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Seasonal effects on the acceleration of largemouth bass and Northern Pike in Toronto harbour

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Abstract

Background Habitats are heterogeneously distributed across landscapes, and animals move through them to access different resources, resulting in energetic consequences. In the Laurentian Great Lakes, nearshore areas provide important habitat for the majority of fish species; however, differences in the distribution and composition of physical (e.g., vegetation, depth, fetch, and substrate type/size and temperature) habitat attributes create habitat heterogeneity. We used high-resolution acoustic telemetry data combined with acceleration sensors to test how spatial and temporal factors relate to acceleration of two ecologically and economically important fish species, Largemouth Bass (*Micropterus nigricans*) and Northern Pike (*Esox lucius*), within a system of coastal embayments in Toronto Harbour, Lake Ontario.

Results For both species, we found that sites characterized by higher vegetation cover, shallower depths, and decreased fetch (i.e., coastal vegetated and wetland sites) were associated with lower acceleration values. We also identified several areas within Toronto Harbour that likely serve as important movement corridors between higher suitability sites. Temporal variation of acceleration was significant for both species and was influenced by season and diel period. Both Largemouth Bass and Northern Pike exhibited increased acceleration during spring and summer. Both species exhibited peak acceleration at dawn and dusk.

Conclusion The use of accelerometers was instrumental in identifying important habitats, movement corridors, and elucidating temporal trends across seasons and diel periods. Our results highlight the importance of incorporating habitat connectivity between habitat patches used for different purposes into conservation and restoration planning.

Keywords Bioenergetics, Movement ecology, Urbanization

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Introduction

Locating suitable habitat is one of the most critical external factors influencing animal movement. Movement decisions result from the interaction between an individual's internal state (i.e., motivation and readiness to move), navigation and motion capacity, and external environmental factors [1, 2]. Theoretically, animals move to acquire energy at a greater rate than they expend it, allowing for a surplus that can be allocated to fitness-enhancing processes such as growth or reproduction [3–5]. Environmental heterogeneity, including variation in food availability, temperature, predation risk, and movement costs, can influence animal behavior, including acceleration [6–9]. For instance, in lakes with smaller or less accessible prey, predators exhibited reduced resting periods and higher overall acceleration [10]. Consequently, animals adjust their acceleration in response to landscape variation, optimizing their movement strategies accordingly [7]. Animals inhabiting small, fragmented, or suboptimal habitats often face increased movement costs due to the necessity of traveling longer distances between quality habitats, whether on a daily timescale (e.g., during crepuscular periods) or seasonally [11]. These increased movement costs can contribute to the spatial and temporal structuring of populations and communities [7]. Movements can range from daily foraging routines within an area of core use to less frequent, longer-distance travel between territories over several days [12].

Regardless of temporal scale, (i.e., seconds, hours, or days), acceleration represents a substantial portion of the energy budget for an animal [13–15]. Standard metabolism (SMR) is considered a primary function and basic maintenance for ectotherms (e.g., fish) and typically requires a minimal amount of energy [13, 16, 17]. Ectotherms rely on temperature to regulate SMR, with warm temperatures resulting in an increase in the rate of physiological processes. This increase results in a greater demand on fundamental systems (e.g., cardio-respiratory systems) causing an exponential increase in SMR causing less available energy for active and maximum metabolism (e.g., energy used for locomotion). Considering anthropogenic impacts to habitat and a warming climate, active metabolism (i.e., measured through acceleration) is likely to be altered, which can influence survival, growth, and reproduction. As movement patterns are shaped by the need to access suitable habitats that keep SMR low, understanding how species use different environments is crucial for predicting their spatial distribution and ecological interactions. Because acceleration reflects the energetic costs of movement, analyzing these patterns across space and time can highlight habitats that either elevate or reduce energetic demand, providing insight into how fish interact with their environment [18]. Such spatial patterns can help outline 'energy landscapes' that reveal where individuals forage, rest, or seek refuge [7], offering a management-relevant view of habitat function. These insights support habitat prioritization and conservation planning in systems facing ongoing environmental change.

The coastal wetlands in the Laurentian Great Lakes support great aquatic biodiversity and provide spawning, refugia, nursery, overwintering, and foraging habitat to many native fishes including Largemouth Bass (*Micropterus nigricans*) and Northern Pike (*Esox lucius*) [19]. Largemouth Bass are classified as a warmwater species throughout North America. Adult Largemouth Bass typically prefer shallow (less than 6 m deep) areas that support submerged aquatic vegetation (SAV) or other submerged cover (i.e., logs, brush piles, and root wads). Largemouth Bass often require deeper areas (up to 15 m) for overwintering habitat [20, 21]. During summer, they are most abundant in areas with 40–60% vegetation cover, as higher vegetation densities can limit prey capture [21, 22]. Adult Largemouth Bass are primarily piscivorous [23] and they use a variety of foraging strategies, including actively searching for prey [24, 25] as well as sit-and-wait "ambush" style predation [26]. Northern Pike are considered a mesothermal or 'coolwater', apex predator throughout the circumpolar range of the species. The specific habitat requirements of Northern Pike are well documented with adults generally found in relatively shallow water in summer, usually ≤ 4 m with some occupancy at depths ≤ 12 m in relatively clear, cool, and well oxygenated areas [27–29]. In winter, Northern Pike tend to move to deeper areas with the onset of inshore ice cover (e.g., up to 8 m deep in Lake Ontario) [30–32]. Throughout the year they are generally abundant at intermediate (30–80% cover) vegetation densities with smaller individuals occupying greater vegetation densities than larger individuals [22, 27]. Northern Pike use aquatic macrophytes for multiple reasons (e.g., refuge from predation and/or forage fish of all sizes) at different life stages [28]. Similar to Largemouth Bass, Northern Pike are also ambush predators [33] where they are often associated with structurally complex habitat [34].

In addition to using biotelemetry to study habitat use, acceleration sensors within acoustic transmitters have become a valuable tool to examine differences across fish species and diverse aquatic environments [18, 35–37]. Despite these advancements, few telemetry studies have tracked acceleration of fish in northern temperate lakes over an entire annual cycle [38] but see [35, 39, 40]. To address this gap, we captured near-continuous telemetry data with associated acceleration to gain insight into the timing, nature, and spatial distribution of fish behavior across a range of habitat types in an urban embayment of Lake Ontario. Our study provides novel information on acceleration of ecologically and economically important Largemouth Bass and Northern Pike in Toronto Harbour, Lake Ontario—a system with a diverse array of habitat types but also pressures [41, 42]. We generated predictions of both species' acceleration across space and time within Toronto Harbour. By exploring when and where these behaviors occur, we provide a deeper understanding of how these species interact with and navigate their environment. Broadly, this study aims to advance our understanding of acceleration in fish and serves as a case study demonstrating how biotelemetry data can reveal patterns of potential fish-habitat interactions and behaviour at different scales.

