abstract

Common carp, *Cyprinus carpio*, are a non-native species that established within the Laurentian Great Lakes more than a century ago and are abundant in some locations. Common carp have negatively impacted freshwater ecosystems, including in the Great Lakes, by increasing turbidity and uprooting vegetation through foraging and/or spawning activities. Knowledge of spatial ecology is necessary to effectively manage non-native species and aid in the development of remediation strategies. The aim of this study was to examine the spatial ecology of common carp across multiple spatial scales within Lake Ontario using passive acoustic telemetry. First, Residency Index (RI), as a metric for habitat preference, was calculated for common carp in Toronto Harbour (TH) and Hamilton Harbour (HH). Linear mixed modelling revealed that season, as well as the interaction between season and physical habitat conditions significantly affected RI. Specifically, during spring and summer common carp had significantly higher RI at sites with increased submerged aquatic vegetation, which could be associated with spawning activities. All common carp tagged in HH were resident, compared to half of individuals tagged in TH. Larger individuals tagged in TH were more likely to be absent from the array during summer. Non-resident common carp tagged at TH made extensive movements in spring and summer along the nearshore of Lake Ontario and were detected throughout the entire basin. Knowledge of spawning habitat could inform efforts to exclude common carp from these specific locations. Based on our findings, common carp should be managed at a regional level, as opposed to single sites, owing to their extensive movements.

Keywords Movement · Management · Invasive species · Control · Fish · Spawning

Introduction

Non-native species are organisms introduced to a novel ecosystem, which can have detrimental economic and environment impacts (NISC 2006). In aquatic environments, non-native species can have direct or indirect biological impacts through predation, competition, hybridization, habitat modification, and transmission of novel pathogens or diseases (Gozlan et al. 2010). Non-native fish species have been introduced for various purposes including for sport, aquaculture, and ornamental trade (Welcomme 1988). Once established, these species can expand their geographical range (Lorenzoni et al. 2010) and rapidly colonize new habitats (Penne and Pierce 2008). Eradication of established populations can be difficult and understanding their ecology is key to guiding effective management strategies (Beatty et al. 2017). The Laurentian Great Lakes of North America have seen numerous introductions of non-native species, which have contributed to the decline and even extirpation of native species (Mandrak and Cudmore 2010). Among the non-native fish species present in the Great Lakes (Mills et al. 1994), one cyprinid species, common carp (*Cyprinus carpio*), first introduced to the American side of Lake Ontario has raised concerns for over 100 years.

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Common carp, native to Eurasia, have been ranked as one of the 100 worst non-native species on the planet (Lowe et al. 2004). Introduced throughout the world for aquaculture and recreational fisheries purposes, common carp have become a dominant species in many freshwater ecosystems (Bajer and Sorensen 2010). Common carp use shallow, vegetated wetlands and floodplains for spawning and use littoral habitat throughout the rest of their life cycle (Penne and Pierce 2008). Once established, common carp populations can reach high abundances, and can drastically alter ecosystems by causing increased turbidity and nutrient mobilization, decreased density of macrophytes, and ultimately lower abundance of macroinvertebrates and fishes (Miller and Crowl 2006; Matsuzaki et al. 2009). These negative impacts are most commonly seen in small, shallow lakes or specific coastal embayments, and do not necessarily occur in all ecosystems where common carp are introduced. Life-history characteristics of common carp enable this species to expand rapidly and attain high biomasses (Britton et al. 2011). These strategies include relatively early maturation (compared to many native fishes), extended adult longevity (up to 64 years; Koch 2014), long breeding seasons in temperate areas (between water temperatures of 17 and 28 °C; Panek 1987), and repeated spawning events in a single year (Smith and Walker 2004).

The Laurentian Great Lakes have long suffered from negative anthropogenic effects, mainly stemming from industry, agriculture, and urbanization (Jones et al. 2006). These deleterious impacts are often concentrated in coastal wetlands (Steedman and Regier 1987). Throughout the Laurentian Great Lakes, coastal wetlands provide spawning, foraging, refugia, or nursery habitat for the majority of native fishes (Jude and Pappas 1992). Despite their ecological importance, over 50% of wetlands within the Great Lakes have been lost (Uzarski et al. 2017), with many of the remaining wetlands impaired or degraded (Chow-Fraser 2006). Additionally, common carp use these wetlands (Lougheed and Chow-Fraser 2001), further contributing to their degradation (Weber and Brown 2009). In light of this impairment, restoration efforts throughout the Great Lakes basin have often included the remediation or creation of aquatic habitat (Hartig et al. 2020); however, the presence of common carp can potentially hinder remediation through removal of aquatic vegetation or increasing turbidity (Lougheed and Chow-Fraser 2001; Miller and Crowl 2006).

Management of non-native species requires an integrated and holistic approach rooted in baseline scientific knowledge (Britton et al. 2011). Biotelemetry can provide important information on the spatial ecology and movement patterns of non-native species (Lennox et al. 2016). Telemetry arrays are broadly accepted as an effective means of studying the spatial ecology of fish including their seasonal habitat preferences and movements (Cooke et al. 2013; Hussey et al. 2015; Krueger et al. 2018). While there have been studies examining common carp spatial ecology within the Great Lakes (see Landsman et al. 2011; Rous et al. 2017; Brooks et al. 2017; Kraus et al. 2018), there remains a need to further understanding of spatial extent, timing, and frequency of movements to inform management actions.

Previous telemetry studies revealed that common carp access shallow areas to spawn during spring, are capable of complex, extensive movements in summer (Jones and Stuart 2007; Banet et al. 2021), and form aggregations at deep overwintering sites (Bajer et al. 2011; Watkinson et al. 2021). Further, Kim and Mandrak (2016) found that common carp dispersed from Lake Ontario to Lake Erie through a system of locks. Preliminary evidence suggests that common carp move large distances in Lake Ontario (Midwood et al. 2019) in a similar manner as other invaded systems (Jones and Stuart 2007; Banet et al. 2021); however, these results have not been fully explored or confirmed. Currently, it is not known how mobile common carp are within Lake Ontario (Midwood et al. 2019), or the extent to which individuals undertake partial migration (Banet et al. 2021), thereby hindering coordinated management measures throughout the basin. Additionally, some observations indicate that common carp within Toronto Harbour (TH) may be part of a larger metapopulation (Midwood et al. 2019). Though there are common carp exclusion structures in some locations (e.g., the Fishway within Cootes Paradise, Hamilton Harbour; Boston et al. 2016), it remains unclear where common carp may be forming seasonal aggregations for spawning in other areas within Lake Ontario. Moreover, effective control measures such as the placement of exclusion structures, will require the identification of areas accessed by common carp during summer for spawning, thereby minimizing recruitment and controlling populations.

