#### **RESEARCH ARTICLE**



# Evaluating the use of a freshwater protected area by northern pike (*Esox lucius*) in a large temperate lake system

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#### Abstract

Freshwater fish populations, especially migratory species and those with larger home ranges, are declining worldwide as a result of numerous direct and indirect anthropogenic factors. Freshwater protected areas (FPAs) are an emerging conservation tool that could help mitigate freshwater biodiversity losses by offering areas within freshwater ecosystems that provide full protection to species and the critical habitats they rely on. Using acoustic telemetry, we evaluated the use of a shallow, heavily vegetated FPA by northern pike (*Esox lucius*; N=29) in a large temperate lake system in Ontario, Canada from 2019 to 2021. Receivers were deployed within the FPA, in the waters adjacent to but outside of the FPA (the "boundary area"), and throughout the open-area lake basins further from the FPA. Telemetry data revealed that 46% of fish captured and released in the FPA departed and did not return (N=6), while the remaining 54% exhibited fidelity (N=7). Notably, northern pike spent a significant portion of time in the boundary area, potentially because it contains deeper waters (maximum 12 m) that may offer thermal refuge or transitional space for movements to the lake's deep main basin (max 95 m). Additionally, three northern pike that were captured and released in the lake's main basin were detected inside the boundary area; however, their use of the FPA was minimal. Our findings underscore the importance of considering habitat requirements and movement ecology of species to inform effective FPA design and identify opportunities to enhance conservation benefits provided by these areas for mobile species.

**Keywords** No-take area  $\cdot$  Movement ecology  $\cdot$  Residency patterns  $\cdot$  Seasonal migration  $\cdot$  Fisheries exclusion zone  $\cdot$  Fish sanctuary

### Introduction

Biodiversity is rapidly declining in freshwater ecosystems as a result of threats like invasive species, habitat loss, pollution, and over-exploitation, among others (Reid et al. 2019a). Drivers of extinction rates are mounting in magnitude and can be difficult to manage given threat complexity and synergies with climate change (Arthington et al. 2016; IUCN 2020). Approximately half of all freshwater fishes are

sity (Tickner et al. 2020) identifies a number of actions to protect and restore freshwater biodiversity such as the use of protected areas to benefit habitats (Piczak et al. 2023) and aquatic wildlife, including fishes (Cooke et al. 2023). Although protected areas are well studied in marine systems (i.e., Marine Protected Areas, "MPAs"), few researchers have quantified the conditions under which freshwater protected areas (FPAs) succeed or fail in supporting conservation. This lack of knowledge makes it difficult to interpret

threatened by global climate change (Darwall and Freyhof 2015), with 31% of described species listed as threatened

with extinction by the IUCN (see Arthington et al. 2016).

The emergency recovery plan for freshwater biodiver-

Protected areas are considered a global cornerstone of biodiversity conservation (Le Saout et al. 2013), including in freshwater systems (Acreman et al. 2020). Promisingly,

what factors lead to effective FPAs that enhance freshwater

fish populations (Bower et al. 2015) and creates uncertainty

around their application as a conservation tool.



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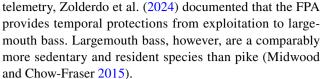
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some studies have reported that FPAs can positively affect (1) fish size (Johnson et al. 1999; Vadeboncoeur et al. 2013; Sweke et al. 2016; Stewart et al. 2014; Zolderdo et al. 2019; de Moraes et al. 2023), (2) abundance (Johnson et al. 1999, 2015; Vadeboncoeur et al. 2013; Stewart et al. 2014; Sweke et al. 2016; Zolderdo et al. 2019), and (3) fish diversity (Vadeboncoeur et al. 2013; Sweke et al. 2016; Zolderdo et al. 2019; Jamu et al. 2023). Importantly, FPAs can also provide spillover benefits (Johnson et al. 1999; Tremain et al. 2004; Zolderdo et al. 2019; Jamu et al. 2023). However, the level of protection provided by static spatial management tools like FPAs for fishes with larger home ranges or that conduct annual migrations has been difficult to quantify because these species transition among different habitats across seasons or life-history phases (Lucas and Baras 2001; Bower et al. 2015; Cooke et al. 2022). Given the staggering global declines in vagile and migratory fishes (~76% since 1970; Deinet et al. 2020), developing tools to support these species is critical to prevent further losses. One such tool to evaluate the use of FPAs is acoustic telemetry, a powerful method for evaluating fish movement dynamics in and around protected areas (Matley et al. 2022). The data generated from acoustic telemetry can support evidence-based delineation of protected area boundaries and help ensure the size and habitats encompassed are suitable depending on the conservation goal(s) of interest (Lennox et al. 2019). Acoustic receivers can be programmed to operate continuously, providing detailed movement data that mark-recapture and active tracking (e.g., radio telemetry) cannot achieve. Acoustic telemetry can determine whether established FPAs are achieving and providing conservation benefits to the species of interest and if their design could be revised to fully achieve the conservation goals for which they were established (e.g., Binder et al. 2017, 2018; Zolderdo et al. 2024).

Here, we evaluated the use of an FPA by northern pike (hereafter, "pike"; Esox lucius), a potamodromous fish that conducts annual spawning migrations (Stott and Miner 2022) and has a larger home range compared to other species in the local fish community (e.g., mostly centrarchid fishes; Midwood and Chow-Fraser 2015). The FPA we monitored is located in Big Rideau Lake, a large temperate lake in eastern Ontario, Canada, and is a fisheries exclusion zone actively patrolled and enforced by the Ontario Ministry of Natural Resources ("OMNR"; a provincial government agency). It is a long-standing FPA, initially established in the 1940s to protect largemouth bass (Micropterus nigricans) from angling exploitation, and has proven an effective conservation strategy in (1) supporting the highest abundances and richness of fishes and providing evidence of spillover (Zolderdo et al. 2019), (2) preserving high-performance phenotypes in populations of largemouth bass (Zolderdo et al. 2023), and (3) positively influencing riparian wildlife biodiversity (Dusevic et al. 2024). Additionally, via acoustic



Pike have long been acknowledged as a keystone piscivore, capable of influencing species compositions, abundance, and distribution in fish communities (Craig et al. 2008), and are one of the most caught and harvested sportfish in Ontario (OMNR 2020). Although pike populations are not listed as of concern or decreasing (Ontario's Endangered Species Act, 2007; https://www.ontario.ca/laws/regul ation/080230), the OMNR have stated that populations in the management zone this FPA is located within are considered to be at relatively low to moderate abundances with signs of high mortality. The OMNR additionally note that these populations lack large, old fish, which may lead to potential negative ecological and economic issues (OMNR 2024a). The reduction of large, old individuals can destabilize fish populations because diverse ages, sizes, and spatial structures are critical for populations to withstand ever-changing environmental conditions (Berkeley et al. 2004). Moreover, evidence shows that larger and experienced (older) spawners can produce a higher quality and quantity of eggs (Wright and Shoesmith 1988; Arlinghaus et al. 2010; Hixon et al. 2014). FPAs that are both large enough and contain suitable habitats for a range of ages would help achieve sustainable fisheries for predators like pike (Hsieh et al. 2010); however, no work has been conducted to evaluate this FPAs ability to protect vagile species like pike. Accordingly, we tracked 29 pike using acoustic telemetry in 2019–2021 to determine (1) size- and season-specific movements relative to the FPA, (2) site fidelity relative to where fish were captured and released, and (3), residency, connectivity, and habitat distribution across the lake system.