Methods

Study site

Toronto Harbour is a large (~ 15 km^2) and heterogenous aquatic system connected to Lake Ontario that contains exposed shorelines, protected embayments, coastal wetlands, rivermouths and port facilities (i.e., industrial and recreational boat slips and associated traffic). It is situated directly adjacent to the downtown core of Toronto, ON, Canada (~ 5 million people) and consists of habitats with varying degrees of anthropogenic degradation. Toronto Harbour is a heavily urbanized area comprised of four zones: Inner Harbour, Toronto Islands, Outer Harbour, and Tommy Thompson Park (TTP). Two zones dominate the Inner Harbour, the city waterfront (urban and industrial landscape with hardened shorelines), which is connected to the Toronto Islands (a series of channels and islands with more naturalized shorelines). The Outer Harbour is bounded by industrial and recreational uses, and TTP, which is an interconnected series of largely, renaturalized embayments. The eastern gap (a channel) joins the Inner and Outer harbours, and both Harbours are directly connected to Lake Ontario proper: one lake connection is via the western gap channel connecting the Inner Harbour to Humber Bay, the confluence between the Humber River and Lake Ontario. While the Outer Harbour is an embayment directly open to the Lake to the southwest. TTP is a man-made peninsula that was constructed in the early 1970's by using ecological restoration techniques to improve the quality of aquatic habitat, with current restoration permitted through infilling. The peninsula is made from clean fill materials and has been modified to naturalize portions of Toronto Harbour, and restore lost coastal features, as well as house contained disposal facilities until they are capped and enhanced naturally. This large aquatic and terrestrial park extends 5 km into Lake Ontario covering a total surface area of over 250 ha [43].

Acoustic telemetry array

An acoustic receiver array was first deployed in Toronto Harbour in 2010 as part of a broader telemetry effort to monitor fish and restoration activity. The present study represents a focused component of that larger initiative and was conducted between August 2014 and August 2016 (see [44]. For this study, 45 acoustic telemetry receivers (VR2W, 69 kHz, Innovasea, Halifax, Nova Scotia) were strategically positioned throughout the harbour to cover a variety of habitat types and environmental gradients, as well as key movement corridors, across 22 different groups (Fig. 1; see Additional File 1). In shallow areas (< 5 m), acoustic receivers were attached to a rope approximately 1 m above a steel or concrete anchor with a Castro float at the top to keep the receiver positioned vertically. Anchors were tethered to the nearest attachment point on shore by submerged steel cable. In deeper water (up to 10 m), the anchor was connected by floating rope to an additional weight approximately 20 m away from the primary anchor weight. Receivers were retrieved every 6 months to download data and to remove any accumulated biofouling and check receiver condition. Receivers were then redeployed in the same locations. Range testing (see Kessel et al. 2014) was conducted at a subset of receivers in different habitat types and in different seasons to inform receiver placement; ranges varied from 400 to 1500 m [45].

Fish tagging

All fish in this study were captured via boat electrofishing (SR-18EH, 6.0–7.0 A, 60 Hz, 340 V DC, Smith-Root, Inc., Vancouver, WA) between August and September 2014 and 2015. After capture, each fish was held in a live well until the boat could be safely docked and set up for transmitter implantation. All individuals were tagged with Vemco (now Innovasea) V13A transmitters [69 kHz, 90 s transmission delay, ± 3.43 g acceleration range, 5 Hz sampling frequency, activity algorithm (root mean square of acceleration = $\sqrt{(x^2 + y^2 + z^2)}$ per transmitter specification sheet, see below for more information, Vemco Ltd., Bedford, Nova Scotia). Fish were immobilized throughout the entire duration of the surgery by holding each individual in a wetted mesh net between the boat electrofisher electrodes (Smith-Root, Inc., Vancouver, WA) – a method that has previously been used to immobilize fish for surgeries (akin to electrostunning; [46]). For transmitter implantation, fish were moved from the live well with a wetted net onto a padded surgical table with the fish in a supine position. Each individual was measured for total length (mm). Prior to implanting an acoustic transmitter into an individual, the transmitter and all surgical tools were disinfected in an iodine solution and rinsed. An incision (< 20 mm) was made with a scalpel on the ventral surface of the fish. Curved forceps were

