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ORIGINAL ARTICLE

WILEY Ecology of FRESHWATER FISH

Tracking bowfin with acoustic telemetry: Insight into the ecology of a living fossil

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Abstract

Little is known about the spatial ecology and behaviour of bowfin (*Amia calva*), despite the fact that it is an important freshwater carnivore, the last living member of the Amiiformes and effectively a living fossil. In the summer of 2013, acoustic telemetry transmitters were surgically implanted in ten bowfin captured in Toronto Harbour on Lake Ontario. Using a stationary acoustic telemetry array that covered most of the 18-km^2 harbour, the residency and movement patterns of bowfin were tracked from their release until November 2014. Detected bowfin ranged in size from 562 to 725 mm total length and included six males and three females (one female was not detected). Bowfin showed high site fidelity with most fish detections concentrated in embayments and within the Toronto Islands, areas characterised by relatively high stable water temperatures and submerged vegetative cover. Statistical modelling revealed that bowfin residency was significantly affected by season, body size, site-specific estimates of vegetative cover and an interaction between body size and season. Bowfin residency increased with vegetative cover and was highest for large fish during the winter and fall months. Despite the overall high site fidelity exhibited by individuals, several bowfin were mobile over the spring and summer months and moved 5.2–12.9 km among telemetry receivers in the inner and outer harbours. The results of this study provide insight into the seasonal habitat preference, home range size and activity level of this unique fish.

KEYWORDS
Amia calva, embayment, nearshore, residency, Toronto, wetland

1 | INTRODUCTION

An integral component of an ecosystem-based management approach for freshwater aquatic systems and the fish populations that they support is an understanding of the spatial and temporal arrangement of habitats as well as their level of connectivity (Lapointe et al., 2014). This is a daunting undertaking given that habitat requirements vary among even closely related species. Resources to determine the species-specific spatial ecology of fish tend to be devoted to commercially or recreationally valuable species or those identified as species at risk (e.g., Cooke et al., 2005). Regardless of a species' perceived importance, the functional resilience of ecosystems with high biodiversity suggests that all species play a role in maintaining healthy and productive ecosystems by filling unique trophic positions, providing functional redundancy or increasing the efficient use of resources (Johnson, Vogt, Clark, Schmitz, & Vogt, 1996; Kerr, Cadrin, & Secor, 2010). Therefore, documenting the ecological requirements for a diverse array of species is an integral component of an ecosystem-based management plan.

Bowfin (*Amia calva* L.) are a carnivorous fish that inhabit warm, vegetated nearshore areas throughout eastern North America including the Laurentian Great Lakes (except Lake Superior) and the Mississippi

River basin (Scott & Crossman, 1998). They are a unique species and the last extant member of the family *Amiidae*, with fossils of bowfin dating back to the Mesozoic era (~250–65 million years ago; Patterson & Longbottom, 1989). While not often considered a recreationally or commercially important species, bowfin have been commonly used as a model in physiological studies because they are facultative air breathers that use their modified swim bladder to survive low-oxygen conditions (Daxboeck, Barnard, & Randall, 1981; Horn & Riggs, 1973) and possess different metabolic functions than those of most teleost fishes (Singer & Ballantyne, 1991).

Despite this interest in their physiological and metabolic adaptations, relatively little research has focused on the ecology of bowfin, largely due to the long-held perception of this species as a "nuisance" predator that competes directly with commercially or recreationally important fishes (e.g., largemouth bass, *Micropterus salmoides* and northern pike, *Esox lucius*; Scarnecchia, 1992; Scott & Crossman, 1998). This perspective is likely unfounded and linked to the perception of higher abundances of bowfin in summer given their preference for shallow, vegetated and warm waterways where they are easily sampled during stock assessment (Scott & Crossman, 1998). It has been suggested that the presence of bowfin may help sport fish because the consumption of small forage fish prevents population stunting, thus benefiting the recreationally important species that share habitat with bowfin (Ashley & Rachels, 1999; Scarnecchia, 1992). Indeed, attempts have been made, albeit unsuccessfully, to use bowfin to manage populations of forage species (e.g., bluegill [*Lepomis macrochirus*]; Mundahl et al., 1998).

More recently, interest in the harvest of bowfin as a source of caviar as well as the development of bowfin-specific angling groups has spurred studies of their population structure and spawning behaviour to improve management and maintain healthy stocks (Daniels, 1993; Davis, 2006; Koch, Quist, Hansen, & Jones, 2009; Porter, Bonvechio, McCormick, & Quist, 2014). These studies have largely focused on the fecundity, timing of spawning and spawning behaviour, with minimal research on spatial ecology or habitat use outside the spawning season. Bowfin preference for shallow, warm waters with dense vegetation (e.g., wetland areas) is well documented and assumed to be associated with a sedentary lifestyle (Davis, 2006; Jude & Pappas, 1992; Scott & Crossman, 1998); however, there is some evidence for diel movements (Cvetkovic, Kostuk, & Chow-Fraser, 2012) and movements among distinct coastal areas (Midwood & Chow-Fraser, 2015). This is further supported in the only telemetry study for bowfin we have identified, which suggested that in Lake Oneida, New York, they are more active than previously thought, occupy unique spawning and foraging habitats, and exhibit seasonal site fidelity (Traslavina, 2010; R. Jackson & A. McCune, unpublished data).

Given the potential ecological importance of bowfin, their unique lineage and their increasing role as a target for commercial and recreational fisheries, a more detailed understanding of their seasonal movements and habitat selection is warranted. In this study, acoustic biotelemetry was used to estimate seasonal residency, seasonal habitat preference and activity over a nearly two-year period in Toronto Harbour on Lake Ontario, Canada. The harbour is a large urban freshwater system that contains diverse and economically important fisheries. The goal was to advance the currently limited information on bowfin spatial ecology and document their seasonal habitat preferences.

1.1 | Study area

Toronto Harbour is a large (18-km^2) freshwater system located along the north shore of western Lake Ontario (43°38′N, 79°22′W). The system is a nearshore environment based on its relatively shallow depth (<10 m) and generally warmer temperatures in contrast to the adjacent main lake. Given its proximate location to the largest urban centre in Canada, Toronto Harbour has a history of development and anthropogenic disturbance such that the system now contains a combination of some remnant natural features (portions of the Toronto Islands), created or remediated habitats (Tommy Thompson Park; TTP), hardened shorelines and structures (e.g., slips along the northern and eastern shorelines), as well as large open areas and dredged shipping channels (Figure 1). Despite a legacy of disturbance, the harbour is still inhabited by a diverse array of warm and coolwater fish species (Dietrich et al., 2008; Murphy, Collins, Doka, & Fryer, 2012). As part of an ongoing study of fish movements within the harbour directed at informing habitat creation and remediation, a large-scale acoustic telemetry array has been deployed in the harbour since 2010 (Figure 1).