# **Materials and methods**

## Study region

This study focused on evaluating pike residency, connectivity, and general space use in relation to an intra-lake FPA in Big Rideau Lake (BRL), Ontario, Canada (Fig. 1). This FPA, referred to as "The Bog" by the provincial managers of FPAs in Ontario (OMNR 2024b), is located in the southeastern corner of BRL in a sheltered back bay and has an approximate surface area of 0.57 km² (Fig. 2; Zolderdo et al. 2024). Little to no boat traffic occurs within FPA boundaries because of its status as a fisheries exclusion, or "no-take", zone coupled with shallow (0.5–2.5 m), heavily vegetated habitats that make for generally poor motorized recreational boating. The FPA is identifiable



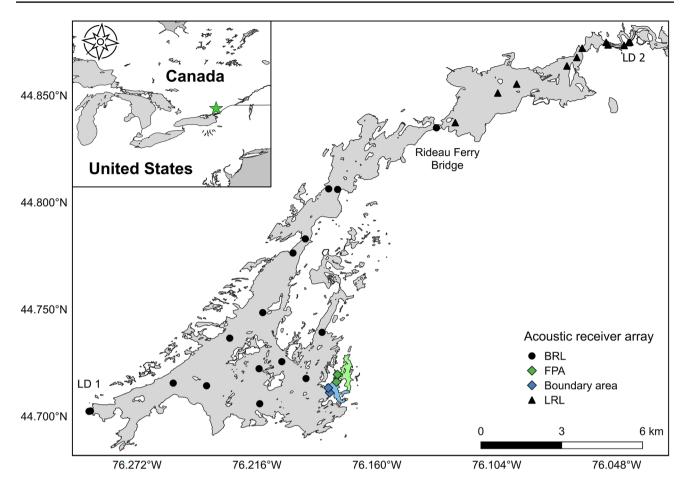


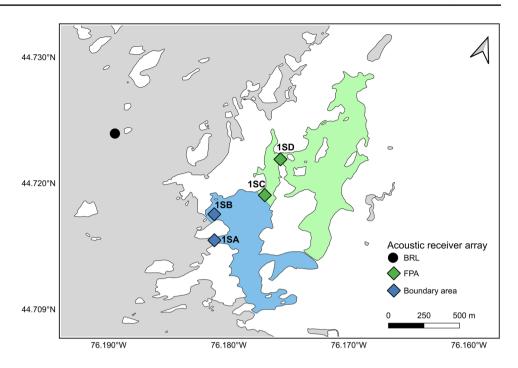
Fig. 1 Full acoustic telemetry array, spanning Big Rideau Lake (BRL; surface area: 44.6 km<sup>2</sup>) and Lower Rideau Lake (LRL; surface area: 13 km<sup>2</sup>), to monitor northern pike space use in relation to a freshwater protected area (FPA). Lockstation 1 (LD1) and Lockstation 2 (LD2) serve as the southern and northern termini, respectively. BRL includes waters between LD1 and the Rideau Ferry Bridge; LRL includes waters between the Rideau Ferry Bridge and LD2. Regions shaded in grey denote open-area, main-basin (unprotected) waters, the blue-shaded region denotes the boundary area (unprotected), and the green-shaded region denotes the FPA (protected). We define the boundary area as the small basin that lies immediately

outside the FPA. Receivers were deployed year-round from 2019 to 2021. Each icon denotes an individual acoustic receiver, with designations as follows: black circles represent the open area of BRL, green rhombuses represent the FPA, blue rhombuses represent the boundary area, and black triangles represent the open area of LRL. Northern pike were caught, acoustically tagged, and released at different locations across the study area including LD1, inside the FPA, in the main basin of BRL~1.5 km from the FPA, and LD2. Water flows in the northeasterly direction. The inset map (top left) indicates the geographic region of our study area relative to Canada and the United States

via signage posted at the entrance (Fig. 3A), and navigation and fishing maps, and is patrolled by the OMNR to ensure fishing does not occur. Members of the public can also assist law enforcement by reporting infractions. Other than two seasonal residences, shorelines within the FPA are natural and undeveloped (Dusevic et al. 2024). Waters outside the FPA, which we refer to as the "open area", are open year-round to recreational pike angling except for six weeks in the spring when fishing is prohibited during their spawning period. Although there is a second FPA in BRL, referred to as "Long Island", surveys indicated primarily rocky substrate (personal communications)—a less preferred substrate by pike compared to vegetated habitats (see Pierce and Tomcko 2005)—and therefore it was not included in this study. Additionally, we selected The Bog FPA to complement previous research that evaluated its efficacy in protecting biodiversity and providing ecological and economic benefits (see Zolderdo et al. 2019, 2023, 2024). BRL is located within the treaty and traditional territories of the Algonquin and Michi Saagiig Anishinaabeg, the traditional territory of the Haudenosaunee, and the ancestral lands of the Huron-Wendat First Nations. The history of Indigenous fisheries pre-dates the existence of Canada, and Indigenous communities in Ontario have constitutionally protected rights to fish in their treaty or traditional territory (OMNR 2024b). Fish hold cultural, social, dietary, and economic significance to Indigenous Peoples and their fishing rights are fundamentally different



Fig. 2 Acoustic telemetry array in the freshwater protected area (FPA) and boundary area relative to the main basin of Big Rideau Lake (BRL). The grey-shaded region and black circle icon represent open-area waters of BRL, the blue-shaded region and blue rhombus icons represent the boundary area, and the green-shaded region and green rhombus icons represent the FPA. Telemetry data indicate significant use of the boundary area by northern pike, potentially because it contains a unique, deeper pool, likely offering thermal refuge that the shallow, heavily vegetated FPA may not. See Online Resource 1 Fig. S3 for a bathymetric view of this region



from the privileges given to licensed recreational anglers. The OMNR have stated that they respect these rights and, as such, the rules of the FPA do not apply to Indigenous harvesters. That said, there is little evidence that those Indigenous groups harvest fish within The Bog FPA.

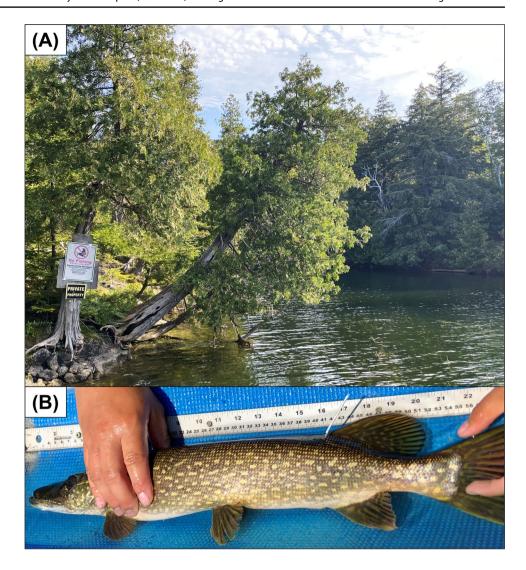
BRL has a surface area of 44.6 km<sup>2</sup> and a maximum depth of 95 m (Forrest et al. 2002). It is hydrologically connected to Lower Rideau Lake (LRL), delineated by Rideau Ferry (44°50′50.9"N 76°08′27.0"W; Fig. 1). Rideau Ferry is a bridge that permits fish movements and is not a biogeographic barrier; we only consider it a border between the two lakes given the size and habitat differences between BRL and the shallower, more riverine LRL (surface area: 13 km<sup>2</sup>, maximum depth 23 m; Forrest et al. 2002). BRL and LRL compose a portion of the 202-km Rideau Canal Waterway (hereafter, "RCW"), a UNESCO World Heritage Site that serves as a navigation network of interconnected lakes and rivers linking the Ottawa River at Canada's Capital City, Ottawa, and the St. Lawrence River at Kingston. The RCW is managed by the federal agency Parks Canada who are responsible for safe navigation, water-level management, and maintenance of the commemorative integrity and outstanding universal value with some aspects of ecosystem management (e.g., federally listed species at risk). The OMNR, not Parks Canada, sets fishing regulations and manages fisheries and FPAs in the RCW. Parks Canada, the OMNR, and other groups (e.g., Conservation Authorities) work together to balance the social-ecological needs of the waters and wildlife with recreational use of the RCW (Bergman et al. 2021).