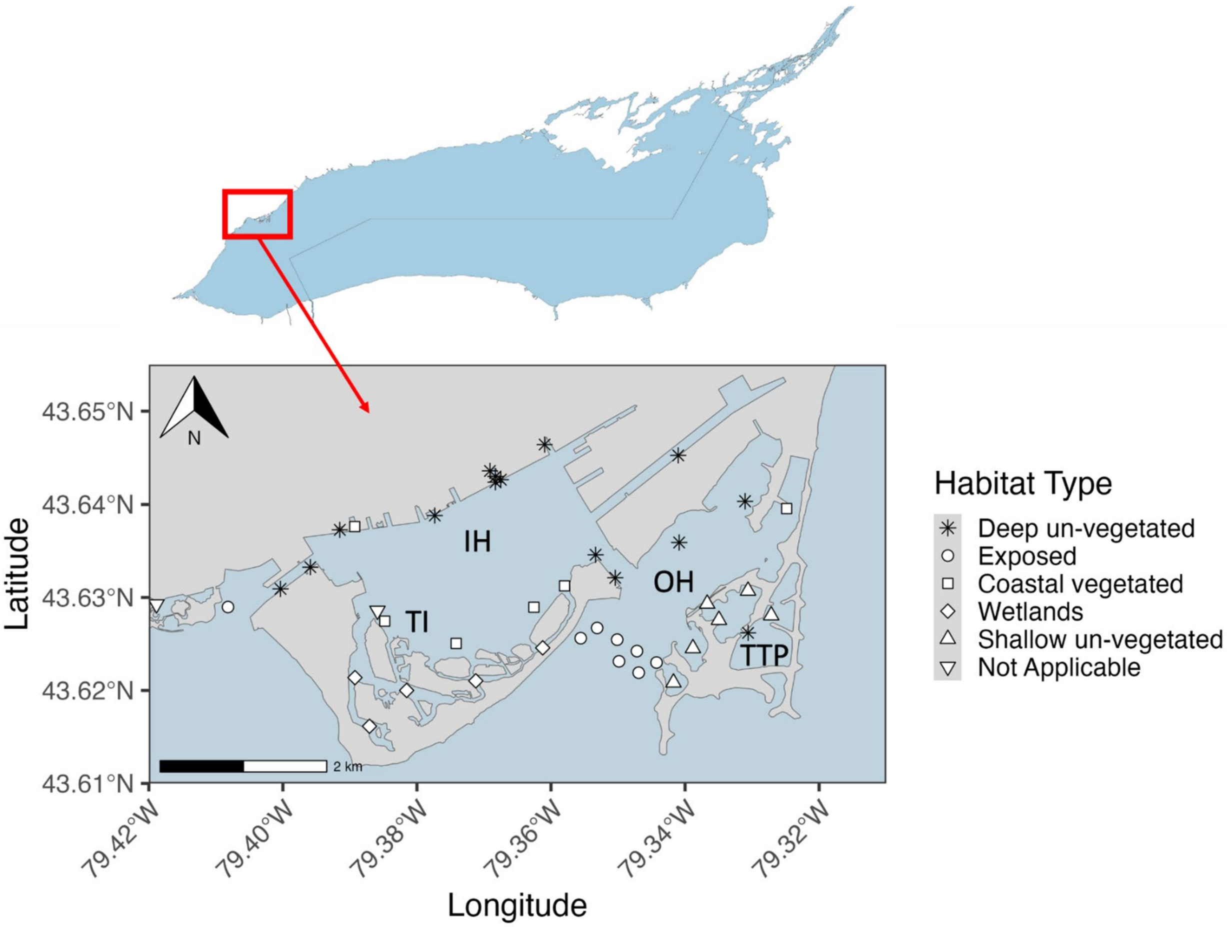

Fig. 1 Map of Lake Ontario and locations of acoustic receivers groups in Toronto Harbour points represent individual receivers in different habitat types. The following regions of Toronto Harbour are defined as the Inner Harbour (IH), Toronto Islands (TI), Outer Harbour (OH), and Tommy Thompson Park (TTP)

used to lift the skin and body wall to avoid any internal injury while making the incision. The transmitter was inserted into the coelomic cavity of the fish. The incision was closed using two simple, interrupted sutures (Ethicon PDS II, 3/0, FSL needle). After surgery, fish were returned to the livewell for recovery, and once recovered, fish were released at their original capture location. Over the course of the study, 37 individual fish were tagged: 2014, 5 Largemouth Bass and 5 Northern Pike and, and in 2015, 12 Largemouth Bass and 15 Northern Pike (see Additional File 1). Fish handling and surgical procedures were approved and followed a Canadian Council on Animal Care protocol administered by Carleton University (Certificate CU 110723).

Data processing

Fish detections were filtered to remove any potential false detections (i.e., detections that occurred from the same tag at the same receiver within a period of less than the minimum tag delay; [47]). Furthermore, a swim-speed filter was applied to the detection data to remove detections that consisted of improbable distances among detections (e.g., two detections that were 5 min apart on two receivers that are 2.0 kms apart from each other). Detections of individual tags were plotted over space and time to visually examine stationary tags (i.e., those not tracking live fish due to fish mortality or tag shedding) and subsequently removed from the dataset. Transmitters measure dynamic acceleration (i.e., acceleration caused by the movement of an animal) and not total acceleration. The transmitter has an onboard processor that first filters out the static component (i.e., gravity and orientation) from the raw acceleration data, leaving only dynamic acceleration. The transmitter then calculates the root mean square [i.e., $\surd(x^2+y^2+z^2)=\mathrm{RMS}$] of this dynamic acceleration over the sampling time period that is then transmitted as the "activity" output. This value dynamic acceleration is transmitted to receivers in a raw unitless value (1-255; ADC) that corresponds to a calibration model provided by Innovasea. These values were transformed into $\mathrm{m\ s^{-2}}$ using the following equation, $y=0+0.013588x$, where ADC values were substituted for

x. For example, if the transmitter is completely still (i.e., no motion, no vibration), the raw accelerometer sensor experiences 1 g (9.8 m/s^2) from gravity but that static acceleration is removed by the onboard filtering process before the RMS acceleration is calculated. Because the tag filters out slow, low-frequency changes caused by gravity and orientation, the remaining dynamic acceleration signal is essentially zero when the transmitter is motionless [48].

Data analysis

Receivers were either treated as a unique station ($N = 14$) or the individual receivers were combined into groups ($N = 9$) that represented locally homogeneous areas with respect to habitat features and had overlapping fields of detections (Fig. 1). For example, at the connection point between the Outer Harbour and Lake Ontario, there were seven receivers deployed as a gate to track fish that may exit the telemetry array for the open lake. These receivers covered a similar habitat type and were in close proximity. Data from all of these receivers were therefore integrated into a single receiver group to represent a "curtain" of receivers (Fig. 1). Herein, both the unique stations and groups of receivers are collectively referred to as "receiver groupings" (see Additional File 1 for details). Importantly, combining receivers into "groups" also increased the total detection area relative to a single receiver (Fig. 1).

Habitat types

Habitats were classified by integrating spatial habitat layers (see [44] for full details). Briefly, Fisheries and Oceans Canada provided a digital elevation model (DEM) for Toronto Harbour. From this DEM, the elevation gradient (slope) was calculated in ArcMap 10.2 (Environmental Systems Research Institute, Redlands, CA, USA; [49]) Mean exposure (i.e., effective fetch) was calculated for the entire harbour at a 10 m^2 grid cell size using a wind-fetch model developed by the United States Geological Survey [50]. An estimate of the percent cover of SAV (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 [51]. Finally, mean benthic water temperature during stratification (June to September) was used for the temperature variable [52]. Only this period was selected since there was considerable spatial variability in temperatures whereas during the pre- and post-stratification periods, the water had uniform temperatures, with minimal variation with depth or spatially throughout the harbour [52]. These habitat layers were then used to generate five habitat categories derived within Toronto Harbour by [44]: (1) wetlands (shallow, low fetch, warm, vegetated), (2) coastal vegetated (moderate depth, moderate fetch, cool-warm, vegetated), (3) shallow un-vegetated (shallow, low fetch, cool-warm, no SAV), (4) deep un-vegetated (deep, moderate fetch, cool, no SAV), and (5) exposed (moderate-deep, high fetch, cool-warm, no SAV; see Additional File 2 for receiver array details). Seasons were defined as spring (1 March until 31 May), summer (1 June until 31 August), fall (1 September until 30 November), and winter (1 December – 28 February).