This study examined seasonal habitat preference, and movements of common carp within Lake Ontario, in the Laurentian Great Lakes. Specifically, we estimated a residency index (RI) in two harbours in western Lake Ontario: TH and Hamilton Harbour (HH). Using this RI, we then examined how habitat preference varied with season and fish sizes. We also investigated the effect of season and fish size on presence and absence within the TH and HH arrays using general linear modelling. Lastly, we documented broad-scale movements in Lake Ontario to examine evidence for movements between TH and HH and to highlight other areas accessed by common carp within Lake Ontario.

Methods

Study sites and telemetry array

Lake Ontario, the most easterly of the Laurentian Great Lakes, has been subjected to anthropogenic activity for over 200 years, particularly in the densely populated western portion, which is home to both the cities of Toronto and Hamilton (43.631–79.369 and 43.285–79.843, respectively; Fig. 1). Due to historic and ongoing anthropogenic disturbance, habitat impairment and loss, TH and HH were identified as Areas of Concern (AOCs) in 1985 and are the focus of considerable remediation efforts (Hartig et al. 2020). Efforts to remediate fish habitat in both harbours target physical habitat enhancement and creation, with the goal of supporting the recovery of native freshwater fishes and other aquatic organisms (Barnes et al. 2020). To assess the efficacy of these efforts, extensive biotelemetry arrays have been deployed in TH and HH, and a variety of fish species including common carp, have been implanted with acoustic transmitters and tracked (Midwood et al. 2019; Brooks et al. 2019).

Toronto, with a population of over five million people, has experienced widespread loss of littoral and wetland habitat along its waterfront (over 400 ha; Whillans 1982) mainly owing to infilling to support urbanization and the expansion of industry (Barnes et al. 2020). A large system (18 km^2) of embayments, TH has four zones; Inner Harbour, Toronto Islands, Outer Harbour, and Tommy Thompson Park (TTP; Fig. 1). TTP is a man-made peninsula consisting of four embayments (A through D; Fig. 1) and a confined disposal facility (CDF) comprised of three cells (1 through 3) that was created and modified to enhance habitat for aquatic species (Barnes et al. 2020). Dredged contaminated materials have been deposited in the CDF cells; however, this has ceased in Cells 1 and 2 (1985 and 1997, respectively), but is ongoing in Cell 3. Subsequently, Cells 1 and 2 were capped and restored with techniques designed to increase shoreline complexity, encourage the establishment of aquatic vegetation, increase structural habitat complexity, and passively exclude common carp with an exclusion structure (Barnes et al. 2020). The majority of the telemetry array within TH was installed in spring 2011, with fluctuations thereafter in coverage due to the loss of receivers or expansion of coverage into new areas of interest (see Supplemental 1 for receiver details). Key movement corridors, as well as various habitat types were strategically instrumented with VR2W 69 kHz acoustic receivers (Innovasea, Bedford, Nova Scotia; Fig. 1). Receivers were combined into 37 groups based on habitat consistency/proximity (Midwood et al. 2019), as well as range-testing results (conservative estimate of 350 m; see Veilleux 2014). Detections in TH were available from fall 2010 to summer 2020, and this entire period was included in the analysis.

Hamilton Harbour, a 21 km^2 protected embayment, is located at the far western end of Lake Ontario. The south shore of the harbour is dominated by industry (mostly steel or concrete walls), whereas the north and east portions are composed of mostly artificial hard and soft shorelines, with more natural shorelines to the west (Gardner Costa et al. 2020). Cootes Paradise Marsh, situated at the western end of the Harbour, is a large (250 ha) degraded coastal wetland. A physical exclusion structure, the Fishway (operational since 1997), connecting the marsh to the main harbour was designed to exclude common carp. The HH telemetry array has been operational since late summer 2015, with receivers deployed throughout the area covering various habitat types and movement corridors. Similar to TH, the array comprises VR2W 69 kHz receivers (27 initially, expanding to 51; Fig. 1) that have been assigned to one of 15 groups (Supplemental 1). Range testing completed in HH showed considerable variability, particularly when the system was stratified in summer. Detection ranges were approximately 300 m during summer and increased to over 400 m during isothermal conditions (Wells et al. 2021). Detection data were available from summer 2015 to summer 2020.

In addition to the TH and HH acoustic telemetry arrays, data from a larger network of receivers deployed in Lake Ontario as part of the Great Lakes Acoustic Telemetry Observation System (GLATOS; Fig. 1) were used. Data sharing through GLATOS network allows tracking of tagged fish tagged throughout much of Lake Ontario. These additional receivers were deployed at various times such that receiver coverage in Lake Ontario was variable with limited coverage prior to 2014.

Fish capture and tagging

Common carp ($n = 102$) were captured from both TH and HH ($n = 81$ and $n = 21$, respectively; see Supplemental 2). All common carp were collected using boat electrofishing (both models SR-18EH, 7.0 A, 340 and 250 V for TH and HH, respectively; Smith-Root, Inc., Vancouver, WA) between 2010 and 2018. After capture, common carp were placed in live wells with ambient lake water and transported to shore for surgery (TH) or surgery was conducted on the vessel (both TH and HH). Fish were immobilized for surgery using either a Portable Electroanesthesia System (Smith-Root; Rous et al. 2015) or electric fish handling gloves (HH; Smith-Root; Reid et al. 2019). Common carp were put in a trough with ambient lake water passed over the gills to aid respiration. All surgical tools and acoustic transmitters were disinfected with an iodine solution and rinsed. An incision (< 15 mm) was made with a scalpel and the transmitter (see Supplement 3 for transmitter details) was inserted into the coelom. Incisions were closed with two or three interrupted sutures. Fish size (total length) was measured, and fish were returned to a live well with circulating lake water. Common carp were released at their point of capture after ensuring full recovery. Fish handling and surgical procedures were approved and followed a Canadian Council on Animal Care

Fig. 1 The receivers deployed as part of the Great Lakes Acoustic Telemetry Observation System (GLATOS) within Lake Ontario are shown with deployment year (**A**). Toronto Harbour (TH; **B**) and Hamilton Harbour (HH; **C**) are located in the north central and western portion of Lake Ontario, respectively. Acoustic receiver groupings across the TH and HH arrays are denoted with different symbols (see Supplemental 1 for additional receiver group information)

protocol administered by Carleton University (Certificate CU 110,723).