# **Acoustic receiver array**

We used acoustic receivers (Lotek Wireless, WHS 4250, 416.7 kHz) to track pike movements continuously from 14 May 2019 to 12 October 2021. This receiver model did not have integrated temperature loggers; instead, water temperature (°C) was measured once per day by an Onset HOBO U20-001-01 water level logger (Bourne, MA, USA) installed on the riverbed in the Rideau River, 77.1 km north of our telemetry array and provided by researchers conducting other work. Receivers were programmed to log on a continuous cycle and were visited twice per year to replace spent batteries and download detection data. Our telemetry array spanned 31.3 km, from Lockstation 1 (44°42′10.8"N 76°17'43.8"W; colloquial name: "Narrows") to Lockstation 2 (44°53′34.6"N 76°03′19.9"W; colloquial name: "Poonamalie"), with receivers deployed relatively evenly across the BRL and LRL basins to investigate general space use and movement patterns. We deployed receivers on the upstream and downstream sides of Lockstation 1 and Lockstation 2 (hereafter abbreviated to "LD1" and "LD2") to evaluate potential departures from the study area and one receiver on either side of Rideau Ferry to detect inter-lake movements. A single, narrow (40 m) channel marks the FPA border through which all fish must pass if they enter or exit. To detect use of the FPA and the small basin that lies immediately outside the FPA (hereafter, the "boundary area"), we deployed one receiver ~ 350 m into the FPA, one receiver at the FPA entrance/exit border, and one receiver near each of the two channels connecting the boundary area to the BRL's main basin (see Fig. 2). Thus, receivers should have detected



Fig. 3 Images of (A): the freshwater protected area (FPA) entrance/exit and (B) the study species northern pike. The FPA boundary sign displayed in (A) states that there is to be no fishing within this provincial fish sanctuary administered by the Ministry of Natural Resources (OMNR), a provincial government organization in Ontario, Canada, and provides a phone number to report resource abuse. Note the white anchor tag inserted into the epaxial muscle beneath the dorsal fin of the northern pike in (**B**); each anchor tag has an email address, phone number, and unique ID so that if an angler recaptures a fish, they can call or email to report the location of that individual. Photo credits: (A) Joel Zhang; (B) Jordanna N. Bergman



when fish entered or exited both the boundary area and FPA. The northern boundary receiver (1SB) was deployed near a unique, deeper pool that descends to 12 m and, as such, may provide potential refuge from warm temperatures in the summer and/or ice phenomena in the winter.

Thirty-one receivers were deployed from May to October in 2019 and 2020, covering the main basins of each lake, riverine areas in LRL, the FPA and boundary area, and near LDs. Receivers were removed from shallow areas near LDs during the winter season to prevent ice damage (N=6). Receivers in the FPA and boundary area were deployed year-round; however, ice-on occurred far earlier than expected in autumn 2019 and we were unable to access the receiver inside the FPA (1SD) to replace batteries prior to winter. The batteries in receiver 1SD were spent by 06 December 2019 and did not record detections thereafter. As such, 24 and 25 receivers were deployed and logging during the 2019-2020 and 2020-2021 winter seasons, respectively. Due to lockdowns and restrictions associated with the COVID-19 pandemic, we were unable to service our telemetry array until late June/early July 2020. We also experienced considerable equipment constraints in 2021 and only serviced and re-deployed 11 receivers in May, covering LD1 (N=2), either side of Rideau Ferry (N=2), LD2 (N=3), and the FPA and boundary area (N=4), until our telemetry array was pulled and the study concluded in October 2021. Information about detection range and efficiency testing can be found in Online Resource 1 (Table S1, Figs. S1 and S2). Briefly, range testing results indicate that receivers deployed in shallow vegetated areas have low detection ranges (< 25 m) with higher detection ranges in more open areas (i.e., up to 13% efficiency at 100 m). We did not conduct formal range testing or detection efficiency evaluation in the lacustrine environments of BRL or LRL; however, Koeberle et al. (2023) found that Lotek WHS 4250 receivers in a similar lake had a detection range of 200-300 m. We did not conduct formal home range analyses, which

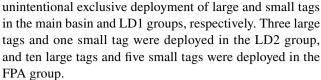


require grid-like receiver arrays with overlapping detection ranges (e.g., Teesdale et al. 2015).

# **Acoustic and anchor tagging**

Experimental protocols were approved by the Carleton University Animal Care Committee (AUP no. 110723) in compliance with guidelines of the Canadian Council for Animal Care. Fish sampling occurred from 31 May to 29 June 2019 during daylight hours between 07:00 and 20:00. Pike were captured using a single method: standard hook-and-line angling with barbed, chatterbait lures. We selected angling as the sole capture method instead of electrofishing or passive nets (or a combination of methods) to control for biases between methods and to catch the most active individuals which potentially represent those most vulnerable to harvest (Monk et al. 2021). Due to time and personnel constraints, we tagged all captured pike that appeared healthy, regardless of size. We conducted acoustic tagging efforts in four regions across BRL and LRL, deploying a relatively even number of transmitters in open areas vs. protected areas: near LD1 (within 1000 m of the LD1 Lock; N=5), in the main basin of BRL~1.5 km from the FPA (an area referred to as "McDonalds Bay" [44°42'41.9"N 76°11'16.9"W]; N=5), inside the FPA near receiver 1SD (N=15), and near LD2 (within 1000 m of the LD2 Lock; N=4). We refer to these four locations as pike "release groups", abbreviated to "LD1", "main basin", "FPA", and "LD2", respectively. All pike were released at their capture location. The exception was LD2 pike, when fishing occurred during poor weather that created unstable boat conditions, so individuals that were captured 500-1000 m into the LRL basin were translocated to the protected LD2 lock channel for tag implantation surgery and released there. These four release groups, in general, represent different regions of the study system and were selected to investigate the degree of inter- and intralake connectivity as well as FPA use.

Upon capture, pike were transferred to a foam-lined V-tray filled with fresh lake water and placed supine so that the head and gills were submerged in water but the incision site was left dry. Twenty-nine pike were implanted with a small (N=11) or large (N=18) disinfected (betadine) Lotek Juvenile Salmon Acoustic Telemetry System (JSATS) Acoustic Micro Transmitter (AMT) (hereafter, "tag"), set to emit a signal at a 20-s interval, into the coelom (small tag: L-AMT-8.2, 3.5-g in air,  $23 \times 9 \times 9$  mm, expected battery life = 1522 d; large tag: L-AMT-14-12, 8.0-g in air,  $45 \times 14 \times 14$  mm, expected battery life = 3114 days). Because all JSAT L-AMT tags use the same frequency and have the same outpower (158 dBm; i.e., both tag models should be detected equally by receivers), we deployed tags at random, and only ensured the use of a small tag if the fish was < 400 mm total length. This, however, resulted in the



To immobilize fish for surgery, Smith-Root electric fishhandling gloves were positioned on the head and caudal peduncle and set to the lowest current setting (4 mA) to immobilize the fish but allow continuous opercular respiration (Reid et al. 2019b). A small (< 1 cm) incision was made centrally on the midline, posterior to the pectoral fins, using a sterilized no. 21 scalpel. The tag was initialized and inserted into the coelom with 1-2 simple, with interrupted sutures (PDS II polydioxanone suture, violet monofilament, 2–0) used to close the incision. The total length (TL) of each fish was measured prior to release. Mass was not measured in the field but instead generated using models from Schneider et al. (2000) to estimate tag burden. We calculated tag burden by dividing the acoustic tag weight in air by the estimated fish mass (both in grams) and multiplying by 100. Tag burden was low across release groups (mean  $\pm$  SD for LD1, main basin, FPA, and LD2 was  $0.37 \pm 0.10\%$ ,  $1.04 \pm 0.28\%$ ,  $0.97 \pm 0.51\%$ , and  $1.02 \pm 0.41\%$ , respectively) and individuals (see Table 1). All pike were marked with an external anchor tag (FLOY TAG & Mfg., Inc., Seattle, WA, USA), inserted into the epaxial muscle alongside the dorsal fin (Fig. 3B), should an individual be recaptured and as part of a broader mark-recapture study. The entire process took 2-4 min. Pike were monitored for post-surgical behaviour changes or distress (e.g., lack of or no movement when gently prodded, equilibrium imbalance, changes in ventilation rate; Tsitrin et al. 2020). No fish showed any apparent deleterious effects from surgery and were released when equilibrium was gained and strong swimming actions were observed (in all cases, occurring within a few minutes postsurgery). Tracking and biological information are provided in Table 1 for acoustically tagged pike.