Acceleration

All statistical analyses were conducted using R version 4.3.2 (R Core Team 2023). The full detection database was grouped into 20-minute time bins to consider fine-scale movement among receivers for each individual and the mean acceleration and location (longitude, latitude) were calculated to create centers of activity (COA; Additional File 3). Considering the detection range of receivers did not overlap, we did not involve the first-detection heard at a receiver in our analysis as we were unsure where that acceleration was measured. Subsequent detections (e.g., 10 detections at a given receiver) were retained and used, because we were certain transmissions occurred near the receiver. To estimate spatial differences in acceleration, we modeled the mean acceleration derived from the COAs using a Generalized Additive Mixed-effects Model (GAMM; using the package {mgcv}; [53]) Prior to modelling, the mean acceleration was transformed using a power transformation to normalize the data (Largemouth Bass – skewness = 2.25, kurtosis = 9.76; Northern Pike – skewness = 6.88, kurtosis = 87.14). The model for Largemouth Bass used a Gamm error distribution with a link function set to log with the model structure being the following:

$$TA_i \sim Gamma(\mu_i, \varphi)$$

$$\begin{aligned}&\log(\mu_i) = \beta_0 + \beta_{\text{season}[i]}\\&+f_{\text{spatial}}(\text{longitude}_i, \text{latitude}_i) + b_{\text{tag}[i]} + \epsilon_i\end{aligned}$$

With transformed acceleration (TA$_i$) as the response, season as a fixed effect (i.e., non-ordered factor; $\beta_{\text{season}[i]}$), longitude and latitude (derived from COAs) as a spatial smoother [thin-plate regression spline; $f_{\text{spatial}}(\text{longitude}_i, \text{latitude}_i)$], fish-tag number as a random effect $[b_{\text{tag}[i]} b_{\text{tag}} \sim \mathcal{N}(0, \sigma^2_{\text{tag}})]$, and an autocorrelation structure defined below (ϵ_i. The models for Northern Pike used a Gaussian error distribution with a link function set to log with the model structure being the following:

$$TA_i \sim \mathcal{N}(\mu_i, \varphi)$$

$$\log(\mu_i) = \beta_0 + \beta_{\text{season}[i]} + f_{\text{spatial}}(\text{longitude}_i, \text{latitude}_i) + b_{\text{tag}[i]} + \epsilon_i$$

The smooth terms were defined with an appropriate number of basis functions to balance model flexibility with interpretability, reduce wiggliness and prevent overfitting (as per [54]). Models included an autocorrelation structure (ϵ_i) that was developed using the package {itsadug} and supplied the correlation matrices for rho [55] using the following:

$$\eta_i \sim \mathcal{N}(0, \sigma^2)$$

$$\epsilon_i = \rho\,\epsilon_{i-1} + \eta_i$$

Model validation was conducted using the package{gratia}for GAMMs [56]. The goal of the model section was to assess whether statistical models that included season (i.e., presumably more complex) indeed were better predictors of acceleration values for Largemouth Bass and Northern Pike.

To determine whether season and diel period influenced largemouth bass acceleration on a more discrete timescale (i.e., season and diel period), we used generalized linear mixed model (GLMM) with a Gamma distribution with the link function set to inverse, while acceleration of northern pike on the discrete timescales was analyzed using a lognormal distribution with a link function set to log. Diel periods were defined using the package {suncalc} into four different time periods dawn, day, dusk, and night, with the duration of each period shifting throughout each season (e.g., day length during summer is greater than during the winter; [57]). We created four separate models to assess whether discrete temporal scales (i.e., season or diel period) influenced acceleration for these two species. These models had the following structure of acceleration as the response variable and season or diel period as categorical predictors. We created separate models for each species considering general behaviour and life-history strategies for each species are different (see [58]). An autocorrelation structure and random effect of individual fish number were included to account for autocorrelation and individual variation. GLMMs were fit using the R package {glmmTMB} [59]. Models were assessed to fit the data using {DHARMa} [60].

Results

Northern Pike represented approximately 84% of the total detections (858,610) and Largemouth Bass 16% (164,047). Individuals were tracked for an average of 68% of the days in the study period (range = 38–374 days; Additional File 2). The number of detections for each tagged individual varied from 122 to 101,161 detections (mean = 27,639). On average, tagged individuals throughout the study period were detected on seven receivers: from a minimum of one and a maximum of 24 receivers. Basic seasonal movement can be inferred by evaluating the number of detections at each receiver and the number of unique individuals that were detected at each receiver which are displayed in Fig. 2.

Largemouth bass

We found that mean acceleration of Largemouth Bass was significantly influenced by spatial differences among seasons (GAMM spatial smoother using latitude and longitude by the fixed effect of season—F = 0.5–2596.7, edf = 0.3–9.8, ref. df = 10, $p \leq 0.001$; Fig. 3A). Spatially, there was minimal variation in acceleration across Toronto Harbour during winter and spring, with bass exhibiting relatively low mean values of ~ 0.3 m s^{-2} in winter and ~ 0.6 m s^{-2} in spring, regardless of habitat type. In contrast, summer showed much greater spatial variation, with the highest acceleration observed in deep, unvegetated areas throughout both the Inner and Outer Harbour (exceeding 1.5 m s^{-2}). Three major areas of high acceleration occurred in Toronto Harbour for Largemouth Bass with two of them being located at the Eastern and Western Gaps which are both deep and unvegetated, where mean acceleration exceeded 1.0 m s^{-2}. The last area that resulted in Largemouth Bass exhibiting high acceleration occurred along the northeast developed coastline (unvegetated) of the Inner Harbour (IH). In comparison, sites within TTP and the Toronto Islands, characterized by shallow, vegetated habitats and reduced wind exposure, had lower acceleration values. During the fall, the highest accelerations (~ 0.6 m s^{--2} occurred in the Outer Harbour, suggesting increased acceleration in these deeper, more exposed areas.