Seasonal delineation

All analyses were completed in R Studio (version 1.1.456; R Core Team; 2021). Water temperature transitions were used to identify seasonal periods (based on Larocque et al. 2020). For TH, temperature-profile data were collected from a chain of temperature loggers deployed nearby in Lake Ontario (Ajax, Ontario; 43.461–78.584). We delineated seasons by taking an average of the temperature loggers: spring started when water temperatures first exceeded 5 °C, until they surpassed 15 °C, which was then designated as summer. Fall occurred when temperatures consistently decreased below 15 °C until falling below 5 °C, which was designated as winter (Table 1). For HH, a chain of temperature loggers (average across the loggers) deployed in the center of the harbour was used to delineate seasons (Table 1) and permitted a different approach to defining seasons. Spring started when temperatures first warmed above 5 °C, shifting to summer when a clear thermocline was established. Fall started when the harbour system "turned over" and lasted until temperatures were consistently below 5 °C. Common carp spawn between 17 and 28 °C (Panek 1987); therefore, spawning likely occurs in late spring or early summer, with staging starting in spring. Due to the COVID-19 pandemic, data were not downloaded from either logger sites in 2020; therefore, some seasons were defined using the average of previous years. Additionally, some monitoring periods did not cover the complete season (Table 1).

Table 1 Season delineation based on water temperatures (based on Larocque et al. 2020) in (A) Toronto Harbour (TH) and (B) Hamilton Harbour (HH)

Year	Spring	Summer	Fall	Winter
TH				
2010	NA	Sept 13[1]	Oct 3	Nov 12
2011	April 22	June 7	Oct 16	Nov 30
2012	April 13	May 21	Sept 22	Nov 15
2013	April 20	June 12	Oct 18	Nov 19
2014	April 26	June 19	Oct 5	Nov 24
2015	April 21	June 17	Oct 14	Nov 26
2016	April 15	May 28	Oct 23	Nov 21
2017	April 9	June 12	Oct 25	Nov 18
2018	April 20	June 11	Oct 16	Nov 27
2019	April 1	June 27	Oct 15	Nov 8
2020	April 16	June 10	Sept 22[1]	NA
HH				
2015	NA	Aug 12[1]	Oct 1	Nov 21
2016	April 30	June 1	Sept 26	Nov 17
2017	April 17	June 18	Oct 14	Nov 25
2018	May 1	June 1	Oct 3	Nov 17
2019	April 12	June 13	Oct 17	Nov 20
2020	April 22	June 8	July 2[1]	NA

[1] Indicates start or stop of study period, and grey shading indicates seasons where averages were taken from all previous years due to missing data

Telemetry data collection and preparation

Data from each telemetry array (TH and HH) were downloaded approximately every six months, once in spring and fall, annually. Receivers were either treated as individual stations or grouped based on their proximity (i.e., overlapping fields of detections) or habitat type (Fig. 1; Supplemental 1), both of which herein are referred to as groups. Erroneous detections were removed if they met criteria for false-positive detections (single occurrences with > 3600 s between successive detections; Pincock et al. 2012). The dataset was also filtered to remove fish that died or expelled their transmitters, which was presumed to have occurred when consistent depth profiles and locations were indicated for an extended period (i.e., stationary horizontal detections at a given station and/or consistent depths; see Klinard and Matley 2020). Additionally, fish that were detected for fewer than 14 days total were removed from the dataset to eliminate those that died following surgery or had malfunctioning tags. To decrease temporal autocorrelation, a reduced dataset was created by randomly selecting one detection per fish once per hour over the course of their period of activity. We also created two different working datasets per harbour: RI (based only on that harbour's array) and total detections in the reduced dataset (including detections outside of the arrays). As noted, prior to 2014 there was limited receiver coverage in western Lake Ontario outside of TH and HH. For example, if a fish left TH in 2013, it would not have been detected in Lake Ontario due to a lack of receiver coverage, thereby leaving extended gaps in detections. We manually identified and removed these extended absences (greater than seven days) from the harbours from the residency datasets, as well as confirmed absences (i.e., individuals detected outside either the HH or TH arrays).

Seasonal residency and habitat conditions

Residency indices are often calculated as the number of days an individual fish was detected at group divided by the total number of days the fish was detected anywhere within the acoustic array. Rather than using raw detections, RI reduces the potential bias of a large number of detections at a given station, generated by a small number of individuals (Kessel et al. 2016). However, in the present study we estimated a modified seasonal RI, which was calculated as the time spent at a given receiver group, divided by the total length of a given season, using the residency function in the GLATOS package (Holbrook et al. 2016). We used this modified RI to avoid potential bias from common carp that had no detections for extended periods of time. Further, due to limited receiver coverage outside both TH and HH during the earlier years of the study, we manually identified periods where common carp were not detected for greater than seven days to determine if individuals remained within or departed either array. For example, if an individual fish was detected continuously throughout a given season, the sum of the modified RI values would be 1, compared to an individual that was not detected continuously (e.g., departed the harbour), the modified RI would sum to less than 1. Mean modified RI was calculated for each season-year combination and for each season across all years of study, for each harbour. Zeroes were added for any receiver group or season combination when an individual fish was not detected during that time period but was known to still be active (i.e., detected elsewhere or detected during a later time period); these zeroes were included in the calculation of the mean seasonal RI.

To estimate habitat conditions within TH and HH, a 350 m circular buffer was created around each receiver group and these buffers were clipped to not include land (see Supplemental 4). The buffer size was used to reflect an approximate receiver detection range based on range testing in each harbour. Percent cover of submerged aquatic vegetation (SAV) was estimated with a model that used the depth, slope, and mean exposure to produce a static estimate of SAV (Doolittle et al. 2010). This model has been determined to be 80% effective at predicting the presence of SAV within HH (Gardner Costa et al. 2020) and was subsequently applied to both HH and TH to produce estimates of mean cover for each receiver group (87.1% accuracy for TH; see Midwood et al. 2020). We acknowledge that percent cover of SAV is highly dynamic both within and among years given that macrophytes grow during spring and senesce in fall; however, we elected to apply a static model due to limited information to support implementation of a more seasonally dynamic approach.

Habitat preference was analyzed by fitting a linear-mixed-effect (LME; package lme4) model with modified RI as the response variable (which was log transformed), as described in Midwood et al. (2018). Each sample in this analysis represented the modified RI (time spent at a given receiver group, divided the total length of a given season) of an individual fish for each season for 1 year. Explanatory variables included season (categorical), total length (mm; continuous), as well as percent cover of SAV (continuous) estimated from a 350 m buffer around receiver groups for both TH and HH (see Supplemental 4). Interaction terms included season by SAV. To account for repeated measures, animal transmitter ID was included as a random effect (categorical). Further, diagnostics were performed for validation and included plotting the residuals (with a Q-Q plot for normality), residuals versus explanatory variables (for independence), and the residuals against fitted values (to verify homogeneity) to visually inspect model fit (Zuur et al. 2009). Spatial autocorrelation was assessed by plotting residuals at receiver coordinates. All procedures were conducted in R statistical environment using the “ggplot2” (Wickham 2016) and “lmer4” (Bates et al. 2015) packages for data visualization and modelling, respectively. Post-hoc Tukey HSD tests were conducted as necessary on categorical variables.