#### **Data analysis**

## Raw detection filtering

All data processing and statistical analyses were conducted using R version 4.4.2 and maps were created using QGIS version 3.34.12-Prizren. Detection filtering followed methods by Bergman et al. (2024). We applied several filters including a minimum lag-interval filter and a minimum power requirement filter to identify and remove likely false positives. We then applied a detection event filter (Holbrook et al. 2019) to the final list of detections, grouping individual detections into distinct events defined by movements between receivers and sequential detections at the same receiver separated by a predefined time frame. Here,



detections occurring in sequence with gaps of < 1 h between detections at the same receiver were considered a detection event. If a full hour passed between sequential detections, the subsequent detection denoted the start of a new event. We filtered out detection events with less than one detection to eliminate improbable detections (e.g., individuals rapidly moving large distances). We generated abacus plots (Online Resource 2) and inspected each to ensure that all detection event timestamps and locations were logically and biologically plausible and to determine whether mortalities or tag shedding occurred via repeated detections of an individual tag at a single receiver over extended periods of time without subsequent detections at other receivers (Klinard and Matley 2020). No tags appeared to exhibit this pattern.

### Lake region residency patterns

To quantify pike space use, a residency index (RI) was calculated. RI is calculated by dividing the total number of days detected at each receiver by the total number of days the individual fish was detected anywhere in the array (using the 'Kessel method' in the GLATOS package; https://rdrr.io/ github/jsta/glatos/man/residence\_index.html). We used RI because it reduces the potential bias of a large number of detections at a given receiver generated by only a few, or more sedentary, individuals (Kessel et al. 2016) and additionally provides a way to assess fish habitat selection and space use in relation to a protected area (e.g., Harasti et al. 2015; Novak et al. 2020; Herrera et al. 2024). RI values are proportional, ranging from 0 to 1, with a value of 1 indicating the highest possible residency. We adjusted RI values from "0" and "1" to "0.001" and "0.999" because our modelling framework (beta regression; see below) is unsuitable with 0 s or 1 s as a response variable. We grouped together the two receivers inside of, and at the entrance/exit to, the FPA (1SC and 1SD, Fig. 2; "FPA receivers"), the two receivers at each of the channels to the basin that precedes the FPA (1SA and 1SB, Fig. 2; "boundary receivers"), all receivers in BRL ("BRL receivers"), and all receivers in LRL ("LRL receivers"). These four receiver groupings are hereafter

**Table 1** Tracking and biological data for acoustically tagged northern pike ("pike"; N=29)

Release lake	Release region	Fish ID	TL (mm)	Tag size	Tag burden	Mean ± SD distance move (m)	Year 1: 2019-2020 ( <i>N</i> =19)	Year 2: 2020-2021 ( <i>N</i> =9)	Year 3: 2021-2022 ( <i>N</i> =6)	Movement type
		1DE5	585	Large	0.66%	152 ± 367	✓			Departed FPA
		B761	411	Large	2.00%	145 ± 257	✓			Departed FPA
		F079	453	Large	1.48%	56 ± 236	✓			Departed FPA
		93F4	835	Small	0.09%	184 ± 716	✓			Departed FPA
		E4AC	475	Small	0.56%	152 ± 212	✓			Departed FPA
		0D40	716	Large	0.35%	336 ± 992	✓	✓		Departed FPA
	FPA -	901B	486	Large	1.18%	96 ± 192	✓	✓		FPA resident
		5918	441	Large	1.61%	126 ± 246	✓			FPA resident
		2A10	543	Large	0.84%	60 ± 171	✓			FPA resident
		57FE	502	Large	1.07%	0	✓			FPA resident
_		CA72	473	Large	1.29%	0	✓			FPA resident
Big Rideau		1BCE	472	Small	0.57%	73 ± 162	✓			FPA resident
		813E	452	Small	0.65%	0	✓			FPA resident
		3289	475	Large	1.27%					Not detected
		BD7E	409	Small	0.89%					Not detected
	Main basin	0B4D	514	Large	0.99%	828 ± 1053		✓	✓	Entered & departed FPA
		8E0F	476	Large	1.26%	128 ± 309	✓	✓	✓	Entered & departed FPA
		AD3D	461	Large	1.40%	107 ± 305		✓	✓	Entered & departed boundary area
		D34B	547	Large	0.82%	1039 ± 1800	✓			Open-area resident
		D08A	564	Large	0.74%					Not detected
	LD1	4EAA	597	Small	0.27%	762	✓			Open-area resident
		07C8	571	Small	0.31%					Not detected
		806E	562	Small	0.33%					Not detected
		BDDB	511	Small	0.44%					Not detected
		EA58	491	Small	0.50%					Not detected
	LD2	8BCF	359	Small	1.34%	94 ± 150	✓			Open-area resident
ver		62E5	507	Large	1.04%	47 ± 295	✓	✓	✓	Open-area resident
Lower Rideau		579E	669	Large	0.43%	268 ± 775	✓	✓	✓	Open-area resident
ш.		6C75	475	Large	1.27%	123 ± 248	✓	✓	✓	Open-area resident

The total length (TL; mm), tag size, tag burden, mean±standard deviation (SD) distance moved during the study (m), and years detected are provided. Fish were captured and released between May 31 and June 29 2019. Seven fish were not detected. Pike were released in four different lake regions to determine inter- and intra-lake connectivity and FPA use. The main basin release site is ~1.5 km from the FPA. A "movement type" was assigned to each fish, indicating if the individual was released in the freshwater protected area (FPA) and departed (departed FPA); released in the FPA and remained for the duration of their detection period (FPA resident); released in the BRL main basin, entered the FPA or boundary area, and departed (entered & departed FPA/boundary area); released in an open area (BRL main basin, LD1, LD2) and remained for the duration of their detection period (open-area resident). The three pike that entered and departed the FPA and/or boundary area did so in early spring, suggesting potential reproductive movements



referred to as "lake regions". RI values were generated for each pike for each lake region to illustrate where fish spent time in relation to their release location (group). A list of acronyms used in this study and their corresponding full-form term is provided in Table 2.

We developed generalized linear mixed models (GLMM) using the glmmTMB function (package glmmTMB; Douma and Weedon 2019; Brooks et al. 2022) to evaluate pike residency patterns and space use relative to the FPA. We only included pike from the FPA and main basin release groups in residency models because these were the only two release groups detected in or near the FPA. Our first GLMM evaluated the effect of release group on residency in the boundary area and FPA. The two FPA receivers remained grouped together as a distinct receiver station. However, because 1SB is located near a unique, deeper pool compared to the shallower 1SA (Online Resource 1 Fig. S3; Pierce et al. 2013), we set each boundary receiver as a unique station. The response data for residency models (RI; continuous) are proportional, so a GLMM with a beta distribution was used to evaluate the potential interactive relationships between release group (main basin or FPA; categorical) and receiver station (FPA, 1SA, 1SB; categorical) on RI. A random intercept of individual fish (pike ID) was included because there were multiple observations from each individual. We used the *DHARMa* package (Hartig 2022) to run residual diagnostics and test model assumptions and the check\_overdispersion to assess overdispersion (from the performance package; Lüdecke et al. 2021). We then fit a second residency GLMM to investigate the possible interactive relationship between fish size (TL; continuous) and lake region use. Due to the considerable reduction in deployed receivers after May 2021, only telemetry data from May 2019-April 2021 were included in the second model. A random intercept for individual fish was included and model assumptions were tested as described above.