Largemouth bass acceleration varied across seasons ($\chi^2_{1,3} = 13840$, $p \leq 0.001$; Table 1; Fig. 4a; see Additional File 3 for centers-of-activity) and diel periods ($\chi^2_{1,3} = 2606$, $p \leq 0.001$; Table 1; Fig. 4c). Acceleration levels for largemouth bass followed general seasonal trends with acceleration lower throughout the winter (0.172 ± 0.001 m s^{-2}) and fall (0.277 ± 0.002 m s^{-2}) compared to spring and summer (0.572 ± 0.013; 0.642 ± 0.004, respectively; Fig. 3b). Largemouth bass acceleration peaked during dawn (0.521 ± 0.012 m s^{-2}) and slowly decreased throughout the day with acceleration being the lowest at night (0.278 ± 0.002 m s^{-2} ; Fig. 3c).

Northern pike

We found that mean acceleration varied across space by seasons for northern pike (GAMM spatial smoother by season—F = 0.06-352.47, edf = 0.42–49.35, ref. df = 18.0–99.00, $p \leq 0.001$; Fig. 3B). During the winter, there was minimal variation in acceleration, where values remained

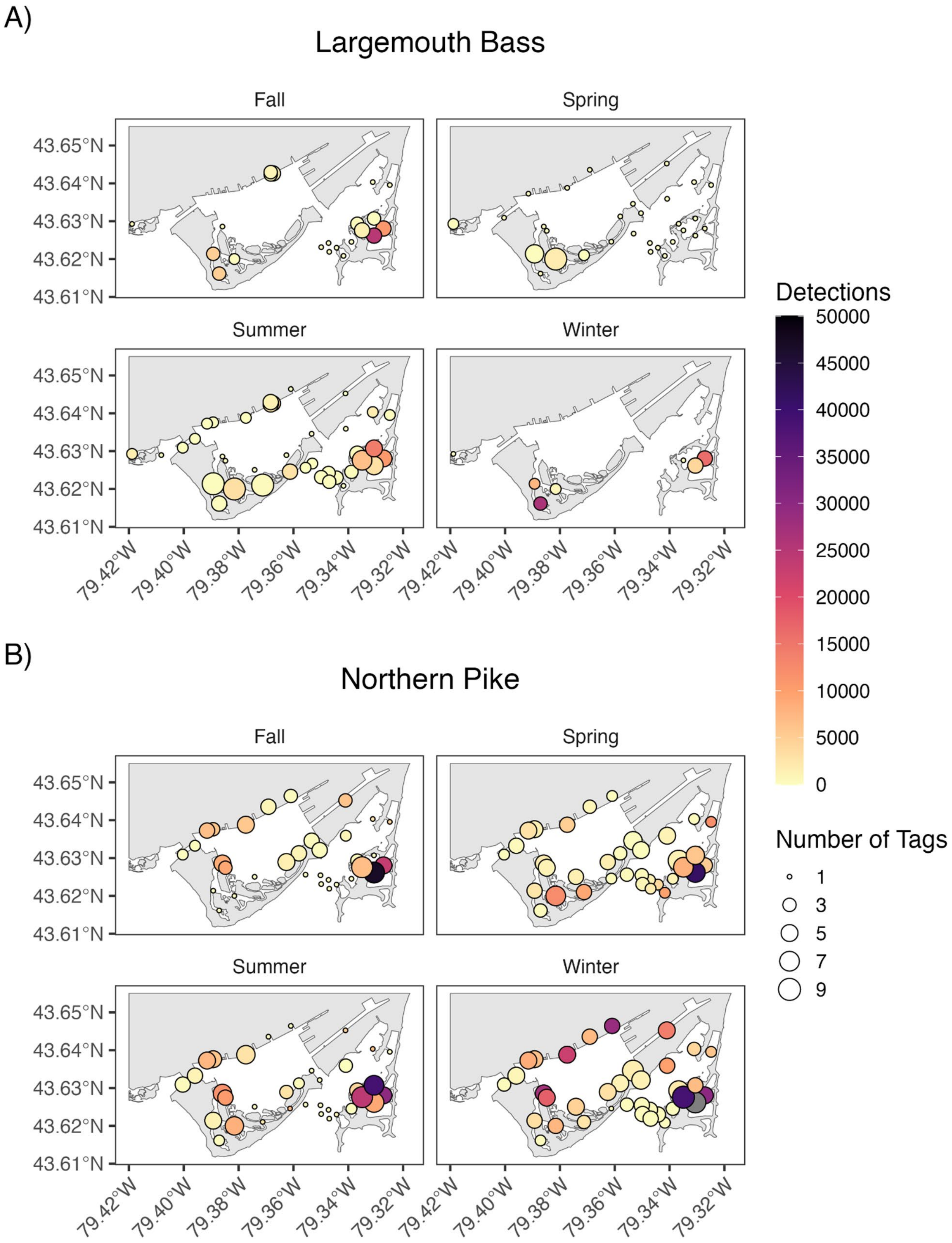

Fig. 2 Maps of detection history for each season for Largemouth Bass **A** and Northern Pike **B** in Toronto Harbour. Colour denotes the number of detections for that receiver within a season while the size of the point is the number of unique individuals that were detected at that receiver