Presence/absence within study areas

To understand drivers of forays (i.e., individual fish that departed the array and subsequently returned) and dispersal (i.e., fish that departed the array and did not return), we documented and described movements beyond each harbour, including associated details (date, time, season, as well as origin and destination when detected). We produced a presence/absence dataset, whereby common carp were absent if they departed either array within a given season and present if they did not leave the array. Absences were denoted when common carp were detected at points of exit within each array (e.g., the curtain or Western Gap in TH or at the Lake Ontario station in HH) and were absent for greater than seven days or detected outside the array (i.e., elsewhere in Lake Ontario). Common carp were designated as non-resident if they undertook forays or resident if they did not depart the array. Each sample in this analysis represented the presence/absences of an individual fish for one season for one given year.

The effects of season (categorical), tagging date (Julian date; continuous) and total length (mm; continuous) on presence/absence from each harbour were tested using generalized linear mixed models (GLMM; package lme4) with a binomial distribution. Interaction terms included season by total length. Diagnostics were performed on the GLMM as per the LME, and animal transmitter ID was included as a random effect (categorical). Diagnostics were performed for validation and included plotting the normalized residuals and the residuals against fitted values. Spatial autocorrelation was assessed by plotting residuals at receiver coordinates.

Large-scale movements

We documented and described movements undertaken by common carp throughout Lake Ontario. Specifically, we mapped detections throughout Lake Ontario on receivers maintained by members of the GLATOS network to examine spatial extent of movements for each season, as well as monthly from May to September (Supplemental 5), which was the time period that captured the bulk of the movements outside the TH and HH arrays. Specifically, for each season we mapped the total number of detections and total number of individual common carp at receivers across all years of study to identify other areas accessed by common carp within Lake Ontario.

Results

Across both TH and HH, there were a total of 6,698,378 detections from 102 common carp. Due to death or transmitter malfunctions, 13 common carp were removed from further analyses ($n = 8$ from TH and $n = 5$ from HH; Supplemental 3) with subsequent analysis focused on 89 common carp ($n = 73$ from TH and $n = 16$ from HH).

Within TH, there was consistently high modified RI in TTP (Cells 2 and 3) and the Western receiver group in HH (Fig. 2). During spring, common carp were found in Cells 1 and 2, as well as Embayment D within TH and in Cootes Paradise and the Western receiver group in HH (Fig. 2). Through the LME, we determined that common carp RI across both harbours was significantly influenced by the interaction term between season and SAV ($p = 0.002$; Table 2). During spring there was a positive correlation between RI and SAV (Fig. 3). During summer and winter, SAV did not influence RI, and there was a negative relationship in fall (Fig. 3).

No common carp tagged in HH were detected outside of the HH array, whereas more than half of the common carp tagged in TH exhibited forays or dispersals outside of the array. Because no common carp tagged in HH left the HH array, they were not included in the presence/absence analysis. The GLMM revealed that both season and total fish length significantly influenced presence/absence of common carp within the TH array ($p = 0.04$ and $p < 0.001$, respectively; Table 3), while tagging date did not ($p = 0.8$; Table 3). Specifically, absences outside the array increased with body size (Fig. 4), with absences were more common in spring and summer and least common during fall.

Of the 73 common carp tagged in TH, 39 were non-resident in that they moved outside the array for at least seven days, while 34 carp were resident and only ever detected within the array. For TH common carp, the mean size for non-resident fish was only slightly larger than the resident carp (665 ± 83 mm and 630 ± 103 mm SD, respectively). Of the non-resident common carp that departed TH, 18 dispersed from the TH array and did not return, and 21 undertook forays (i.e., ultimately coming back to the TH array). Most of these movements outside the TH array occurred during summer as evident by higher total number of detections and number of individual common carp on receivers in Lake Ontario during this season (Fig. 5). Fourteen of the common carp tagged in TH were detected elsewhere in Lake Ontario (via the GLATOS network) and six of these individuals were detected within HH (Fig. 5). There were also extended absences outside the TH array (i.e., periods with no detections) prior to the expansion of the GLATOS network in Lake Ontario and the location of common carp during these periods is unknown.

The majority of forays outside the TH array occurred during summer ($n = 59$), followed by spring ($n = 27$), winter ($n = 4$), and fall ($n = 3$). Movement during spring was not as extensive as summer; however, individual common carp were still detected in Credit River, as well as throughout the middle portion of Lake Ontario (albeit infrequently) near Presqu'ile Provincial Park and Braddock Bay, outside of Rochester, USAduring this season (Fig. 5). Additionally, there were detections throughout the Niagara River, Credit River, and Bronte Creek in spring (Fig. 5) for a total of six receiver groups. In summer, common carp were detected at 30 different receiver groups (outside the TH array) throughout Lake Ontario, followed by five in fall, and one in winter (Fig. 5). Multiple common carp undertook extensive movements in summer, with some detections recorded at the eastern end of Lake Ontario in July (over 300 km from the tagging site assuming fish followed the nearshore (i.e., not direct Euclidean distance; Fig. 5). During summer, common carp were also detected throughout the western portion of Lake Ontario, ranging from Duffins Creek to the Niagara River, and as far east on the south shore as Braddock Bay (Fig. 5). During fall, common carp were detected at Duffins Creek and Niagara River receiver groups. Finally, the only location common carp were detected outside the HH and TH arrays during winter was in the Niagara River (Fig. 5). At a finer temporal resolution, there was a gradual increase of distance moved from TH for common carp movements from May to a maximum in July, where individuals were detected in the far eastern portion of Lake Ontario (Supplemental 5). There were also extensive movements undertaken in August and September, where common carp were detected as far away as Braddock Bay (Supplemental 5).

Discussion

We examined the spatial ecology, seasonal habitat preference, and movements of common carp within Lake Ontario. We found that common carp habitat preference was highly variable across individuals and seasons, but was influenced by season and SAV. Specifically, we determined that common carp were associated with SAV coverage in spring and summer, though many fish also left TH during summer. We also found that larger common carp were more likely to leave TH during summer, with some individuals exhibiting extensive movements. Further, only common carp tagged

Fig. 2 Mean modified Residency Index of common carp (*Cyprinus carpio*; $n = 89$) by season in Toronto Harbour (**A**; $n = 73$; 2010–2020) and Hamilton Harbour (**B**; $n = 16$; 2015–2020). Residency Index was calculated as time spent at a given receiver group, divided by the total length of a given season. Receivers were either treated as individual stations or grouped based on their proximity or habitat type (see Supplemental 1 for additional details)