# Seasonal FPA and boundary area use

While *RI* was more appropriate to evaluate general area use of our full telemetry array, *duration* assesses the amount of time fish actually spent near each receiver station. We therefore assessed the duration that fish spent in the FPA and at each of the two boundary receivers to examine the FPA's protective capacity across seasons. We chose "duration" as the response variable in this analysis because it provides a finer-scale resolution of space use for this smaller geographic scale vs. the use of RI which we applied to the full telemetry array. With RI analysis, a fish may have been detected for only a few minutes for one day at a single receiver and generate an RI value of 1 for that station. Seasons were defined as spring (March, April, May), summer (June, July, August), autumn (September, October,

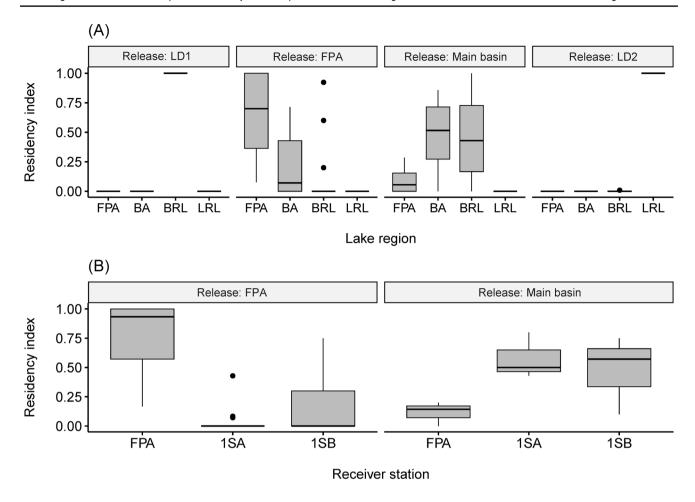
Table 2 A list of acronyms used in this study with full-form terms provided

Acronym	Full-form term
BRL	Big Rideau Lake
LRL	Lower Rideau Lake
FPA	Freshwater protected area
LD1	Lockstation 1 (southern terminus)
LD2	Lockstation 2 (northern terminus)
1SA	Receiver station: Boundary area
1SB	Receiver station: Boundary area
1SC	Receiver station: Freshwater protected area
1SD	Receiver station: Freshwater protected area
RI	Residency Index

November), and winter (December, January, February). Duration was calculated by summing the total time in minutes that fish spent at 1SA, 1SB, and the two (grouped) FPA receivers. We fit a GLMM with duration as the (continuous) response variable and season (categorical) and receiver station (FPA, 1SA, 1SB; categorical) as predictor variables. Duration data were not normally distributed (positive skew), so a gamma distribution was applied. Individual pike ID was included as a random effect as above, as well as "year" to control for biased numbers of detections by season due to our deployment schedule (e.g., there are no spring 2019 detection data because tagging did not occur until summer). An interaction between season and receiver station was not applied because of insufficient data and low sample sizes.

We used freely available, high-resolution (10 m horizontal RGB) Sentinel-2 images via the ESA Copernicus browser (https://browser.dataspace.copernicus.eu/) to determine iceon and ice-off in winter (December, January) and spring (March, April), respectively. Ice-on and ice-off periods were used as a proxy to investigate potential seasonal barriers to movement (i.e., ice) in and out of the FPA and boundary area, in particular because pike commence their annual spring spawning migration to flooded vegetation in littoral, sheltered areas, usually soon after winter ice-off, when shallows have warmed to 8-12 °C (Casselman and Lewis 1996). In BRL, these spawning temperatures are typically reached between the end of March and mid-April. Surface ice and anchor ice or ice dams (Nafziger et al. 2017; Thellman et al. 2021) may form at the shallow (<3 m) boundary area and FPA entrance/exit channels, fragmenting connectivity among the FPA, boundary area, and main basin of BRL. We defined "ice-on" and "ice-off" to have occurred when most (> 80%) of the FPA and boundary were fully covered or mostly free of surface ice, respectively. We inspected all images, regardless of cloud cover, to assess when ice coverage and ice dissipation occurred each year.





**Fig. 4** Boxplots illustrating the interactive relationships between residency index (RI) and (A) release location at different lake regions and (B) release location and receiver stations. (A): Acoustic receivers were grouped together to provide residency data across four lake regions including the FPA, the boundary area (BA), BRL, and LRL. (B): The two boundary area receivers, 1SA and 1SB, were set as distinct stations to evaluate space use in the region immediately outside

the FPA. The two FPA receivers remained grouped for residency analysis. For information on receiver locations and RI values, see Figs. 1 and 2 and Tables 3 and 4, respectively. Boxes represent the boundaries of the upper and lower quartiles, lines inside boxes represent medians, and whiskers represent the minimum and maximum values from the raw data

## **Results**

The final acoustic telemetry dataset consisted of 1213 detection events (19,590 detections) for 22 individuals (76% detected) from 31 May 2019 to 24 June 2021. Seven individuals were not detected: four LD1 pike, two FPA pike, and one main basin pike (Table 1). Tracking durations were mixed, ranging from one to 729 days, with an average of 155 days. Four fish were detected for the full three-year study, 4 fish were detected for 2 years (either 2019 and 2020, or 2020 and 2021), and the remaining 14 fish were detected for 1 year in 2019. Of those 14, 5 fish were detected for < 7 days. Only one pike from the LD1 release group was detected for a few minutes near the LD1 Lock (Online Resource 2). Fish released (and detected) at LD2 spent 100% of their time in LRL, except for one individual (#579E) that briefly crossed Rideau Ferry into BRL where it spent 8 min

before returning to LRL. We also recorded one LD2 pike (#62E5) moving across the LD2 Lock several times. This fish conducted two lock passages, one downstream and one upstream, ultimately returning to LRL and remaining there for the duration of the study. We did not detect any inter-lake movements.

During our study, the farthest a fish moved from its release point was 8.5 km. This movement was conducted by the same LD2 pike that travelled and crossed Rideau Ferry. The farthest distance moved by fish from the main basin and FPA release groups was 4.3 km and 4.9 km, respectively. Pike in the main basin release group moved on average the most (mean  $\pm$  SD: 298  $\pm$  700 m) compared to LD2 (104  $\pm$  426 m) and FPA (126  $\pm$  461 m) pike. The LD1 pike moved 762 m from its release location to the LD1 Lock for its single detection event. The average distance moved for each acoustically tagged pike is provided in Table 1.



We observed 46% (6/13) of detected FPA pike departing the FPA with no detectable return. Pike that left the FPA and entered the boundary area spent a considerable amount of time there, with three individuals spending more than half of their detected time in this region. Presumably, the remaining 54% of FPA pike remained within, or at least near, the FPA if their last detection was at the receiver inside the FPA (1SD) or at the FPA border receiver (1SC). We documented three main basin pike entering and residing within the boundary area, two of which also were detected inside the FPA. These two fish were detected inside the FPA briefly (#0B4D and #8E0F for 20 min and 3.5 days, respectively; Online Resource 2) before exiting. A summary of all statistical test outputs is provided in Online Resource 3.

## **Residency patterns**

We evaluated pike residency patterns from all release groups to illustrate where fish spent time in relation to their release group (Fig. 4A). Pike released at LD1 and LD2 displayed RI values of 1 in BRL and LRL, respectively, only being detected on receivers in the basins of each of their respective release lakes. The exception, as mentioned above, was the single LD2 pike that was detected briefly on the BRL side of Rideau Ferry before returning to LRL. Mean RI  $\pm$  SE values for each lake region appear to be linked with release group: fish released in the FPA showed the highest mean RI values for the FPA  $(0.65 \pm 0.10; N = 13)$  and fish released in the (BRL) main basin showed the highest mean RI values for BRL  $(0.47 \pm 0.22; N=4)$ . Interestingly, both the main basin and FPA release groups resided in the boundary area, although the main basin group spent more time in the boundary area  $(0.47 \pm 0.19; N = 3)$  than FPA pike  $(0.23 \pm 0.08;$ 

N=7). Residency values from this analysis are provided in Table 3.