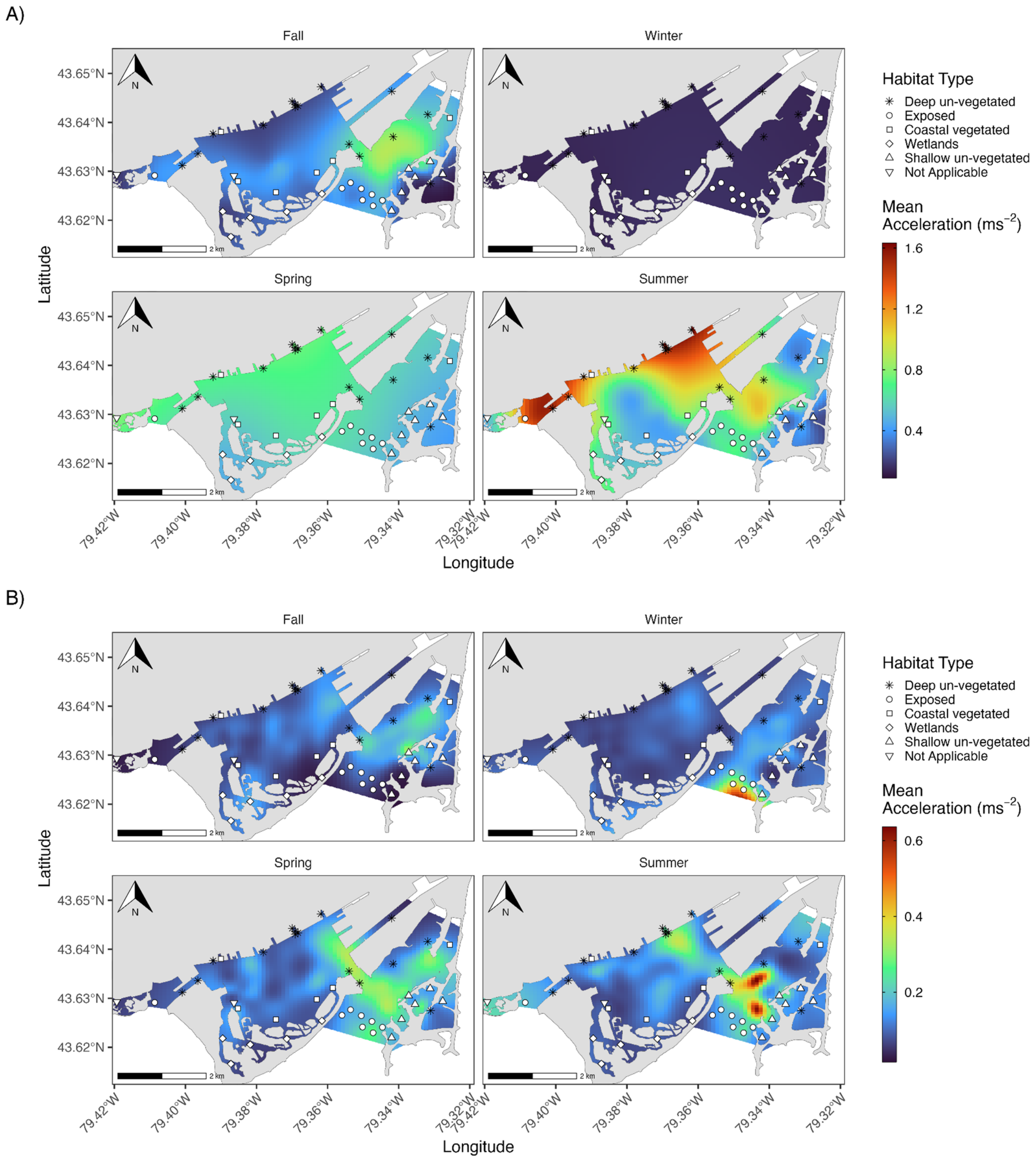

Fig. 3 Predicted mean acceleration values derived from Generalized Additive Mixed-effect Models for **A** for Largemouth Bass and **B** Northern Pike in Toronto Harbour across habitat types denoted by different symbols

below 0.2 m s^{-2} throughout most of Toronto Harbour. We observed higher acceleration values for Northern Pike in the Outer Harbour during winter, particularly near the confluence with Lake Ontario, where fish moved faster in exposed habitats with minimal vegetation (Fig. 3B). In spring, acceleration remained low across most of Toronto Harbour, except in the Outer Harbour, where values reached ~ 0.3 m s^{-2} in deep, unvegetated areas. Similar to Largemouth Bass, Northern Pike exhibited the greatest spatial variability in acceleration during summer, with the highest values occurring in the Outer Harbour near the Eastern Gap. In contrast, acceleration values were lower

Table 1 Significant predictors of activity estimated with a generalized linear mixed effects model

Species	Predictor	χ^2	df	*p*
Largemouth bass	Season	13840.00	3	≤ 0.0001
	Diel Period	2606.00	3	≤ 0.0001
Northern pike	Season	1937.80	3	≤ 0.0001
	Diel Period	2644.90	3	≤ 0.0001

Transmitter ID was included as a random effect

throughout the Toronto Islands and TTP, which were characterized by shallow depths, high vegetation cover, higher temperatures, and reduced wind exposure (i.e., wetlands and coastal vegetated habitats). During the fall, acceleration values were largely uniform across the Harbour, generally remaining below 0.2 m s^{-2}. As in other seasons, the highest fall values were again found in deep, unvegetated habitats of the Outer Harbour (Fig. 2B).

Northern Pike acceleration varied across seasons ($\chi^2_{1,\ 3}$ = 1937.80, $p \leq 0.001$; Table 1; Fig. 4b; see Additional File 3 for multiple comparisons) and diel periods ($\chi^2_{1,\ 3}$ = 2644.90, $p \leq 0.001$; Fig. 4d; Table 1). Seasonal trends in acceleration levels for northern pike were generally lower throughout the winter (0.114 ± 0.001 m s^{-2}) and fall (0.140 ± 0.001 m s^{-2}) compared to spring and summer (0.176 ± 0.001 and 0.175 ± 0.001, respectively; Fig. 4b). Northern pike acceleration peaked at dusk (0.212 ± 0.003 m s^{-2}) and dawn (0.178 ± 0.003 m s^{-2}) compared to during the day (0.153 ± 0.001 m s^{-2}) and night (0.121 ± 0.001 m s^{-2}; Fig. 4d).

Discussion

Using acoustic telemetry with accelerometer sensors, we examined how acceleration varied across space and time for both Largemouth Bass and Northern Pike within a heterogeneous system of coastal embayments. We found that acceleration was highest at sites throughout Toronto Harbour that were deep and unvegetated, with elevated values particularly evident in the Outer Harbour across all seasons. For both species, acceleration was influenced by season and diel period, with values increasing during