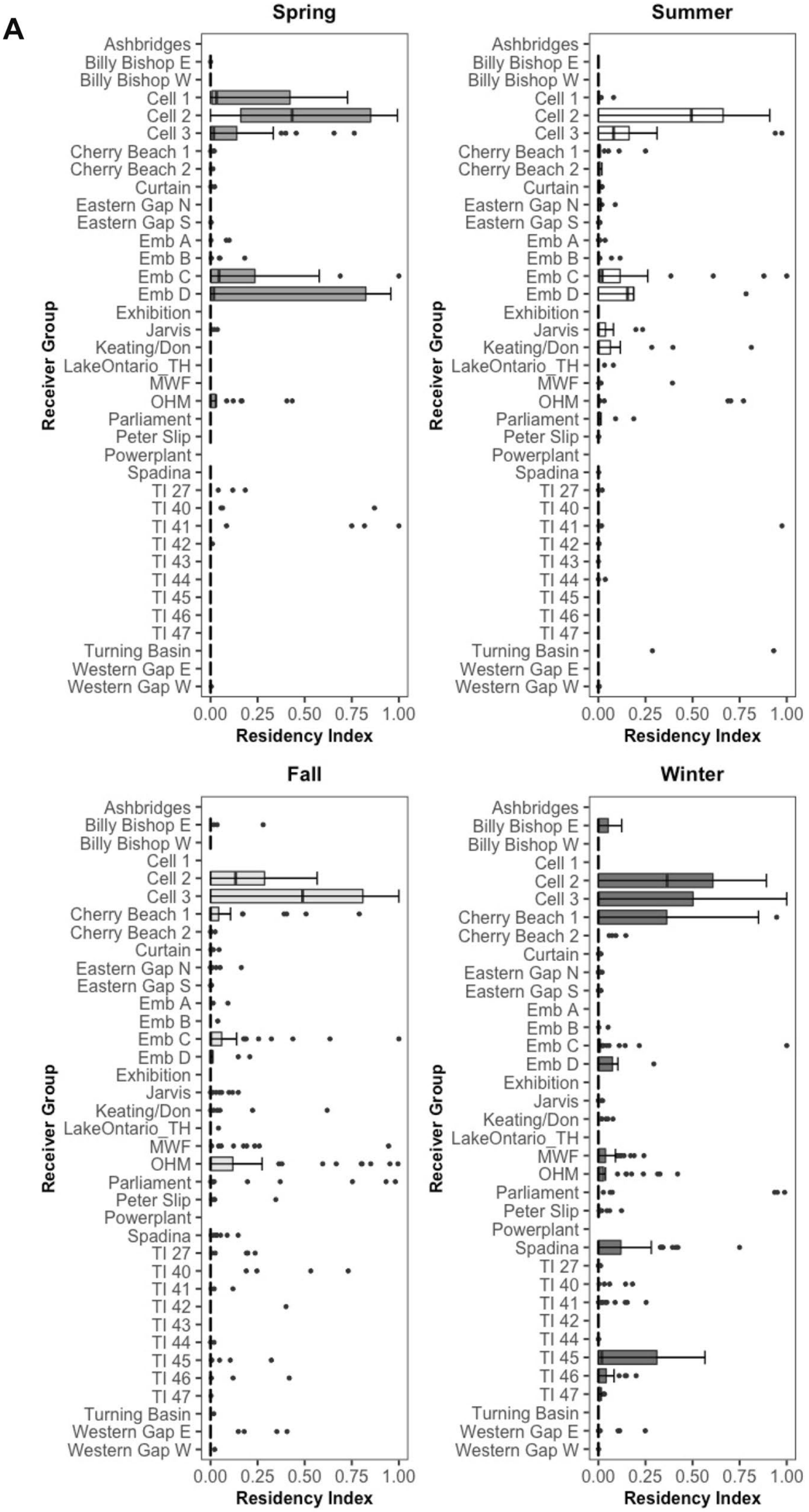

Fig. 2 (continued)

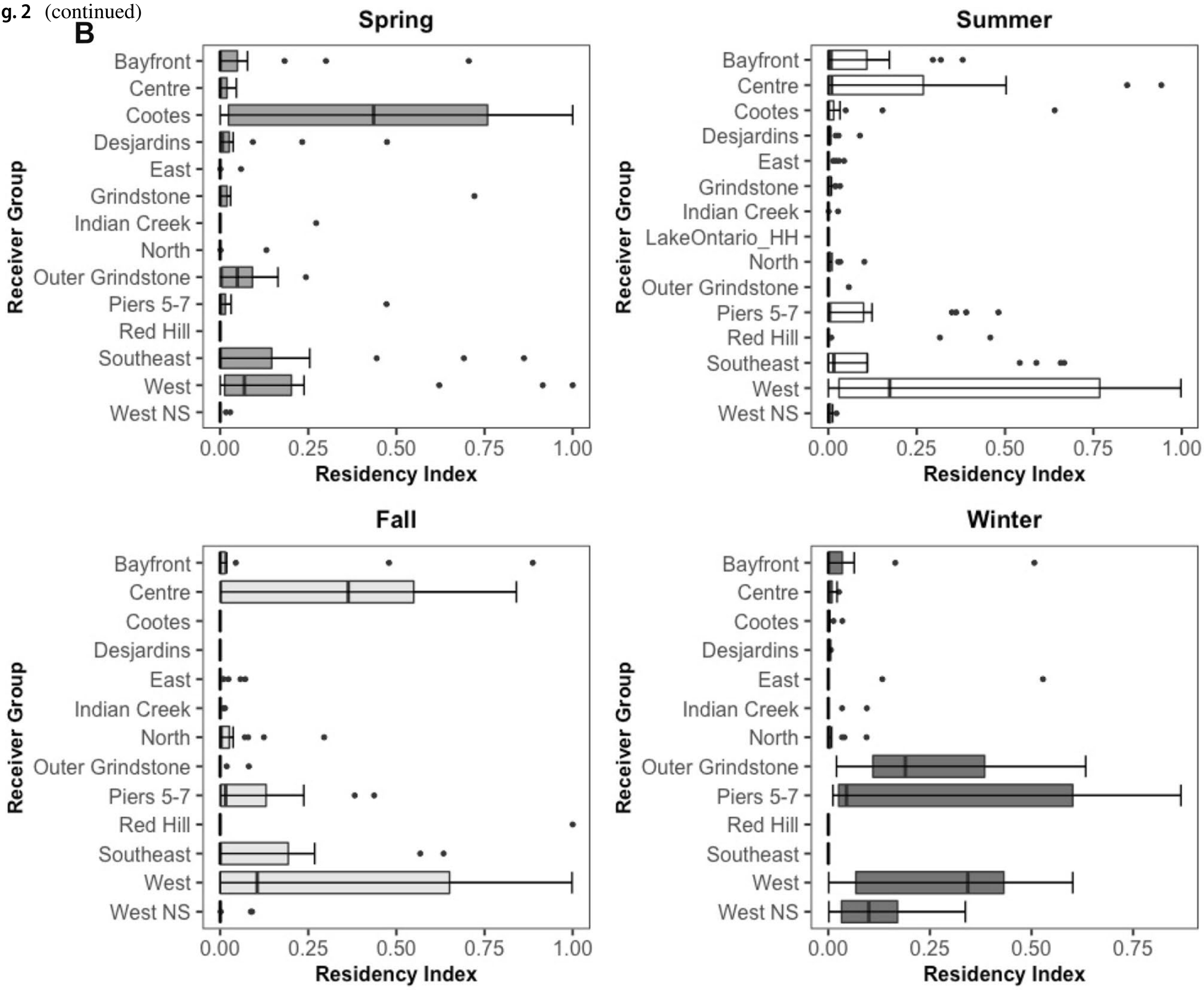

Table 2 The importance of individual terms and interactions for the linear mixed effects model of common carp residency index ($n = 1193$)