For statistical analysis of residency in relation to the FPA, only pike from the main basin (N=4) and the FPA (N=13) release groups were included because LD1 and LD2 pike were not detected near or in the boundary area or FPA and therefore acted as outliers. Results from our first GLMM that evaluated the relationship between release group and boundary area and FPA residency revealed significant differences in residency at each receiver station, which were related to release location (Fig. 4B; Model 1—Online Resource 3 Table S1). Pike released in the FPA showed the highest RI values (mean RI  $\pm$  SE) for the FPA  $(0.77 \pm 0.09)$  and spent significantly more time there (p < 0.001) than at either of the two boundary area receivers (1SA: p = 0.21, 1SB: p = 0.45). Although FPA pike did not select for 1SB significantly more than 1SA, residency was four times higher at 1SB (1SA:  $0.05 \pm 0.03$ vs. 1SB:  $0.20 \pm 0.08$ ). Main basin pike that entered the boundary area resided nearly equally at 1SA and 1SB, displaying similar mean RI  $\pm$  SE values of  $0.58 \pm 0.11$  and  $0.48 \pm 0.19$ , respectively. Main basin pike showed significantly lower residency in the FPA (p < 0.001) with a mean  $RI \pm SE$  of  $0.12 \pm 0.06$ . The mean  $RI \pm SE$  values provided here are given in Table 4.

We documented an interesting relationship between fish size and lake region residency via our size-residency GLMM (Fig. 5; Model 2—Online Resource 3 Table S1). This model indicates that larger fish spent significantly more time in the main basin of BRL (p=0.006;  $R^2=0.6$ ), whereas smaller fish displayed higher residency in the FPA (p=0.06;  $R^2=-0.48$ ). There was overlap in residency across fish sizes in the boundary area (p=0.41;  $R^2=-0.071$ ).

**Table 3** Residency index (RI) for acoustically tagged northern pike, by release group, at four different lake regions: the freshwater protected area (FPA), the boundary area that denotes that small basin adjacent to the FPA, Big Rideau Lake (BRL), and Lower Rideau Lake (LRL)

Release lake	Release group	Mean RI±SE by lake region   number of northern pike detected					
		FPA	Boundary area	BRL	LRL		
Big Rideau (BRL)	LD1 (N=1)	0	0	1   N = 1	0		
	Main basin $(N=4)$	$0.10 \pm 0.07 \mid N = 2$	$0.47 \pm 0.19 \mid N = 3$	$0.47 \pm 0.22 \mid N = 3$	0		
	FPA $(N = 13)$	$0.65 \pm 0.10 \mid N = 13$	$0.23 \pm 0.08 \mid N = 7$	$0.13 \pm 0.08 \mid N = 3$	0		
Lower Rideau (LRL)	LD2 (N=4)	0	0	$< 0.01 \pm < 0.01 \mid N = 1$	1   N = 4		
Number of northern pike	detected	N = 15	N = 10	N=8	N=4		

RI and standard error (SE) across the 3-year study (2019–2021) are provided for each release group with the number of detected pike denoted. Data from May–October 2021 were not included in this analysis because our telemetry array was considerably reduced during this period due to equipment constraints. The values provided here are reflected in Fig. 4A



#### Seasonal habitat use

We evaluated the amount of time (duration) pike spent near boundary area receivers and in the FPA to determine whether residency might be related to season, revealing significant effects of both season and receiver station on habitat use (Fig. 6; Model 3—Online Resource 3 Table S1). Pike spent the most time at receiver station 1SB (p = 0.01; mean  $\pm$  SD: 2.95  $\pm$  5.02 min) compared to receiver station 1SA (p = 0.10; mean  $\pm$  SD: 1.45  $\pm$  2.69 min) or within the FPA (p = 0.81; mean  $\pm$  SD:  $0.96 \pm 1.53$  min). Although our model did not detect a statistical difference in duration among spring (p = 0.65; mean  $\pm$  SD:  $2.46 \pm 0.11$  min), summer  $(p = 0.81; \text{ mean} \pm \text{SD}: 2.28 \pm 4.29 \text{ min}), \text{ and}$ autumn (p = 0.86; mean  $\pm$  SD:  $0.98 \pm 1.48$  min), spring and summer durations were approximately  $2.5 \times \text{greater than}$ autumn and 30 × greater than winter duration. Pike spent significantly less time in the FPA and boundary area in the winter  $(p < 0.001; \text{ mean} \pm \text{SD}: 0.08 \pm 0.11 \text{ min})$ . Notably, our HOBO temperature logger recorded warm water temperatures between ~ 25 and 29 °C from 3 July to 8 August 2019, 1 July to 18 August 2020, and 9-28 August 2021. The maximum temperature recorded was 28.87 °C on 10 July 2020.

Sentinel-2 satellite imagery revealed ice-on occurred by 20 December 2019 and 09 January 2021 and ice-off occurred by 23 April 2020 and 29 March 2021 (Online Resource 1 Figs. S4 and S5). We did not detect fish moving among the FPA, boundary area, and main basin of BRL during the ice-on period. However, we did document three main basin pike using the boundary area and/or FPA in the spring, close to the ice-off dates. Pike #8E0F moved from the boundary area into the FPA in early April 2021, and pike #AD3D was documented moving from the BRL main basin into the boundary area at the end of March 2021. Pike #0B4D was detected in the boundary area and FPA at the end of March 2020. It departed and was detected in the BRL main basin, subsequently re-entering the boundary area to be detected in December 2020 and March 2021. Pike #0B4D's boundary-area detections in December 2020

Table 4 Residency index (RI) for acoustically tagged northern pike, by release group, at the three receiver stations used to evaluate the protective capacity of the freshwater protected area (FPA) and surrounding region (the boundary area)

Release lake	Release group	Mean RI $\pm$ SE by lake region   number of northern pike detected				
		FPA	1SA	1SB		
Big Rideau (BRL)	Main basin $(N=4)$	$0.12 \pm 0.06 \mid N=2$	$0.58 \pm 0.11 \mid N=3$	$0.48 \pm 0.19 \mid N = 3$		
	FPA $(N=13)$	$0.77 \pm 0.09 \mid N = 13$	$0.05 \pm 0.03 \mid N = 3$	$0.20 \pm 0.08 \mid N = 5$		
Number of northern	pike detected	N = 15	N=6	N=8		

We assessed residency at each of the two boundary area receivers (1SA and 1SB; Fig. 2) and inside the FPA. The two FPA receivers were grouped together for RI analysis. Only fish detected on a boundary area or FPA receiver were included here; as such, LD1 and LD2 pike were excluded from this analysis. RI and standard error (SE) across the full 3-year study, from May 2019 to October 2021, are provided for each release group with the number of detected pike denoted. The values provided here are reflected in Fig. 4B

and March 2021 suggest the fish was restricted to this region during the ice-on period. Its detections at the end of March in both 2020 and 2021 may be reproductively linked and indicate site fidelity given overlap in timing with spawning water temperatures.