The focus of this project has largely been on recreationally important and managed species (e.g., northern pike, largemouth bass and walleye (*Sander vitreus*)) as well as non-native common carp (*Cyprinus carpio*), but in 2013, funds became available to conduct a small-scale study of the movement of bowfin within the harbour. As warm water fishes preferred temperature between 28°C and 32°C (Scott & Crossman, 1998), portions of the harbour are ideally suited as bowfin habitat, particularly the shallow, vegetated areas among the Toronto Islands, as well as some of the created and remediated habitats in TTP that also provide similar habitat. Given the scale of the harbour, as well as the more pelagic areas that separate the Toronto Islands and TTP, there is good potential to capture movements of bowfin in or through these deeper water habitats.

2 | MATERIALS AND METHODS

To avoid their spawning window (typically May or June), in early July 2013, ten bowfin were captured by boat electrofishing in Toronto Harbour (five in TTP and five in the Toronto Islands; Figure 1). These individuals were anesthetised using a portable electroanesthesia unit (Smith-Root Inc., Vancouver, WA, USA) set at 90 V, 100 Hz and 3 shock seconds. Mass and length measurements were collected, and the sex was determined for each individual based on external characteristics (i.e., presence of a tailspot twice the size of the eye in males and green coloration in fins; Scott & Crossman, 1998). They were then placed supine in a v-shaped trough, and lake water was pumped over their gills for the duration of the procedure. A 2- to 3-cm incision was made along the ventral midline anterior to the pectoral fins. A V13 acoustic transmitter (13 × 48 mm, 13 g in air, 69 kHz, mean delay = 200 s, Vemco Ltd. Halifax, NS, USA) was placed into the body cavity, and the incision was closed using two sutures. Surgeries lasted between 150 and 330 s, after which time individuals were allowed to recover in a 100-L container with harbour water before being returned and released at their initial site of capture. A similar approach with bowfin documented 94% survival post-tagging (Traslavina, 2010).

2.1 | Analytical approach

Data from the 72 Toronto Harbour receivers were downloaded at approximately six-month intervals from April 2013 to October 2014. Once collected, erroneous detections resulting from tag collisions and false detections (e.g., propagated from environmental noise) were removed from the database. The first bowfin detection occurred on 8 July 2013, and this was consequently the start date of data acquisition for this study.

2.2 | Seasonal residency

For the residency analysis, receivers were either treated as a unique station (*N* = 22) or the individual receivers were combined into groups (*N* = 7), which represented locally homogeneous areas with respect to habitat features but also increased the total detection area relative to a single receiver (Figure 1). For example, at the connection point between the outer harbour and Lake Ontario, there were eight receivers deployed to track fish that exited the telemetry array for the open lake. These receivers covered a similar habitat type (deep, open water) and were in close proximity, which resulted in single-transmitter pings frequently being detected at all eight receivers. Data from all of these receivers were therefore integrated into a single receiver group to represent this "curtain" of receivers (Figure 1). Herein, both the unique stations and groups of receivers are collectively referred to as "receiver groups," which were individually named based on their ordered location within the harbour (inner harbour [A1–A8], outer harbour [B1–B6], TTP [C1–C7], Toronto Islands [D1–D6] and outside the harbour [E1]; Figure 1). When detected, seasonal residency time was determined for each bowfin in a given receiver group, and this was used to calculate the proportion of continuous time spent at each receiver group during each season for all animals. Seasons were defined as spring (1 April until 31 May), summer (1 June until 31 September), fall (1 October until 30 November) and winter (1 December until 31 March). These classifications were used for data collected in 2013 and 2014. To ensure that all individuals were tracked for the same total time period, bowfin were assumed to remain in the proximity of the station where they were last detected until detected elsewhere. This provided continuous positions for each bowfin in every season and also helped to decrease a bias in our determination of habitat selection that may have occurred due to a higher probability of detection in areas where there was greater receiver coverage or for individuals that were more active (and therefore more likely to be detected). For all situations where a bowfin was absent from the array for an extended period of time (>7 days), their first and last detections for this window were at the same receiver group.

Bowfin seasonal residency was analysed by specifying a global linear mixed-effects model (LME) that included the following explanatory variables: season (categorical); body size (continuous); mean exposure (i.e., effective fetch; continuous); and per cent cover of submerged aquatic vegetation (SAV; continuous). Interactions included body size × season, body size × mean exposure and body size × SAV per cent cover. The response variable (proportion of detections at each receiver by individual) was log-transformed to meet the assumption of normality and heterogeneity in the residuals.

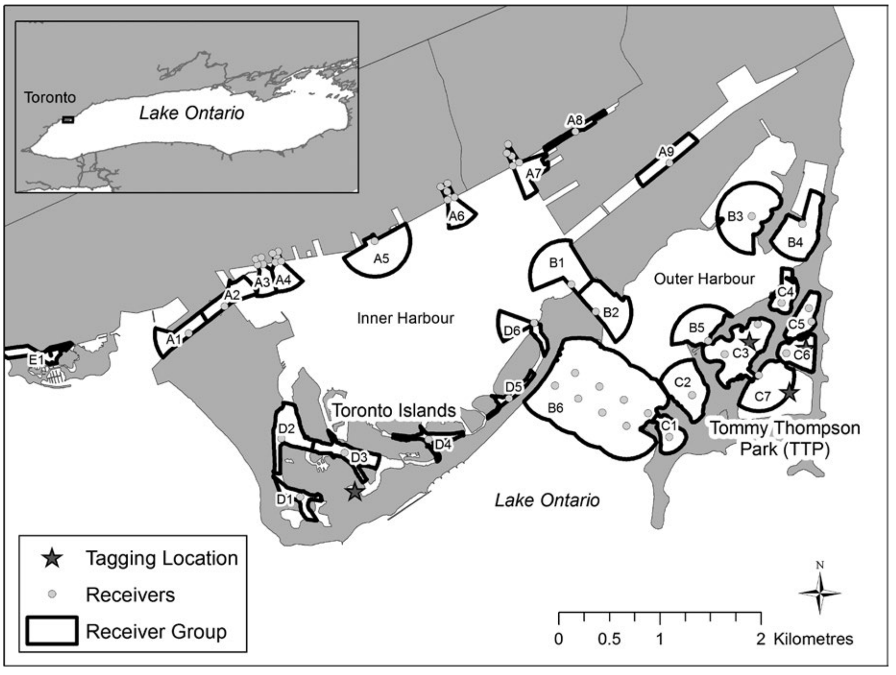

FIGURE 1 Layout of the receiver array in Toronto Harbour with buffered (350 m) receiver groups. Receiver groups are labelled with their site ID, as defined in Table 4, and the initial bowfin capture and tagging locations are indicated. Inset map at top left shows the location of Toronto Harbour in Lake Ontario

Using Akaike information criterion (AIC) model selection, fish ID, receiver group and fish ID nested in receiver group were evaluated as possible random effects. For the global model, backwards model selection was performed using log-likelihood ratio tests at $\alpha = 0.05$. The final model was updated using restricted maximum likelihood and validated by plotting the normalised residuals against the fitted values, all possible explanatory variables, and by plotting the size and direction (i.e., positive and negative) of the residuals at each receiver coordinate (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Residual heterogeneity across seasons precluded the inclusion of a variance structure to allow for different variances for each stratum. All procedures were completed in the R statistical environment (R Core Team 2014) using "ggplot2" and "nlme" for data visualisation and modelling respectively (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2014; Wickham, 2009).