Model term	Chi square	*df*	*P* value
Total Fish Length (mm)	2.87	1	0.08
Season	42.07	3	< 0.001*
SAV (%)	2.76	1	0.09
Season x SAV (%)	14.11	3	0.002*

Percent cover of submerged aquatic vegetation is SAV and animal transmitter ID (categorical; $n = 89$) was included as a random effect

in TH departed the array (i.e., forays and dispersals), while individuals tagged in HH did not leave the area. The results from our study highlight potential spawning areas within TH and HH, as well as areas within Lake Ontario accessed by common carp during spring and summer.

Our study highlighted potential areas within TH and HH where common carp could be spawning during spring and summer. Specifically, within TH and HH, we found that in spring and summer common carp were seeking sites with increased SAV and it has been shown within TH that SAV presence is dictated by fetch and depth (Midwood et al. 2020), suggesting that common carp seek shallow, protected areas that support SAV growth. Indeed, it has been well documented that common carp migrate in spring to shallow, littoral areas (floodplains, shallow lakes, ponds or wetlands) with SAV (Lougheed et al. 2004; Hennen and Brown 2014; Sorensen and Bajer 2020; Banet et al. 2021). Further, Banet et al. (2021) determined that common carp exhibited homing during spawning migrations, with consistent use of sites across multiple years. Although we did not explicitly study homing or site fidelity, we did find consistent preference of specific sites within TH (Cells 1 and 2) and HH (Cootes Paradise Marsh) across years (10 and 5 years, respectively), future studies should look to confirm if these behaviours are representative of homing during spawning.

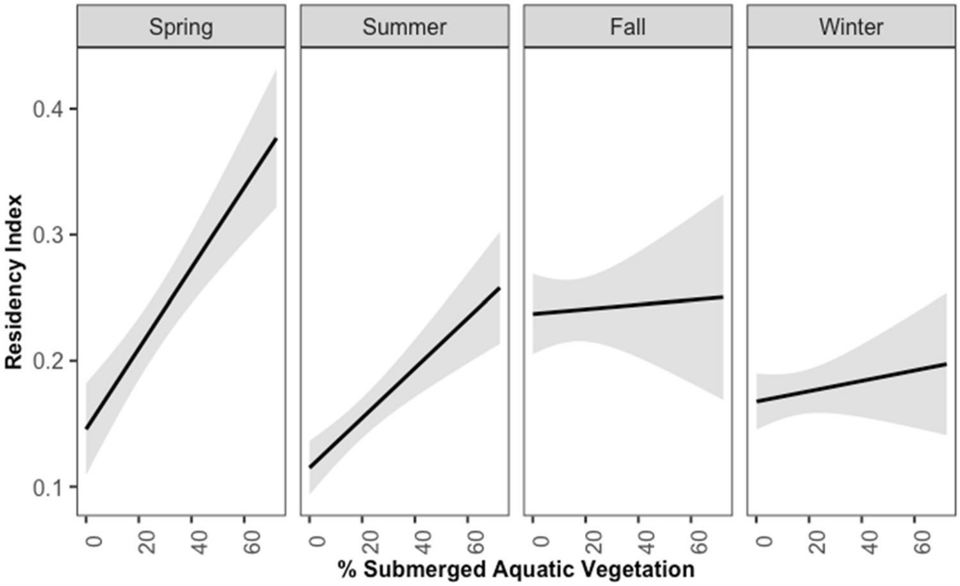

Fig. 3 Impact of percent cover of submerged aquatic vegetation (SAV) on common carp (*Cyprinus carpio*) residency across seasons in Toronto Harbour and Hamilton Harbour as determined by the linear mixed effects model. There was a strong positive relationship between the Residency Index and SAV during the spring and summer

Table 3 The relative importance of terms in the generalized linear mixed model with a binomial distribution for common carp that were present or absent from the TH array ($n = 843$)

Model term	Chi square	*df*	*P* value
Total Fish Length (mm)	9.86	1	0.04*
Season	8.45	3	< 0.001*
Season x Total Fish Length	1.74	3	0.63
Tagging Date	0.06	1	0.80

Animal transmitter ID was included as a random effect (categorical; $n = 73$)

There were increased absences of common carp from the TH array during spring and summer, which coincided with some extensive movements throughout Lake Ontario. This is consistent with a previous study where large-scale movements, likely for the purposes of spawning, were documented during spring in the Murray-Darling Basin in Australia (up to 650 km; Jones and Stuart 2009). It is possible that movements (albeit infrequently) off the TH array during spring and summer in Lake Ontario could be indicative of common carp movements to spawning areas including Hamilton Harbour, Bronte Creek, Credit River,

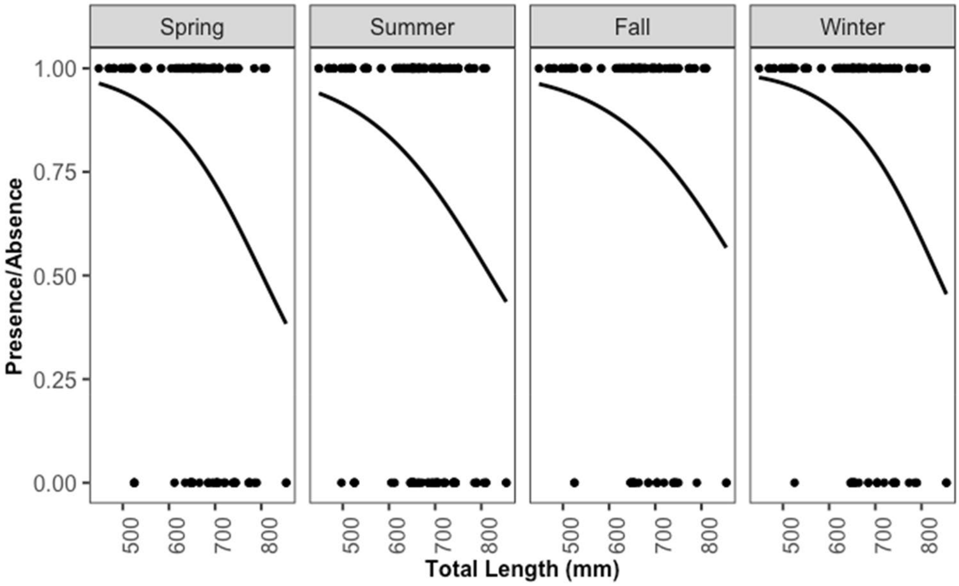

Fig. 4 Impact of season and total length on common carp (*Cyprinus carpio*) presence/absence on the Toronto Harbour array (as no common carp tagged in Hamilton Harbour departed the array) as determined by the generalized linear mixed model with a binomial distribution.