### **Discussion**

# Inter- and intra-lake connectivity

Our telemetry data indicate limited inter-lake connectivity, as none of our acoustically tagged pike relocated from BRL to LRL or vice versa. Pike from the main basin release group moved more than the other release groups, on average moving 3 × and 2.4 × further than LD2 and FPA pike, respectively. Kobler et al. (2008) suggests that a pike's activity centre size may be related to the size of the waterbody itself, which could be why we documented main basin pike-caught and released in openarea waters of the larger, deeper BRL—moving the most. The recorded maximum distance moved by pike in other research appears to vary considerably, with Miller et al. (2001) reporting 26.5 km in a large lake, Vehanen et al. (2006) reporting 7.4 km in a connected river-lake system, and Midwood and Chow-Fraser (2015) reporting 3.9 km in a coastal wetland system. Several studies have suggested that most adult northern pike are resident and do not move extensively (Vehanen et al. 2006), with subpopulations of pike thought to exist, broadly characterized as "sedentary or resident" or "highly mobile" (see Jepsen et al. 2001; Cittadino et al. 2024; Lukyanova et al. 2024; Rittweg et al. 2024). Our data supports this suggestion, given the variability in average and furthest distances moved by pike. Regardless, because our receivers detected most pike moving on average < 500 m, and that BRL and LRL have a large combined surface area spanning 57.6 km<sup>2</sup>, FPAs in the RCW are likely only available to pike residing nearby. We did detect three main basin pike inside the boundary area, with two of those individuals also entering the FPA,



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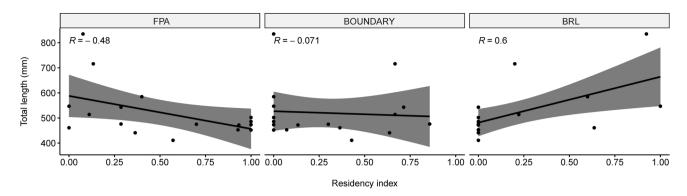


Fig. 5 Scatterplot illustrating the interactive relationship among residency index (RI), lake region (the freshwater protected area [FPA], the boundary area [BOUNDARY], and the main basin of Big Rideau

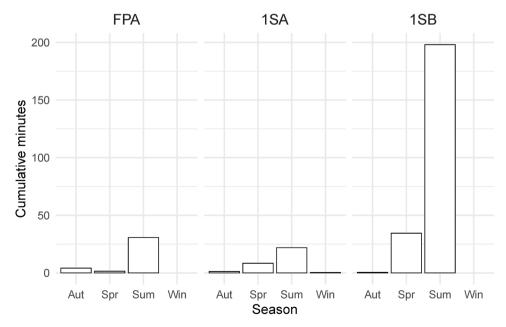
Lake [BRL]), and fish size (total length, mm). A Pearson correlation coefficient is provided for each lake region. The solid line represents the best-fit regression line with 95% confidence intervals

indicating that fish with home ranges within a few kilometers of the FPA may access and use it.

Notably, the farthest distances moved were by two LD2 pike. These two individuals travelled close to double the maximum distance moved by any other pike in our study. These larger movements from riverine areas towards deeper waters may be purposeful, as they occurred in the summer (June, July) and winter (December), potentially as pike search for waters that provide thermal refuge from warmer, shallower regions or protection from ice phenomena (Pierce et al. 2013). Although LRL offers vegetated, littoral areas and deeper pools that should provide pike with habitat throughout the year, these comparably farther movements may suggest searching behaviour to find new, or potentially better, habitat (Lucas and Baras 2001). It is not entirely clear, however, why these two pike did not continue into BRL. It could be that the narrow, deep channel connecting LRL to the BRL main basin is not a suitable migratory corridor or that the region near Rideau Ferry, which experiences considerable boat traffic, produces high levels of anthropogenic noise that pike avoid (i.e., avoidance behaviour; Mickle and Higgs 2018).

One goal of our study was to evaluate whether pike tagged and released within the FPA remained inside its protective boundaries or showed movement patterns indicating site fidelity. Telemetry data revealed that 46% (N=6) of our tagged pike left the FPA and did not return. The remaining 54% (N=7) were detected exclusively on FPA receivers and therefore assigned as "FPA residents" (Table 1). Unpublished mark-recapture data on pike from the FPA also suggest residency or fidelity, as multiple individuals were both marked and recaptured within the FPA up to 1000 days later (average number of days between mark and recapture: 293) (Bergman JN, unpublished data). Notably, FPA residents were detected only in 2019, which is likely an artifact of poor receiver detection ranges and a lack of additional

**Fig. 6** The duration (in minutes) northern pike spent in the boundary area and freshwater protected area (FPA) across seasons. Duration was cumulatively summed by season: autumn (Aut), spring (Spr), summer (sum), and winter (Win). Note that fish were not detected in the FPA or at 1SB in the winter. Although northern pike spent more time in the FPA and near 1SA in the summer relative to other seasons, duration was highest at 1SB and especially in the summer. Northern pike likely selected for 1SB because it is located near a deeper, unique pool (see Online Resource 1 Fig. S3) that may offer cooler waters and thermal refuge to fishes





receivers extending into the FPA. The FPA is shallow and heavily vegetated, with dense macrophyte growth that creates highly complex habitat structure; as such, while the FPA may offer excellent spawning habitat and refuge for pike and other species, these same factors can contribute to poor detection ranges. Additionally, it is most likely that these pike remained within the FPA because, even if a fish exited undetected, we expect the boundary area receivers placed near each of the entrance/exit channels to have recorded movements.

# **Residency patterns**

Our results suggest that a combination of abiotic (e.g., temperature, depth, submerged vegetation) and biological (e.g., fish size) factors probably influenced residency patterns, as well as differences in anthropogenic disturbances across lake regions with the FPA serving as a refuge from angling pressure and motorized vessels. In addition, fish release locations (groups) affected residency. Perhaps one of the most important findings of this study was the significant proportion of time fish spent in the boundary area, specifically near receiver 1SB. Pike spent  $6.5 \times$  and  $7.3 \times$  the cumulative amount of time near 1SB compared to the FPA and 1SA, respectively, with pike from both the FPA and main basin release groups residing near 1SB. However, pike that entered the boundary area from the main basin were rarely detected inside the FPA. Although we were unable to conduct an interactive model that evaluated where fish spent time at each of the boundary area receivers and FPA by season, Fig. 6 illustrates the substantially greater time fish spent at 1SB in the summer. The boundary area, similar to the FPA, offers spawning habitat and vegetated littoral regions; however, it also provides a unique, deeper pool that descends to ~ 12 m (Online Resource 1 Fig. S3) and, as such, potential thermal refuge or transitional space for movements to and from BRL's deep main basin.

The FPAs established throughout the RCW were created for largemouth bass, a warm-water species that prefers temperatures ranging from 24 to 30 °C (Stuber et al. 1982; Brown et al. 2009). In contrast, pike are a cool-water species with comparatively lower thermal optima ranging from 19 to 21 °C (Casselman and Lewis 1996). Water temperatures between 25 and 29.5 °C are considered stressful to pike, and lethal when > 29.5 °C (Macuch and Klug 2020). Our water temperature logger, located upstream in a faster-flowing riverine portion of the RCW, indicated extended periods of warm temperatures between 25 and 29 °C for multiple weeks each summer. In shallow (1–3 m), wetland-like waters of the FPA, it is likely that water temperatures exceeded those recorded by our logger. As such, though largemouth bass withstand warmer summer temperatures inside the FPA year-round (Zolderdo et al. 2024), it is possible that pike departed in search of cooler waters and resided in the pool near 1SB instead. By extending the FPA to include the boundary area, pike would be afforded protection from disturbances (e.g., angling, boating) during the warmer summer seasons, as the existing FPA does not include these deeper, cooler areas.

We also recorded an increase in time spent near, and directed movements towards, the boundary area and FPA in the spring. We documented three main basin pike entering the boundary area and/or FPA, displaying purposeful movements in the direction of these regions, in late March and early April in both 2020 and 2021. These movements coincided closely with ice-off (Online Resource 1 Fig. S4), suggesting these movements are reproductively driven. One individual (pike #0B4D) was detected in the boundary area and FPA in March 2020 and 2021, suggesting potential fidelity given repetitive use. An FPA resident (pike #901B) was also recorded in the FPA in early April 2020, suggesting an additional tagged fish using the area for spawning. Indeed, these four pike were longer than or near the size at which they mature (> 462 mm; Malette and Morgan 2005). Reproduction in most temperate fish species is triggered by seasonal water temperature changes and, accordingly, warming temperatures can alter fish reproductive phenology (e.g., shifting the timing of spawning events; Winslow et al. 2017). Although the pike recreational fishery is closed from April 1 to the second Friday in May, presumably protecting their spawning season, during warmer years these restrictions may not protect fish during the reproductive period (e.g., early ice-off in March 2021). As such, extending the FPA boundary to include the boundary area would also protect spring spawning activities.