2.3 | Habitat

To evaluate environmental metrics at each receiver group, a 350-m circular buffer was created around all receivers within each group, and this was refined to include only the portions of these buffers that (i) fell within the water and (ii) were in a direct "line of sight" from the receiver(s) (Figure 1). This buffer size was selected to reflect a moderate receiver detection range based on range testing that has been completed in Toronto Harbour (S. Cooke, unpublished data).

Fisheries and Oceans Canada provided a digital elevation model (DEM) for Toronto Harbour. From this DEM, the gradient of the elevation (slope) was calculated in ArcMap 10.2 (Environmental Systems Research Institute, Redlands, CA, USA). Mean exposure (i.e., effective fetch) was calculated for the entire harbour at a 10 m^2 grid size using a wind fetch model developed by the United States Geological Survey (Rohweder et al., 2012). An estimate of SAV per cent cover (calculated using DEM, slope and mean exposure) was generated from an equation developed for Hamilton Harbour, an urban harbour located approximately 40 km southwest of Toronto Harbour on Lake Ontario (Doolittle, Bakelaar, & Doka, 2010). Finally, mean benthic water temperature prestratification (May to June), during stratification (June to September) and poststratification (September to October) was determined. For this, temperature data were collected in 2012 and 2013 and used to develop spatial models of the mean water temperature during the prestratified, stratified and poststratified period throughout the harbour (presented and discussed in Hlevca et al., 2015). Generally, during the pre- and poststratified periods, the water had fairly uniform temperatures, with minimal variations with depth or spatially around the harbour. During the stratified summer period, there was much greater spatial and temporal variability (Hlevca et al., 2015). The warmest waters were located in the protected and sheltered embayments on the Toronto Islands and TTP. During cold upwelling events, these sheltered sites had minimal reductions in temperature. In contrast, the deeper and more exposed open waters in the outer harbour were consistently cooler and had much more variable temperatures in response to the dramatic movements of the thermocline in Lake Ontario, which affect coastal areas the most (Hlevca et al., 2015).

Temperature data were not collected at the same spatial resolution during the winter (Hlevca et al., 2015), and therefore, temperature selection was not evaluated during this season. Using the DEM, mean exposure, SAV and the three seasonal temperature spatial layers, a mean value for each of these environmental metrics was calculated for each receiver group within its 350-m buffer zone.

In addition to the aforementioned use of a LME to explore seasonal residency, a more descriptive evaluation of bowfin habitat preference was undertaken. Principal component analysis (PCA) was used to combine the DEM, SAV per cent cover and mean exposure environmental variables at each receiver group into a single parameter. As an estimate for habitat preference, the proportion of time all bowfin spent in proximity to each receiver group during each season was then plotted against the resulting PC Axis-1. An important caveat of the assessment of bowfin habitat preference is that the array did not cover all potential habitats in Toronto Harbour; therefore, noted preferences are based solely on areas where bowfin could be detected.

2.4 | Large-scale movements

For each bowfin, their spatial distribution was visually assessed in a GIS to determine whether they moved between the inner and outer harbours and, more specifically, between the Toronto Islands and TTP. For those individuals that did make these larger movements, the total distance moved (based on the shortest linear distance through the water between stations) and the timing of these movements were determined.

3 | RESULTS

Of the ten bowfin tagged, nine (six males and three females) were detected within the array and these individuals ranged in size from 562 to 725 mm total length (mean = 632 ± 56 standard deviation [*SD*]) with a mean mass of 2.9 ± 0.7 kg (Table 1). The number of detections was highly variable among bowfin, with some individuals disappearing from the array for extended periods of time (Table 1; Figure 2). This was particularly evident for bowfin that were primarily resident in the Toronto Islands, especially during the winter. In contrast, bowfin active in the TTP region were more continuously detected across all seasons (Figure 2).

3.1 | Seasonal residency

Bowfin were detected at most receiver groups during the spring (2013, $N = 23$), an intermediate number of groups during the summer (2013 and 2014, $N = 14$ and 19 respectively) and fall (2013 and 2014, $N = 19$ and 9 respectively) and the fewest receiver groups during the winter ($N = 4$; Table 2). The proportion of time spent at

TABLE 1 Summary information for bowfin tagged in Toronto Harbour during summer 2013. Bowfin 734 was not detected post-tagging (*). The tracking window represents the time in days between the first and last detection of a bowfin.

ID	Sex	Length (mm)	Mass (g)	Tagging site	Tracking window (days)	No. days detected
Bowfin 734*	F	734	3,584	Cell 2 and 3	–	–
Bowfin 615	M	615	2,336	Cell 2	296	205
Bowfin 615b	M	615	2,138	Cell 2	480	389
Bowfin 600	M	600	2,490	Toronto Islands	480	44
Bowfin 655	M	655	2,862	Toronto Islands	480	58
Bowfin 725	F	725	4,165	Toronto Islands	480	208
Bowfin 655b	M	655	3,210	Toronto Islands	480	78
Bowfin 562	F	562	2,124	Toronto Islands	480	341
Bowfin 701	F	701	3,850	Cell 3	480	163
Bowfin 612	M	612	2,442	Embayment C	470	300