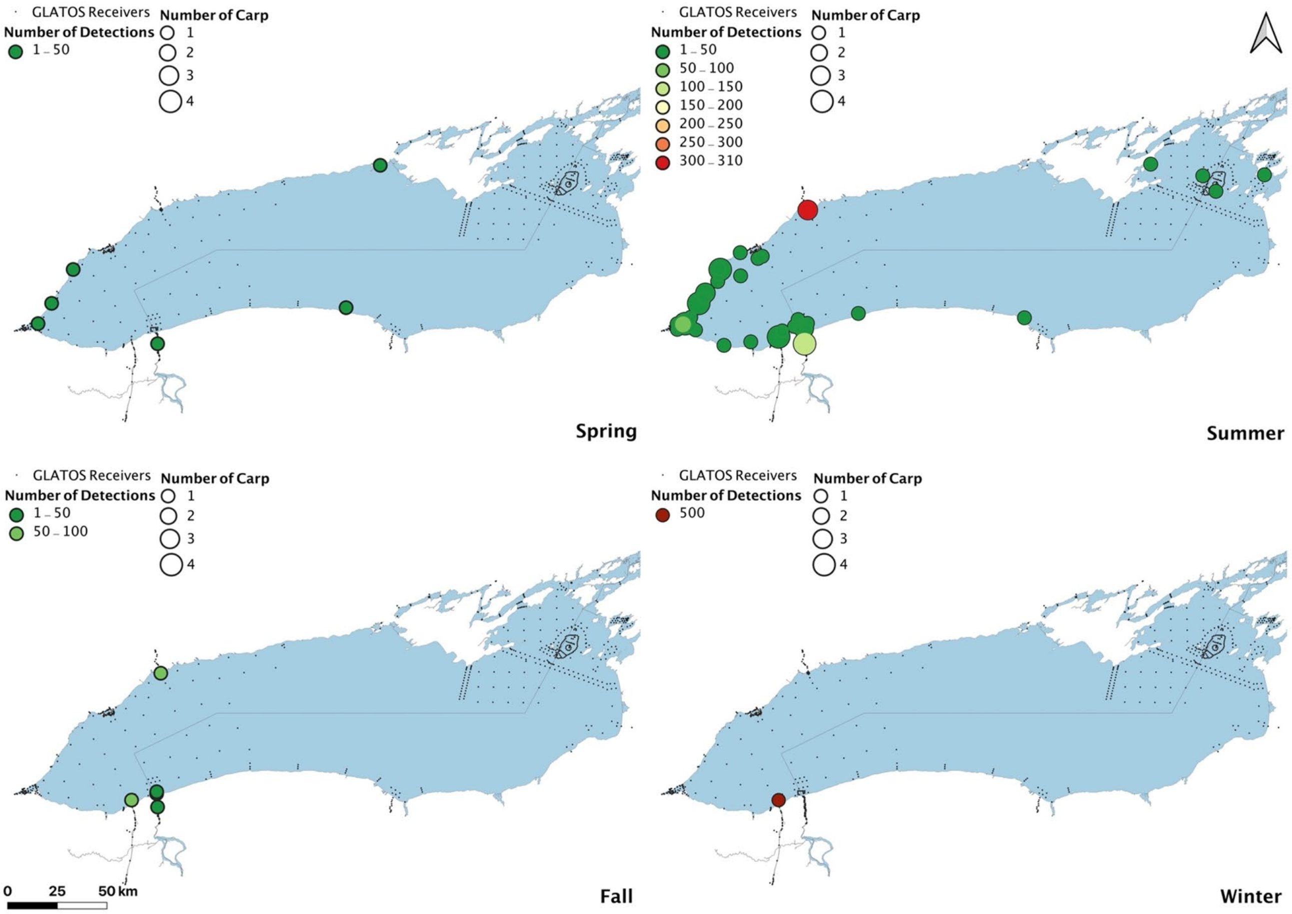

Fig. 5 Locations of detections throughout Lake Ontario (outside of the Toronto Harbour array) of common carp (*Cyprinus carpio*); seasons are shown to highlight differences across spatial extent and distances moved. Colour gradient represents numbers of detections, with size of circle depicting the number of individuals detected at a receiver. Receivers within of the GLATOS array are also displayed (small black points) to show the full extent of coverage as of 2020. More spatially extensive movements by some common carp are evident in the spring and summer compared to fall and winter (Color figure online)

near Presqu'ile Provincial Park, and southern Lake Ontario (near Hamlin Beach State Park, USA). Other individuals may have spawned in their resident harbours, given that most common carp in TH and all individuals in HH remained resident during spring. Management implications of these extensive movements undertaken by common carp during spring include the identification of additional areas where physical exclusion structures could be placed to minimize access to spawning habitats.

During summer, common carp were detected over 300 km away from TH, throughout the entire basin of Lake Ontario. In addition to spawning activities, it has been suggested that these extensive summer movements may be associated with environmental factors, such as foraging or prey resources, and/or climatic factors, including temperature or wave action (Hennen and Brown 2014). Banet et al. (2021) found that in the Rice Creek Watershed, Minnesota, common carp movements were extensive throughout June, July, and August, similar to our findings (see Supplemental 5). Further, it has been hypothesized that increased movements during summer by common carp could be related to strategies to avoid eating their own eggs or to forage in different areas than spawning (Banet et al. 2021; Watkinson et al. 2021). In addition to increased absences during spring and summer, we found that larger common carp were more likely to be absent from TH. While the relationship between total fish length of common carp and distance moved has not been previously examined, it may be that larger individuals require greater resources and thus travel further to acquire them, have more energetic resources to support long-distance movement, or more apt to move because they face lower risk of predation. Based on these movements undertaken by common carp throughout Lake Ontario across international borders, management of this non-native species should be carried out at a large spatial scale across jurisdictional boundaries.