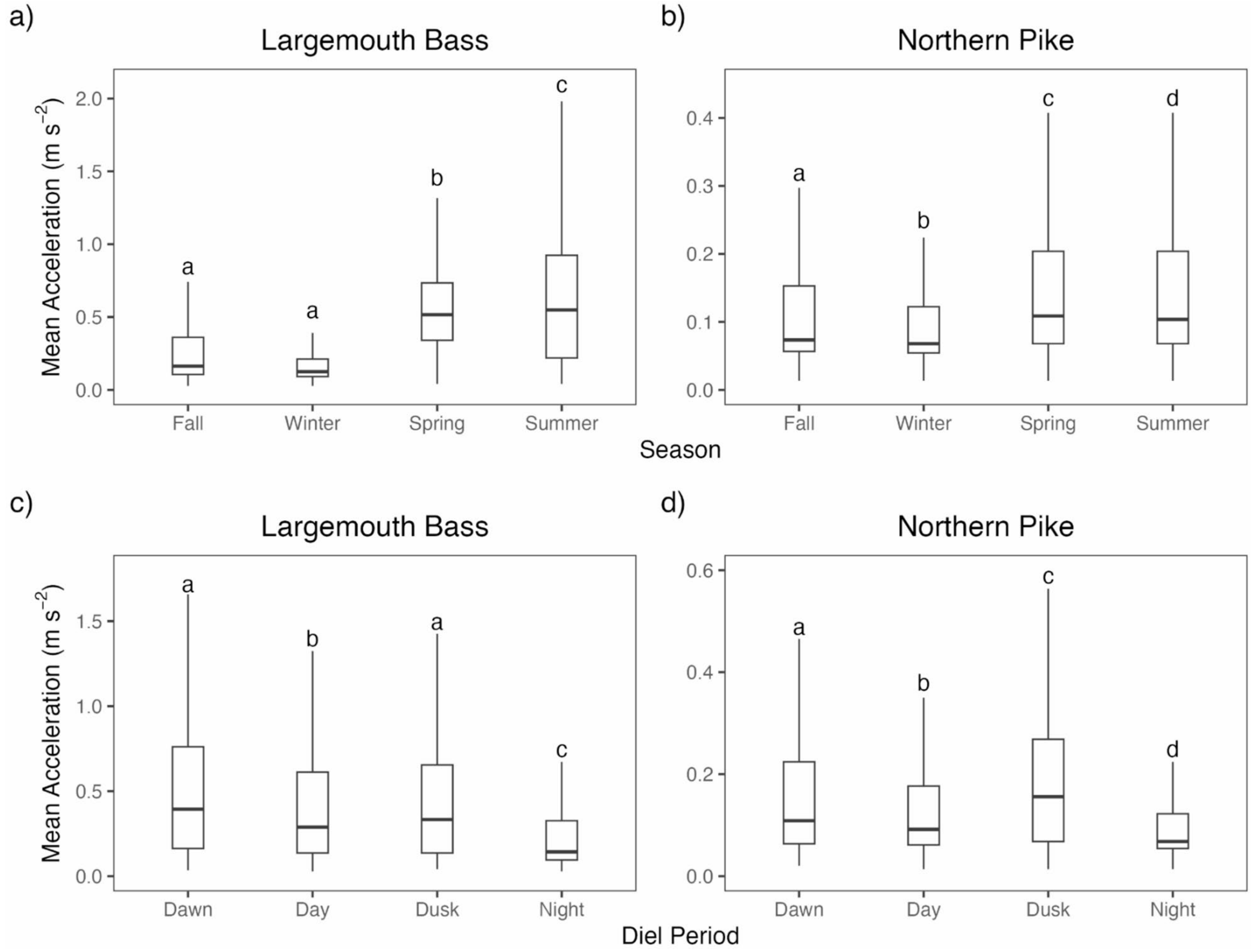

Fig. 4 Mean acceleration (m s^{-2}) for Largemouth Bass and Northern Pike in Toronto Harbour delineated by season (top panels **a** and **b)** and diel period (bottom panels **c** and **d**). Letters in all panels represent statistical significance among groups with alpha set to 0.05

spring and summer, and peaking around dawn and dusk (crepuscular). Acceleration patterns for Largemouth Bass and Northern Pike, suggested that exposed, deep, and unvegetated areas may function as movement corridors connecting patches of preferred habitat. This interpretation aligns with previous research showing low residency and occupancy at exposed sites lacking vegetation [44] and with the observed spatial separation between high-quality vegetated habitats across Toronto Harbour [42]. Several high-acceleration areas also corresponded with regions of intense water exchange and current velocity (e.g., upwellings; [61]), such as the Eastern and Western Gaps, indicating that both species may increase swimming effort and therefore likely energy expenditure in these dynamic environments to maintain position or move between preferred habitat patches [61]. Although both species are generally associated with vegetated habitats, elevated acceleration was also observed at some vegetated coastal sites, particularly for Largemouth Bass, which may serve as transitional zones between areas of low acceleration. For example, vegetated sites north of the Toronto Islands lie between sheltered wetland habitats and the more exposed Inner Harbour, potentially requiring more active movement. It is important to note that acceleration values were averaged across 20-minute intervals, which captures broader movement effort but may not detect short bursts of high activity associated with behaviors such as foraging. As such, the high-acceleration areas identified here are more likely to reflect sustained swimming or transit between habitats rather than short-burst predation events. Together, these findings emphasize the importance of transitional zones and suggest that both species use a combination of habitat types, including high-acceleration corridors, to navigate the heterogeneous landscape. To better understand the energetic consequences of these high acceleration movements in areas of high flow, future work should calibrate acceleration values to metabolic cost at varying thermal conditions using swim tunnel experiments (e.g [62]). , . These measurements could help facilitate estimating yearly energetic budgets that rely on relating standard and active metabolism to food consumption and thus providing an index of available energy for survival, growth, and reproduction [3, 63]. This would be especially valuable in an urbanized system like Toronto Harbour, where habitat heterogeneity and degradation may impose increased energetic demands on resident fish [64].

Acceleration values for both species remained relatively low throughout the year in the Toronto Islands and TTP, areas characterized by vegetated habitats such as wetlands and coastal vegetation. These findings align with previous research in Toronto Harbour showing high occupancy of both Largemouth Bass and Northern Pike in these locations, indicating consistent habitat use [22]. Specifically, Largemouth Bass exhibited the highest occupancy within the Toronto Islands and TTP, while occupancy remained low across the Inner and Outer Harbour [22]. This pattern is consistent with known habitat preferences for Largemouth Bass, which favour areas with SAV, shallow depths, and low exposure [65, 66]. Similarly, Northern Pike were also found to have high occupancy in these same areas, consistent with their known association with vegetated, shallow habitats, typically less than 12 m in depth [27, 32]. In addition, Northern Pike showed high occupancy along the northwest shoreline of the Inner Harbour, including boat slips that have undergone ecological restoration specifically for this species [67]. Our results are consistent with these prior studies, as acceleration values were predicted to remain low across seasons in these vegetated areas. Taken together, the observed low sustained acceleration values, combined with previously documented high occupancy, underscore the ecological importance of the Toronto Islands and TTP as key habitat for both Largemouth Bass and Northern Pike in this highly urbanized harbour.