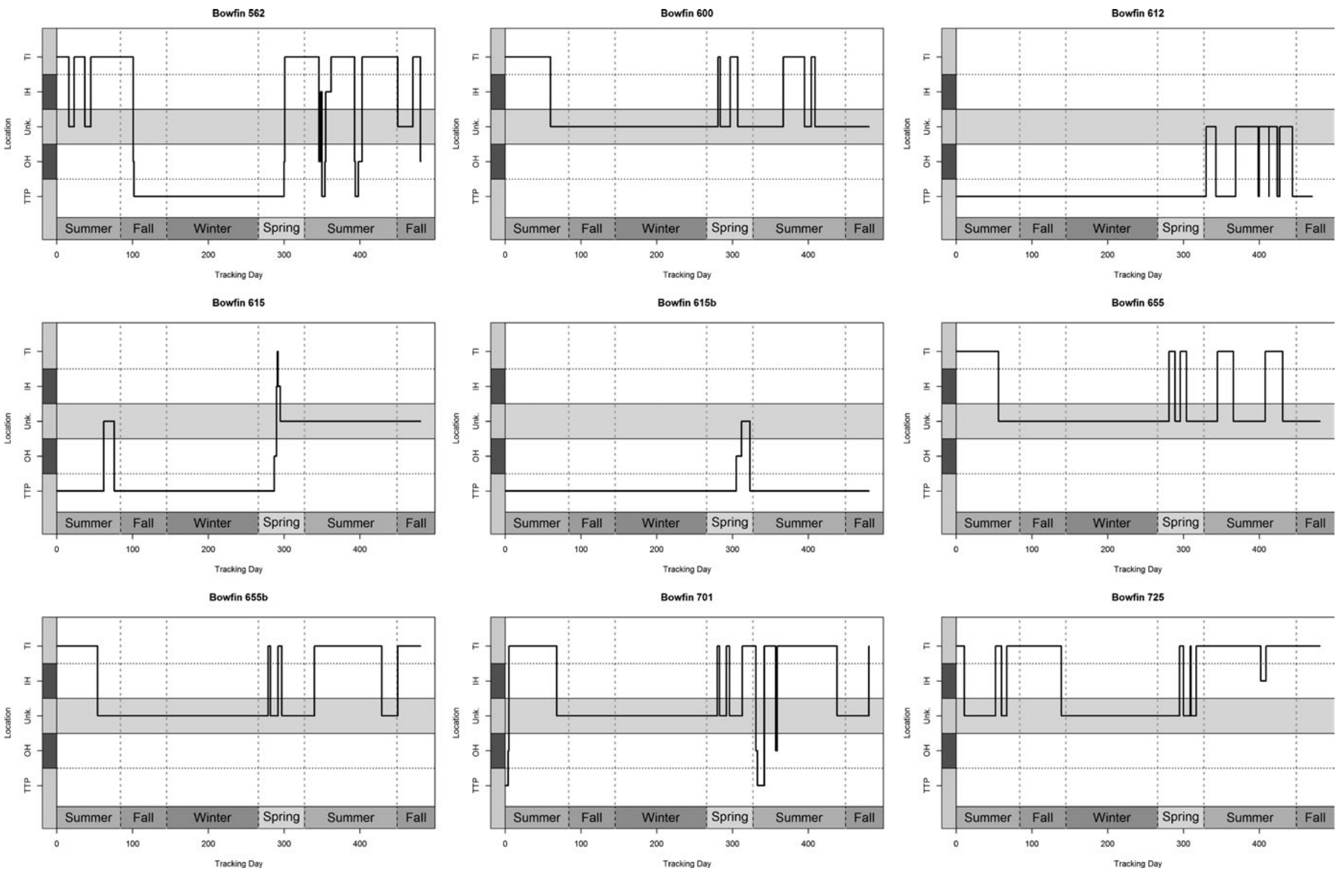

FIGURE 2 Movement timing and duration of residency in Tommy Thompson Park (TTP), outer harbour (OH), inner harbour (IH) and Toronto Islands (TI) for all bowfin. An additional category is also included (Unk.) showing when a bowfin was not detected on the array for 7 days or more. In all instances, following an extended absence on the array, the bowfin either returned to the same general region or was not detected again. For bowfin 562 and bowfin 701, movements between TI and TTP were evident and typically occurred quickly, with minimal time in other regions. In contrast, bowfin 615 left TTP and has not been detected in the Toronto array since. All other bowfin were exclusively detected in either TTP or TI

a receiver group varied across seasons and receiver groups. During the winter, bowfin were found almost exclusively near D1 in the Toronto Islands (0.56) and C6 (0.39), although they also spent time in C7 (0.05) and C3 (0.02; Table 2). During both the summer of 2013 and the summer of 2014, bowfin exhibited high fidelity to the Toronto Islands (specifically D1, D3, D4 and D5; combined totals of 0.61 and 0.68 respectively) and C6 (0.31 and 0.14 respectively), although C5 was also frequented in 2014 (0.14). These same three areas were commonly occupied in both fall 2013 and fall 2014 (combined means equalling 0.79 and 0.65 respectively) with the

TABLE 2 Proportional residency of bowfin at receiver groups throughout Toronto Harbour by season. The proportion of time during each season that each individual bowfin spent in proximity to a receiver group was first calculated, and the mean value for all nine bowfin was then derived. Based on these values, it is clear bowfin spent the majority of their time across all seasons in the Toronto Islands and Tommy Thompson Park (TTP).

			Mean proportion of time in proximity					
Location	Receiver group name	Site ID	Summer 2013	Fall 2013	Winter 2013–2014	Spring 2014	Summer 2014	Fall 2014
Inner Harbour	W Western Gap	A1	0.000	0.000	0.000	0.001	0.009	0.000
Inner Harbour	E Western Gap	A2	0.000	0.000	0.000	0.000	0.000	0.000
Inner Harbour	Spadina Slip	A3	0.000	0.001	0.000	0.001	0.001	0.000
Inner Harbour	Peter Slip	A4	0.000	0.001	0.000	0.001	0.000	0.000
Inner Harbour	Middle Waterfront	A5	0.000	0.000	0.000	0.002	0.000	0.000
Inner Harbour	Jarvis Slip	A6	0.000	0.000	0.000	0.000	0.000	0.000
Inner Harbour	Parliament Slip	A7	0.000	0.000	0.000	0.001	0.000	0.000
Inner Harbour	Don River	A8	0.000	0.000	0.000	0.000	0.000	0.000
Inner Harbour	Turning Basin	A9	0.000	0.000	0.000	0.000	0.000	0.000
Outer Harbour	N Eastern Gap	B1	0.000	0.000	0.000	0.000	0.000	0.000
Outer Harbour	S Eastern Gap	B2	0.000	0.000	0.000	0.006	0.001	0.000
Outer Harbour	Cherry Beach	B3	0.000	0.000	0.000	0.004	0.002	0.000
Outer Harbour	Outer Harbour Marina	B4	0.000	0.000	0.000	0.004	0.001	0.000
Outer Harbour	Outside Emb. C	B5	0.000	0.000	0.000	0.000	0.000	0.000
Outer Harbour	Curtain	B6	0.001	0.001	0.000	0.002	0.001	0.009
TTP	Embayment A	C1	0.000	0.000	0.000	0.002	0.000	0.000
TTP	Embayment B	C2	0.000	0.000	0.000	0.000	0.000	0.000
TTP	Embayment C	C3	0.037	0.174	0.002	0.143	0.005	0.008
TTP	Embayment D	C4	0.000	0.000	0.000	0.000	0.000	0.000
TTP	Cell 1	C5	0.002	0.000	0.000	0.049	0.125	0.167
TTP	Cell 2	C6	0.295	0.161	0.393	0.152	0.129	0.119
TTP	Cell 3	C7	0.000	0.078	0.050	0.010	0.000	0.219
Toronto Islands	Station 40	D1	0.206	0.531	0.556	0.099	0.086	0.240
Toronto Islands	Station 27	D2	0.007	0.044	0.000	0.014	0.004	0.026
Toronto Islands	Station 41	D3	0.216	0.007	0.000	0.271	0.211	0.079
Toronto Islands	Station 42	D4	0.101	0.000	0.000	0.204	0.233	0.132
Toronto Islands	Station 43	D5	0.108	0.001	0.000	0.018	0.180	0.000
Toronto Islands	Station 44	D6	0.028	0.000	0.000	0.000	0.013	0.000
Outside Harbour	Exhibition Grounds	E1	0.000	0.000	0.000	0.018	0.000	0.000