Our study revealed that individual common carp within Lake Ontario have different movement strategies, with only portions of the population foraying and/or dispersing. Sample sizes differed between tagging sites (73 and 16 for TH and HH, respectively) and other (non-tagged) common carp in HH may undertake movements outside the array. Different movement strategies across TH and HH could be due to spatial and temporal variation in resources (Dingle and Drake 2007), potentially with additional resources and habitat throughout Lake Ontario being accessed by TH individuals. It is also possible that there is higher resource or other habitat availability within HH, as indicated by movements by some TH fish to access the harbour and further supported by a lack of common carp leaving HH. Previous studies have found other common carp populations exhibiting various movement strategies (Stuart and Jones 2006; Chizinski et al. 2016; Banet et al. 2021). Further, through these individualistic movements, common carp can locate periodically shallow habitats, inundated floodplains and forests to seek spawning sites (Jones and Stuart, 2006). We found that there were movements outside the TH array during both spring and summer, which could be indicative of breeding (to access spawning sites) and non-breeding (for foraging; Banet et al. 2021). At this point, the purpose of movements throughout Lake Ontario during spring and summer cannot be explicitly determined, although coincident with spawning and expanded summer foraging, future works could aim to confirm these activities through surveys of recruitment, such as egg and fry collection. Individualistic movements along with other adaptive and flexible life history traits, such as early maturation, extended breeding season, and adult longevity (Jones and Stuart 2009) contribute to the success of common carp (Weber and Brown 2009), as well as challenges with their management.

Understanding the spatial ecology of common carp is critical to producing effective management strategies. We identified sites within TH and HH, as well as Lake Ontario, that common carp accessed during spring and early summer, which could be indicative of spawning or spawning staging areas. Currently within HH, adult common carp have decreased access Cootes Paradise Marsh due to a physical exclusion structure (the Fishway) that was installed in 1997 to exclude common carp from shallow spawning habitat (Lougheed et al. 2004; Boston et al. 2016). Within 5 years of installation, there was a 50% decline in common carp biomass within HH, suggesting these efforts were successful (Boston et al. 2016). Other studies have similarly documented success from the use of common carp exclusion structures to not only reduce biomass (e.g., Tempero et al. 2019), but also improve water quality and establishment of aquatic vegetation (Lougheed and Chow-Fraser 2001; Lougheed et al. 2004; Knopik and Newman 2018). Additional exclusion barriers could be constructed in areas across Lake Ontario that common carp accessed during the spring and summer, in efforts to decrease access and improve aquatic habitat conditions.

Evidence of extensive movements beyond the TH common carp population during spring and summer suggests that some individuals may be spawning at additional sites throughout Lake Ontario (as observed in Smith and Walker 2004). Our emerging understanding of the scale of common carp movements during spring and summer not only highlights other areas throughout the western portion of Lake Ontario where management efforts may be required, but also indicates that population control measures need to be coordinated throughout Lake Ontario to ensure individuals blocked from accessing one spawning area are restricted from alternate spawning habitat within their movement range. Physical exclusion structures, such as the Cootes Paradise Fishway could be a potential management strategy in other areas where common carp aggregate.

In addition to supporting population management, findings from the present work can also inform current restrictions on consumption related to bioaccumulation of contaminants. For example, common carp, among other species, within Great Lakes AOCs Lakes have been shown to accumulate polychlorinated biphenyls (PCBs; Brooks et al. 2017; Visha et al. 2021), which has led to restrictions related to consumption and continued impairment of the AOCs. Determining the extent of movement for fishes, such as common carp, has been identified as a key element in assessing whether actions taken within Great Lakes AOCs aimed at reducing contaminant levels will be successful (Bhavsar et al. 2018) because resident fishes are likely to benefit from local reductions of contaminants while migratory or wide-ranging fishes may still be exposed in other locations. Our finding of limited movement by common carp in HH compared to those in TH suggests that potential sources of PCBs from HH fish likely come from within the harbour, whereas sources for more mobile fish in TH are more difficult to determine. Future studies should attempt to confirm sources of PCB contamination within common carp in Great Lakes AOCs as well as explore other potential sources of contaminants that mobile individuals may be exposed to.

To confirm habitat preference, consistent and thorough receiver coverage of all habitats in TH and HH is needed; however, in some shallow areas there was limited coverage because of the need to minimize receiver damage from boat collisions or ice scour and limited detection range because of dense SAV. Therefore, despite efforts to achieve total coverage with receivers and consistent detections, individual fish can "disappear" (i.e., out of line-of-sight of a receiver or in dense SAV; Midwood et al. 2019), therefore impacting RI analyses. We aimed to alleviate this limitation with large sample sizes across multiple years of study (ten years in TH and five in HH). Additionally, we also attempted to account for these periods where fish could "disappear" (i.e., imperfect detections) by manually identifying times when common carp were not detected to determine if they departed the array or not. Next, our estimations of SAV were coarse, in that we assigned one, static mean for a given group; however, these conditions are highly variable over time (i.e., the cycle of SAV growth both within and among years; Tang et al. 2021). Therefore, the estimate of SAV throughout fall and winter is likely an overestimate. Finally, for multiple years of this study there were considerable gaps in receiver coverage outside of TH and HH. Due to these gaps, our coverage of common carp movements outside of our arrays was limited and it is highly likely they are using more parts of Lake Ontario than were documented here. The Lake Ontario array was expanded in 2021 to provide near complete coverage of the main basin of the lake as well as numerous nearshore areas (https://glatos.glos.us/). This expanded infrastructure will support future studies of movements of common carp and other fishes throughout Lake Ontario, which will further inform more targeted and effective management.

Conclusion

Knowledge of the spatial ecology of non-native species is necessary for effective control and management. With the use of passive acoustic telemetry, we have identified areas within both TH and HH where common carp could be spawning and that sites accessed during spring and summer had increased SAV. We also determined that common carp tagged in Toronto Harbour undertake individualistic, extensive movements throughout the entire Lake Ontario basin, mostly during summer and spring. These extensive movements coincide with increased absence outside of the TH array, which was positively related to the total fish length of the individual. Based on these extensive movements, population control measures for common carp need to be coordinated throughout Lake Ontario to ensure individuals blocked from accessing one spawning area (i.e., with exclusion structures) are restricted from alternate spawning habitat within their movement range. Our study contributes to the identification of places within both harbours and Lake Ontario (i.e., Toronto Islands and the western portion of HH, Bronte Creek and the Credit and Niagara Rivers) where control measures could be implemented, including passive management measures such as exclusion structures that may decrease access during spring and summer. Ideally, minimizing access of common carp to their spawning habitat will decrease recruitment and biomass, thereby bringing balance back to Lake Ontario's struggling aquatic ecosystems.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00027-022-00917-9.

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Author contributions MLP wrote the paper and analyzed data, with guidance from NWRL, JDM and SJC. MLP, SED, RP, NWRL, JDM and SJC conceived and designed the study. MLP, JLB, CB and NWRL performed fieldwork, with direction from RP. Equipment was contributed by SED, RP, JDM and SJC. Editing and proofreading was done by all authors. SED, RP, JDM and SJC provided research funding.

Data availability The data and source code that support the findings of this study are available from the corresponding author upon reasonable request.

Declarations

Conflict of interest The authors declare that there are no conflicts of interest.

Consent for publication All the authors consent to publication.

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