We determined that acceleration for both species varied across seasons, and that acceleration was generally higher in spring and summer for both species. Increased acceleration in spring may be in preparation for reproductive activities of both Largemouth Bass and Northern Pike. During this time fish will actively seek out food and warmer water temperatures to enable gonad development needed for spawning [68–70]. Additionally, as SAV can be sparse during spring, Northern Pike and Largemouth Bass could be quite active as they search for suitable areas to forage, and stage for spawning activities, after ice-out. Acceleration continued to increase in spring and into the summer. Fish may show increased acceleration during late summer and early fall as they intensify foraging activity to build overwinter energy reserves [71, 72] or to locate overwintering regions with suitable water quality conditions (e.g [73]). , . We did, however, determine that acceleration of both species decreased substantially in fall as fish resumed low acceleration as water temperatures became cold and isothermal. Each species also exhibited decreased acceleration during the winter, particularly Largemouth Bass, although neither species were completely quiescent. Average acceleration was slightly higher (0.17 ± 0.0013 m s^{-2}) for Largemouth Bass compared to Northern Pike during winter (0.11 ± 0.0005 m s^{-2}); however, Northern Pike did exhibit a greater number of isolated, high-acceleration events, consistent with their overall acceleration patterns throughout the rest of the year (Additional File 3). Overall, our findings highlight that although both species reduced acceleration during colder months, seasonal and species-specific differences in acceleration were evident, reflecting underlying life history traits and habitat use strategies.

Largemouth Bass and Northern Pike acceleration were also influenced by diel periods. Largemouth Bass had the highest acceleration levels at dawn, followed by day and dusk, with the lowest values at night, although there were movements undertaken at all times of the day. These observations are similar to a previous study that determined that Largemouth Bass acceleration levels were higher during the day compared to night [74]. Higher foraging success is likely driving increased activities for Largemouth Bass during periods of more intense daylight as previous research has found that feeding drastically decreased during night [75]. Northern Pike were also found to have increased acceleration levels during dawn and dusk across all seasons, but were more pronounced during the summer, similar to other studies [40, 76]. Higher acceleration by Northern Pike during low-light conditions is likely due to increased foraging because reaction time of prey is diminished with decreased light, conditions that are favourable for ambush predators (see [77]) These patterns suggest that diel variation influences both foraging activity and broader movements between foraging areas, with peaks in acceleration likely reflecting periods when individuals optimize foraging efficiency while minimizing energetic costs. Both species are piscivorous, consuming small-bodied fish such as Yellow Perch (*Perca flavescens*) [23, 78]; future studies could further examine foraging movements on a fine scale for both predators and prey (e.g., with YAPS; [79]) particularly given that technological advances in acoustic telemetry are now making this possible [80].

Our study had several limitations, which should serve as sources for future research. First, while acceleration is useful for determining speed of animals in relation to their habitat, it does not distinguish among specific behaviors such as predator avoidance, or reproduction [81]. Future studies integrating acceleration with additional environmental or physiological data could help refine interpretations of movement behavior. Next, the number of detections was much lower for Largemouth Bass relative to Northern Pike, which could have influenced our analysis and interpretations. Future research would benefit from increased sample sizes and longer monitoring periods to maximize the comprehensiveness of assessing acceleration over space and time. The habitat types were assigned at individual receiver stations; however, it would have been beneficial to have higher temporal resolution for the vegetation, depth, and exposure values to ensure adequate coverage for the fish movements. While all values for vegetation, depth, and exposure were static, ideally there would be vegetation estimates across seasons, to capture variability both within year and interannually (see [82]). Additionally, the acoustic receiver array was designed to capture specific habitats and features, as well as navigation needs within Toronto Harbour; however, examination of accelerations across space would be more conducive to a grid design where receivers and spread uniformly across space (see [83]), to minimize bias introduced by the locations of the receivers [84]. Environmental variables beyond habitat type, such as water exchange (e.g., upwelling events) and prey availability, may also contribute to spatial and seasonal variation in acceleration but were not directly measured in this study.

Management implications and conclusion

Our findings of differing acceleration patterns in both Largemouth Bass and Northern Pike have implications for habitat management and conservation. We have built upon previous research [18], demonstrating the utility of incorporating acceleration sensors into acoustic telemetry studies. Here, accelerometers complemented standard movement information to elucidate which habitats within Toronto Harbour were used as movement corridors between preferred habitats, as demonstrated by high accelerometer values. As previously noted, aquatic habitat is often heterogeneously distributed in space, and this is true for Toronto Harbour. Since both species exhibited increased acceleration in exposed sites, these areas may represent energetically costly corridors rather than preferred habitats, yet they likely remain important for connectivity and transit. Consequently, restoration planning should consider the spatial configuration and distance between high-quality habitats, as movement through less suitable areas still contributes to overall connectivity across the energy landscape. For example, if wetlands are restored within a system but are disparately spaced with extensive exposed sites in between, these sites could remain fragmented due to the increased energy expenditure associated with movements between wetlands. Our results suggest that areas associated with high acceleration may act as movement corridors, allowing fish to travel between essential habitats. Therefore, habitat restoration should not only focus on creating or enhancing habitat patches but also consider how fish move between these sites, including the energetic costs of these movements across different habitat types (see [85]). Additionally, given that both species had lower acceleration in coastal vegetated and wetland habitats with higher SAV cover, these habitats should be prioritized during conservation planning. Specifically, our findings regarding acceleration, in combination with previous research [22], demonstrate the importance of these habitats to both species, particularly in urbanized areas where high-quality habitat may be scarce [64]. Therefore, wetlands and coastal vegetated habitats should be prioritized for both protection and ecological restoration for

Largemouth Bass and Northern Pike (see [86, 87]). Conserving a diversity of habitat types and maintaining functional connectivity through both high-use corridors and refuge areas will be critical for sustaining fish populations within increasingly fragmented urban environments unless active restoration is included in planning [88, 89].

Supplementary Information

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Supplementary Material 1

Supplementary Material 2

Supplementary Material 3

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Author contributions

All authors contributed to the design of the study. Field work and sampling were conducted by A.M.R. Data analyses and figures were done by A.M.R., M.L.P, and B.L.H. The manuscriptwas written by A.M.R., M.L.P, and B.L.H, with all authors contributing to revisions.

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Data availability

Telemetry data are available at the following [GitHub repository.](https:/github.com/benjaminhlina/toronto-lmb-np-accel).

Declarations

Competing interests

The authors declare no competing interests.

Ethics approval and consent to participate

Not applicable.

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