additional use of C3 in 2013 (0.17) and C7 in fall 2014 (0.31). While bowfin were detected at the greatest number of receiver groups during spring (N = 24), core residency by bowfin was still focused in the Toronto Islands (D1–D6 inclusive, 0.63), the C5–C7 at TTP (0.18) and C3 (0.15).

Receiver group alone was the most important random effect in the global LME to predict bowfin seasonal residency (AIC_{RG} = 1,126.7; $AIC_{RG/FishID}$ = 1,130.7; AIC_{FishID} = 1,242.8). Backwards model selection indicated that season, body size, per cent cover and body size × season were significant fixed terms (Table 3). Model estimates illustrated that during the summer months, bowfin residency (%) tended to decrease with body size, whereas the opposite pattern was inferred during all other seasons (Figure 3). In general, residency increased with SAV cover; however, while residency was still the lowest in sites where vegetative cover was minimal (i.e., <30%) in the spring and summer of 2014, bowfin also exhibited the lowest overall residency during these seasons (Figure 3). The highest per cent residency occurred for the largest bowfin in sites with relatively high vegetative cover (i.e., 50%) during the winter and fall months (Figure 3).

TABLE 3 The importance of individual terms, including a variance structure (*var*), for the final linear mixed-effects model (LME) of bowfin residency. The variance of the random intercept is 2.29 with a residual error of 4.65. Body size (continuous covariate) is not shown as an individual term because it is included in an interaction

Model term	L ratio	*df*	*p*-value
Season	11.25	5	.047
Per cent cover SAV	11.16	1	<.001
Body size × season	11.74	5	.038
(*var*)	9.58	1	.088

3.2 | Habitat

There was considerable overlap in the receiver groups that had the highest mean prestratified, stratified and poststratified water temperatures; these included C5 and C6 as well as D1–D4 (inclusive) in the Toronto Islands (Table 4). Similarly, C5, C6, D4 and D5 all had mean modelled per cent SAV cover of over 50% (Table 4). PC Axis-1 (eigenvalue = 2.2) explained 73% of the variance among receiver groups based on their depth (loading = 0.63), SAV per cent cover (loading = 0.63) and mean exposure (loading = −0.46). Across all seasons, bowfin spent proportionally more time in proximity to receiver groups with positive PC Axis-1 values, suggesting an affinity for shallow water, high SAV per cent cover and low mean exposure (Figure 4). These shallow backwater areas were characterised by the warmest temperatures during the data collection period (Table 4), and, compared to the rest of Toronto Harbour, these shallow backwater areas warmed first in the spring and remained warm longer into the fall (Hlevca et al., 2015).

3.3 | Large-scale movements

In general, the spatial distribution of bowfin in Toronto Harbour can be categorised as being either focused around the Toronto Islands or C5–C7 and C3 at TTP (Table 2; Figure 2). For two bowfin (B615b and B612), virtually all of their detections occurred in or near TTP either in C5–C7 or C3 (which connects the three other sites to the outer harbour; Figure 5). Similarly, four bowfin (B600, B655, B655b and B725; Figure 5) were almost exclusively detected among the Toronto Islands (with the exception of four detections). For these six individuals, their core detection areas were consistent with their initial capture and tagging locations. In contrast, three individuals were detected making large-scale movements within Toronto Harbour; B562 and B701 (both females) appeared to move readily between TTP and the Toronto Islands, covering between 5.2 km and 10.7 km during any single movement event (Figure 5). The final individual, B615, exited the harbour via A1 and A2; however, in contrast to B562 and B701, this individual made only a single large-scale movement covering approximately 12.9 km in 8 days in their movement from C6 to E1 located along the shore west of the harbour (Figure 5). Based on their detection at the slips along the north shore of the inner harbour, it is likely that B615 used the open water area of the inner harbour as part of its movement corridor.

4 | DISCUSSION

While not uncommon in their natural range, bowfin represent a distinct taxonomic lineage and, to date, their spatial ecology and seasonal habitat preferences have been seldom studied. In keeping with the concept of a more holistic community-based approach to telemetry (Lapointe, Thiem, Doka, & Cooke, 2013), the present study is the first exploration of bowfin spatial ecology using acoustic telemetry. It is now clear that bowfin exhibit variable levels of activity dependent on both the season and the individual's size. Movements outside their core habitat were most often undertaken by larger bowfin during the spring and summer, and residency was highest during the winter. This would suggest that the long-held perception of bowfin as a sedentary species is likely valid during winter, but following the spawning season, there is strong evidence of movements of several kilometres by at least

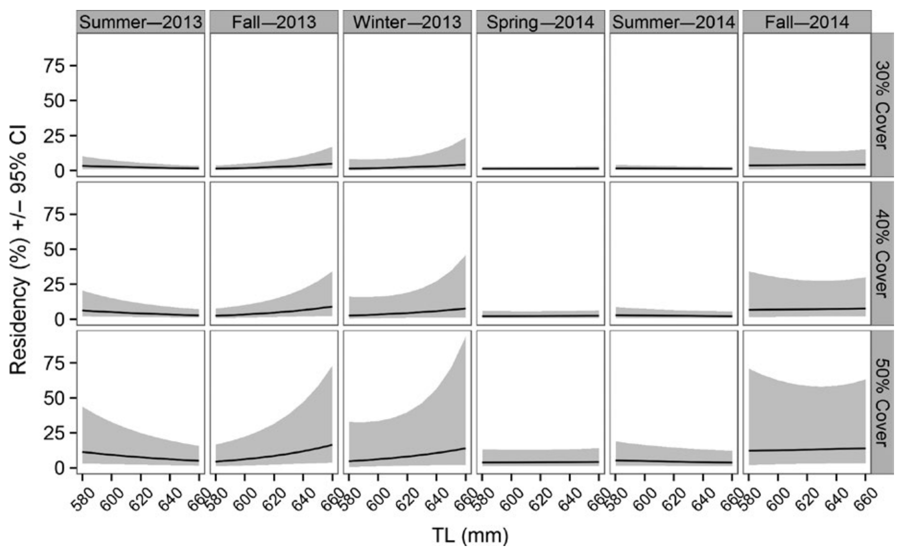

FIGURE 3 Estimated bowfin residency (%) ±95% CI as a function of total length (TL), season and per cent cover of submerged aquatic vegetation

TABLE 4 Environmental variables summarised for each receiver group. Receiver groups are categorised by their relative location within the harbour (e.g., Tommy Thompson Park; TTP), and their site ID, which is used in Figure 1, is shown. Results are presented as mean with *SD*. Depth data were derived from a DEM of the harbour, exposure was measured, and SAV cover was estimated based on a model by Doolittle et al. (2010). Temperature data were derived from a temperature model (Hlevca et al., 2015), and areas outside the harbour were not included in the model; therefore, no data were available for the exhibition grounds

Location	Site ID	Depth (m)	Exposure (m)	SAV cover (%)	Prestrat. temp. (°C)	Stratified temp. (°C)	Poststrat. temp. (°C)
Inner Harbour	A01	6.99 ± 2.63	1,276 ± 608	2.4 ± 8.1	13.2 ± 0.9	15.2 ± 0.9	10.0 ± 0.5
Inner Harbour	A02	7.11 ± 2.36	695 ± 227	2.3 ± 8.8	13.3 ± 0.8	15.5 ± 0.8	10.2 ± 0.5
Inner Harbour	A03	6.53 ± 2.02	830 ± 225	2.8 ± 10.3	13.4 ± 0.8	16.0 ± 1.1	10.6 ± 0.9
Inner Harbour	A04	7.79 ± 1.59	867 ± 201	0.9 ± 6.3	13.5 ± 0.7	16.3 ± 1.0	11.0 ± 0.7
Inner Harbour	A05	8.05 ± 0.87	1,050 ± 100	0.2 ± 2.9	14.1 ± 0.3	17.3 ± 0.6	11.9 ± 0.3
Inner Harbour	A06	7.65 ± 2.05	922 ± 266	2.2 ± 9.7	14.0 ± 1.0	15.6 ± 1.1	11.5 ± 0.7
Inner Harbour	A07	6.31 ± 2.22	650 ± 233	4.8 ± 13.8	13.7 ± 0.9	13.4 ± 1.0	10.9 ± 0.8
Inner Harbour	A08	2.70 ± 1.00	110 ± 97	31.8 ± 18.4	14.1 ± 0.4	19.3 ± 0.9	15.4 ± 0.7
Inner Harbour	A09	6.96 ± 3.04	157 ± 12	7.0 ± 16.3	13.4 ± 0.0	11.2 ± 0.0	9.7 ± 0.0
Outer Harbour	B01	8.43 ± 2.16	898 ± 184	0.7 ± 4.1	13.8 ± 0.8	15.4 ± 0.8	10.9 ± 0.6
Outer Harbour	B02	9.13 ± 2.70	2,026 ± 1,356	1.2 ± 5.7	13.4 ± 1.1	14.5 ± 1.4	10.3 ± 1.1
Outer Harbour	B03	7.77 ± 3.27	1,547 ± 621	2.5 ± 9.2	11.1 ± 0.1	9.7 ± 0.1	7.8 ± 0.1
Outer Harbour	B04	5.04 ± 1.96	520 ± 268	7.8 ± 17.8	14.0 ± 0.7	15.4 ± 0.8	10.2 ± 0.6
Outer Harbour	B05	3.78 ± 2.09	1,725 ± 970	14.3 ± 23.7	11.9 ± 0.6	11.3 ± 0.9	8.7 ± 0.6
Outer Harbour	B06	6.50 ± 2.96	4,903 ± 946	0.6 ± 4.4	12.7 ± 0.7	12.8 ± 1.9	8.7 ± 1.0
TTP	C01	2.39 ± 1.94	222 ± 174	32.2 ± 27.6	13.6 ± 1.5	14.8 ± 1.1	9.4 ± 1.1
TTP	C02	1.34 ± 0.67	1,161 ± 882	42.6 ± 18.0	13.6 ± 0.6	17.6 ± 1.8	11.8 ± 1.7
TTP	C03	2.96 ± 2.08	234 ± 59	27.4 ± 28.3	14.1 ± 1.2	16.0 ± 2.9	11.5 ± 1.4
TTP	C04	0.04 ± 0.65	276 ± 249	69.4 ± 6.4	13.9 ± 0.9	21.8 ± 1.7	17.2 ± 1.3
TTP	C05	0.41 ± 0.64	155 ± 27	63.6 ± 8.9	15.0 ± 1.1	21.3 ± 2.1	15.5 ± 1.7
TTP	C06	1.43 ± 0.62	181 ± 40	58.6 ± 10.0	14.7 ± 0.8	18.8 ± 1.0	13.1 ± 0.8
TTP	C07	8.46 ± 2.89	299 ± 38	2.5 ± 9.6	14.7 ± 0.6	17.3 ± 0.9	12.6 ± 0.4
Toronto Islands	D01	2.49 ± 1.18	94 ± 13	36.1 ± 17.9	14.5 ± 0.0	18.8 ± 0.0	13.9 ± 0.0
Toronto Islands	D02	3.06 ± 1.25	181 ± 36	24.3 ± 21.5	14.5 ± 0.3	18.0 ± 0.1	13.0 ± 0.2
Toronto Islands	D03	2.26 ± 1.00	140 ± 25	42.7 ± 17.0	14.6 ± 0.0	18.5 ± 0.1	13.8 ± 0.1
Toronto Islands	D04	1.80 ± 0.73	78 ± 28	52.3 ± 10.2	14.2 ± 2.2	17.9 ± 2.7	12.3 ± 1.9
Toronto Islands	D05	1.37 ± 0.74	105 ± 88	54.5 ± 15.1	13.7 ± 2.2	18.4 ± 3.0	12.2 ± 2.5
Toronto Islands	D06	3.72 ± 2.06	782 ± 376	21.1 ± 24.3	13.7 ± 1.1	15.9 ± 1.3	11.2 ± 0.9
Outside Harbour	E01	2.04 ± 0.55	283 ± 526	46.3 ± 9.9	NA	NA	NA

some individuals in an urban freshwater system. An important caveat, however, is that many of the bowfin were not detected on the array for extended periods of time (particularly during winter). Therefore, a key assumption of this study is that when not detected on the array, bowfin behaviour and habitat selection were consistent with periods when they were detected. This is an inherent limitation with studies where total coverage of all available habitats is unrealistic.

Movement away from their core habitat was greatest for larger bowfin during the summer. These individuals also tended to be female, although a small sample size prevented us from exploring an effect of sex on seasonal residency and we caution too strong of an interpretation of size-based differences until a focused study with a wider range of sizes is undertaken. In a study of bowfin in Lake Oneida, New York, a sex-specific effect was detected such that females both departed earlier from spawning areas and occupied larger home ranges during the summer relative to males (R. Jackson & A. McCune, unpublished data). Earlier departure by females and larger summer ranges are consistent with the role of males as nest guarders (Reighard 1903 in Davis, 2006). Expanding their foraging area and summer activity also likely allows females to collect sufficient and diverse nutrients for egg development, as is commonly the case for other freshwater fishes (e.g., Gutowsky et al., 2015; Wootton, 1998). The two females in the present study that made large-scale movements did so through the open waters of the outer harbour and these movements were repeated in both years of the study, suggesting they

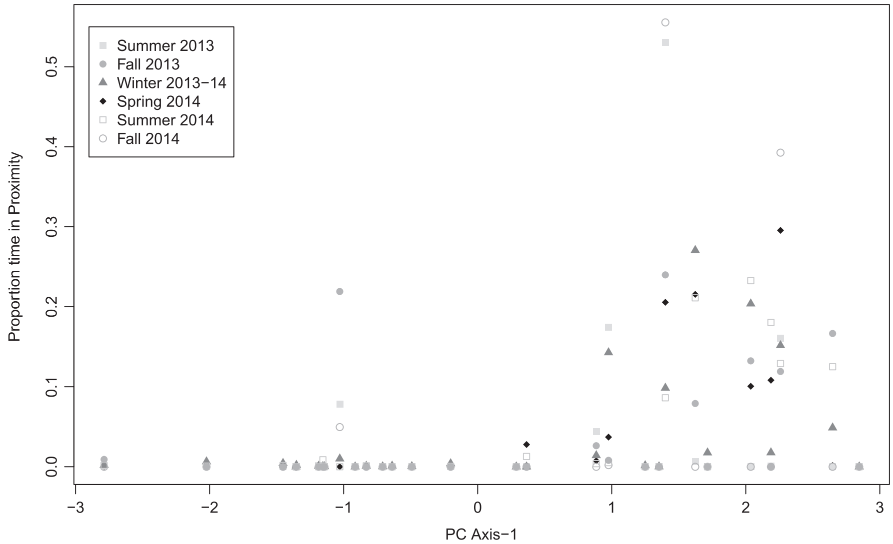

FIGURE 4 Proportion of time during a given season that bowfin spent in proximity to different receivers based on the receivers' PC Axis-1 (PCA1) score. This axis integrates mean exposure, depth and per cent submerged aquatic vegetation cover (%SAV). Higher values of PCA1 are given to shallow, low-exposure sites with high %SAV. PCA1 explained 73% of the variance among receiver groups. It is clear that bowfin spent more time in areas with low mean exposure, shallow water and high %SAV. The sole exception (negative PC Axis-1 value) was in Cell 3, which has deeper water (mean >8 m) than most other sites where bowfin were typically found

may be a regular occurrence for a subset of the bowfin in Toronto Harbour.

Mark–recapture studies have documented movements by bowfin among distinct wetlands units (Midwood & Chow-Fraser, 2015); however, the movements observed in the present study are orders of magnitude larger. This discrepancy is at least partially due to the techniques as mark–recapture is known to underestimate movements (Gowan, Young, Fausch, & Riley, 1994). Additionally, differences in the characteristics of the ecosystems studied may partially explain this discrepancy as overall habitat supply and the size of high-quality habitat patches likely differ. The mark–recapture study was conducted in Georgian Bay, Lake Huron, an area that has thousands of small (<2 ha) wetlands (Midwood, Rokitnicki-Wojcik, & Chow-Fraser, 2012) and comparatively little human influence (Chow-Fraser, 2006). Bowfin in Toronto Harbour may therefore simply have to move farther to reach distinct areas of preferred habitat types. Regardless of the mechanism behind the distances they travelled, a subset of the bowfin population in Toronto Harbour connect spatially distinct habitats and contribute to the transfer of energy among the nearshore areas. Documenting this type of connectivity is an essential component of developing regional fisheries management strategies and indeed has frequently been identified as a pressing research need but seldom pursued (Fullerton et al., 2010).

Consistent with previously documented habitat preferences (Davis, 2006; Jude & Pappas, 1992; Scott & Crossman, 1998), there was also definitive selection of shallow vegetated areas, which also tended to have warmer waters (Table 3). Bowfin were rarely detected in the more developed and less vegetated portions of the harbour even though depth and temperature are consistent with other areas where they were found. Across all seasons, bowfin were often associated with areas that had a higher per cent coverage of SAV. This was particularly true during the fall and winter, which is an important observation considering SAV is senescing during these seasons. Therefore, during the winter, a preference for SAV-dominated areas may not represent direct use of SAV per se, but rather a preference for the conditions that promote SAV growth (i.e., mean exposure <300 m and water depth less than 2.3 m).

The LME suggested that residency was strongest during the winter and, with only a few exceptions, all bowfin detections during this season were in the south-western portion of the Toronto Islands and in C6. From a management perspective, this suggests that protection of bowfin overwintering habitat is critical for population maintenance. These areas were the core habitat in the Toronto Harbour, especially for males which resided here virtually year-round. They are also likely spawning and nursery habitat, and their habitat type (i.e., shallow, sheltered, warm, vegetated) is consistent with conditions that have previously been documented as important for bowfin reproduction (see Davis, 2006; Scott & Crossman, 1998) as well as other species that would be concentrated in these remnant and restored but rare locations in Toronto Harbour.

Evidence for increased residency during the winter raises an important caveat for the present study, which was our assumption that bowfin remained in proximity to the receiver group where they were last detected. Analytically, we did explore only using known positions of bowfin; however, this underestimated the importance of TTP for overwintering habitat and increased the apparent level of activity for the bowfin as they were only detected as they moved outside their overwintering habitat. We are also confident in this assumption as, when a bowfin was absent for an extended period of time (>7 days), the next detection was always either at the receiver group where it was last detected (i.e., suggesting it had remained in

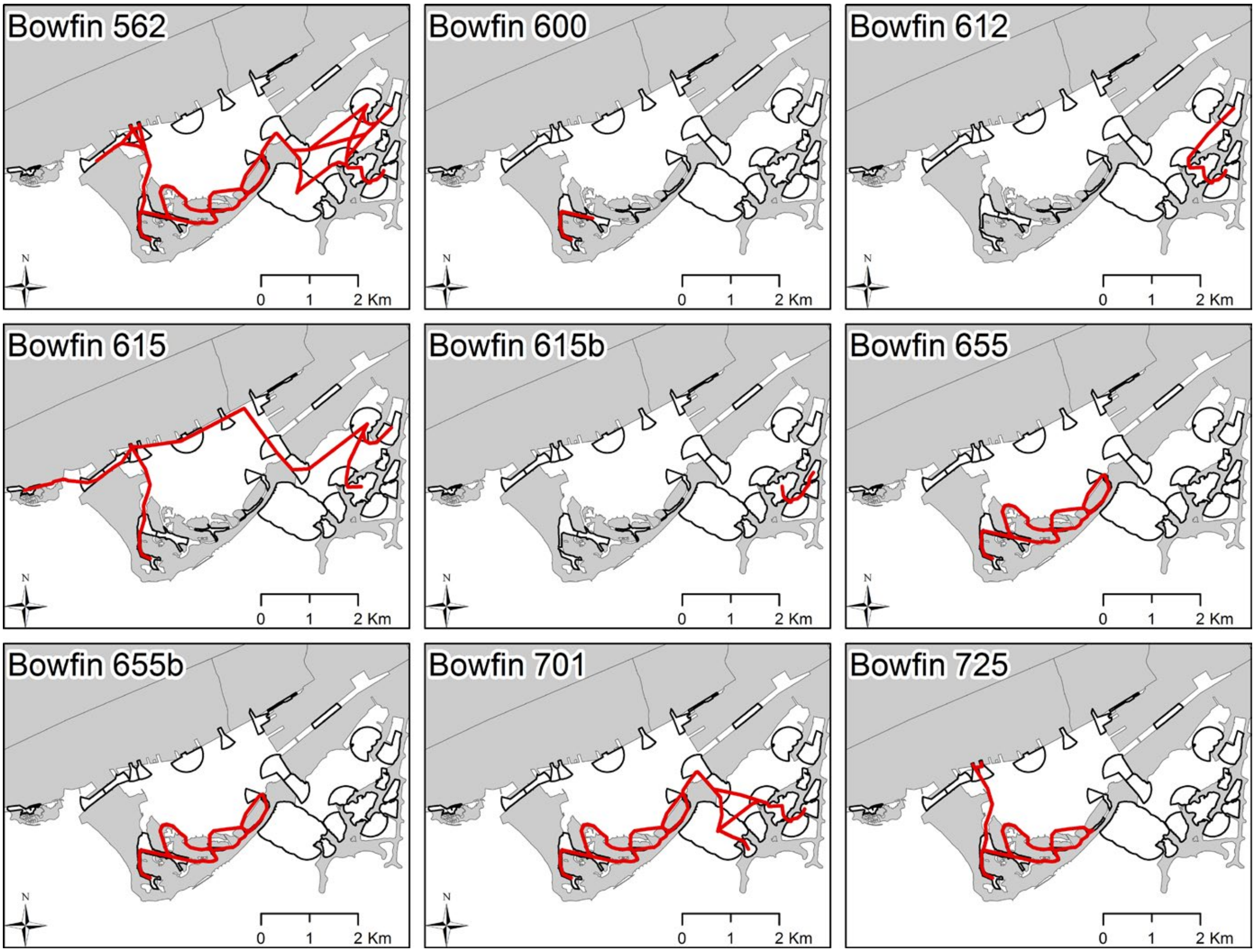

FIGURE 5 General movement paths for the nine bowfin tracked within the harbour (red lines). These paths represent the shortest in water distances connecting receiver groups (black lines), and, in cases like the Toronto Islands where there is more than one path that connect the receiver groups, both options are shown. Despite extensive movements for some individuals (e.g., bowfin 562, bowfin 615 and bowfin 701), their core areas were still focused around the Toronto Islands and Tommy Thompson Park

close proximity but not in a direct line of sight) or the next closest receiver group (i.e., suggesting it had remained in an intermediate location).

The strong association with the south-western portion of the Toronto Islands during the winter is largely a result of bowfin in this area being last detected at D1 before disappearing for extended periods of time. This indicates that the receiver array is missing a critical area of bowfin habitat. Consequently, our interpretation of bowfin habitat selection, particularly during the winter, is biased towards the habitat conditions in proximity to our receiver groups. While we did find that bowfin selected areas that were comparatively warmer, shallower and more densely vegetated than other parts of the harbour, there are some regions that are still shallower, more vegetated, warmer and where we were unable to deploy receivers. Their very affinity for these types of habitats (Scott & Crossman, 1998) likely make bowfin a challenging species to study using passive acoustic telemetry as transmitter signals are attenuated by dense vegetation (Cooke et al., 2013) and stationary receivers in shallow water can pose navigational hazards, be frozen in ice or be exposed when water levels drop. While our assessment of overwintering habitat conditions may not represent the ultimate habitat bowfin are selecting, it is still reflective of their regional habitat preferences. Active bowfin tracking during the winter would help to refine their position and habitat preferences.

While the present study identified a variety of habitat features that are linked to bowfin use, future work should explore the influence of substrate type, specific SAV species use and dissolved oxygen profiles on bowfin habitat selection. This last component is of particular interest as bowfin are facultative air breathers that can tolerate very low dissolved oxygen levels (<1 mg L^{-1}; Kilgore & Hoover, 2001). An exploration of the seasonal dynamics of dissolved oxygen levels in their core habitat warrants further study as their tolerance to anoxic conditions may help bowfin outcompete native freshwater water carnivores that are more intolerant of these conditions (e.g., largemouth bass or northern pike). As the spatial and temporal scales of acoustic telemetry monitoring programmes continue to expand (Cooke et al., 2016), tracking bowfin across a larger range (lakewide) and longer time span may provide a more complete understanding of the annual and seasonal scale of movements by this species.

5 | CONCLUSION

Bowfin are an ecologically important top-level freshwater predator. They have long been considered a sedentary species, and while the present study confirms their reliance on a relatively small core habitat, particularly during the winter, we also found evidence of substantial movements postspawning. In contrast to their surprising large-scale movements, this work supports their documented preference for shallow, densely vegetated habitat, and indeed, the environmental conditions that favour the development of dense SAV (e.g., shallow protected embayments) also appear to be important features of bowfin overwintering habitat. Given their documented site fidelity and reliance on their overwintering aggregation sites, protection of these areas is essential for maintaining healthy bowfin populations in the future. Similarly, changing the perception of this ancient species as purely sedentary will be important for establishing spatially appropriate management strategies for their populations.

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