### Size-specific habitat use

Our telemetry data revealed a pattern in lake region preferences whereby the largest pike displayed significantly higher residency in the deeper, lacustrine main basin of BRL—an area open to angling—whereas smaller pike selected the shallow, wetland-like regions of the FPA (Fig. 5). Size-specific habitat use is common with ontogenetic shifts, whereby smaller conspecifics rely on habitats that minimize resource competition and/or predation (Casselman and Lewis 1996). Our finding of smaller fish being detected more in the structurally complex, densely vegetated FPA, potentially as a form of predation refuge, is not unexpected as other work has noted these habitats support higher levels of smaller pike in other systems and geographic regions (e.g., Casselman and Lewis 1996; Eklöv 1997; Pierce et al. 2013). Pierce et al. (2013) found that larger pike sought out deeper habitats and suggested that these individuals follow the thermocline into cooler water as upper water layers warm, with preferred



habitats related to shifts in temperature-linked metabolic processes (e.g., growth). Similarly, Midwood and Chow-Fraser (2015) used radio telemetry to monitor pike movements in a Laurentian Great Lakes coastal wetlands system, finding that larger pike tended to be in deeper waters adjacent to wetlands and proposed that smaller pike use wetlands for nursery habitat. Additionally, because smaller pike are more tolerant to oxygen depression, with lower critical values, they may be able to remain within the FPA for extended periods (Casselman and Harvey 1975). We note, however, that the two largest pike captured and released in our study originated from the FPA (Table 1), so this area appears to provide habitat to individuals of varying sizes. In addition, we acknowledge that shifts in thermal habitat can be difficult to decouple from intraspecific interactions like competition (Pierce et al. 2013).

### Limitations

While our study provides novel findings on the use of an FPA by a vagile fish species, as with any telemetry study, there were limitations. First, we encountered considerable equipment and personnel constraints during our study. Due to COVID-19 restrictions and lockdowns in 2020, we experienced reductions in personnel for safety purposes, delays to field work, and could not service receivers until late June/ early July in 2020, resulting in the loss of some spring data. In addition, our telemetry array was reduced by ~50% during May-October 2021, contributing to a lack of open-area detections and removing our ability to conduct lake region residency analysis for that time period. Second, although we deployed acoustic receivers to provide relatively even coverage of BRL and LRL to potentially capture larger-scale and inter-lake movements, because of low detection ranges and long distances between receivers (up to 5 km), our telemetry dataset was composed of discrete detection events that, in some cases, may have been separated by months. The lower number of fish tagged in the open-area release groups likely contributed to this disparity. Notably, we did not detect most LD1 pike. Data from both our study and Bergman et al. (2024) suggest that the small-size tags may be driving data deficiency patterns as these tags may suffer from early battery failure or lower power outputs. Indeed, only individuals implanted with large tags were detected for multiple years, and five of the seven undetected fish had small tags (four of which were LD1 pike). As such, if the body size of target species permits it, we recommend researchers consider using the large-size tags. Third, due to the low number of detections for some individuals, we lacked the statistical power to include interactions in some of our models. We recommend future work to include higher sample sizes of both fishes and receivers or conduct a more focused study in specific regions of BRL and/or LRL. Deploying "gates" of receivers with overlapping detection ranges may help better detect use of the FPA and inter-lake connectivity (e.g., Koeberle et al. 2023). In addition, a study that evaluates sex-specific habitat use by pike would be an interesting aspect for future research to consider given that males and females may have different migration patterns (Larsson et al. 2015) and could elucidate the size-specific habitat use patterns we noted given that female pike are usually larger than males (Malette and Morgan 2005).

# **Management considerations and conclusions**

This research highlighted important findings related to FPA design and siting. The benefits of no-take MPAs are well established (e.g., Sciberras et al. 2015; Sala and Giakoumi 2018) and there is evidence that inside of protected areas, populations increase and individuals live longer, grow larger, and develop an increased reproductive potential, resulting in spillover benefits (Bohnsack 1998). Indeed, previous research has shown that no-take zones in MPAs can positively affect the spawning stock of pike by increasing abundances and biomass (Bergström et al. 2022; Roser et al. 2024). That said, we are not aware of an analogous study on pike in freshwater systems, and there is currently no review-style article that comprehensively evaluates the effectiveness of no-take FPAs like the FPA monitored in our study. Given concern with the lack of large pike in eastern Ontario (OMNR 2024a), FPAs could offer a safe haven year-round that can ensure fish have a chance to reproduce and reach larger sizes. However, as noted earlier, many fish departed the FPA and resided in the boundary area just past the protective boundary. Our work here demonstrates the importance of using movement ecology to inform decisions: evidence from our telemetry data indicates that pike would be offered considerably more legal protections if the FPA boundary were extended by even 500 m into what we called the "boundary area", which includes deeper water.

Given our telemetry data revealed no examples of interlake connectivity and generally small distances moved (< 500 m), it is unlikely that most pike in the system benefit from our monitored FPA. The FPAs established in the RCW, as is the case with most FPAs, are small, obscurely placed, and were not created with consideration for fish with larger home ranges (Bower et al. 2015; Hermoso et al. 2016). Promisingly, there are examples of FPAs providing tangible conservation benefits to vagile and migratory species. For example, Watson et al. (2021) evaluated and compared the effectiveness of closed, partially closed (fishing restrictions), and open streams in New Zealand on the abundance, biomass, and egg production of Galaxias maculatus, a migratory galaxiid, finding that closed areas increased outputs for all three metrics compared to partially closed or open waters. They also found evidence of fisheries benefits conferred by



partial closures, suggesting that even some restrictions may be a worthwhile management tool if complete closures are not feasible. Cucherousset et al. (2017) provide an additional example, evaluating a no-take marsh in France to support a threatened, migratory European eel (Anguilla anguilla). They discovered that the proportion and mean production of silver eels were  $4.5 \times$  and  $3.6 \times$  higher in the protected area than the fished area, respectively. The effectiveness of FPAs that are fisheries exclusion zones warrants a thorough review to identify what key elements lead to their conservation success and could help increase their use in freshwater systems.

Although fishes in FPAs benefit from legal protections while residing within borders, a panoply of pressures jeopardize wild fish populations and could destabilise an FPAs ability to support healthy fish communities. In the RCW, invasive species that threaten ecosystem stability are prevalent, including nonnative common carp (Cyprinus carpio), which have been detected within the FPA (personal observations), and the relatively newly discovered round goby (Neogobius melanostomus) (Bergman et al. 2022). As with many freshwater waterways globally, the RCW is additionally plagued with poor water quality and issues relating to decreased longitudinal connectivity and habitat degradation (Bergman et al. 2021). The most logical next steps will be to investigate the FPA's current capacity to maintain or increase pike populations and determine it's ability to serve as effective spawning, nursery, foraging, and refuge habitats in the face of these threats, with careful consideration for an evaluation that determines successful spawning (i.e., the presence of young-of-year and/or juvenile fish). Finally, because no-take FPAs have the capacity to preserve high-performance phenotypes in a population by protecting individuals from fisheries-induced evolution (FIE; e.g., Zolderdo et al. 2023), and pike in other systems have shown differing behavioural responses in open areas vs. FPAs (Roser et al. 2024), an evaluation of potential FIE effects would offer a physiological testament to the potential effectiveness of the FPA in BRL. From this perspective, it will be important to consider the capture method used (e.g., passive nets vs. angling vs. electrofishing), given angling may sample the most active individuals in a given population (Monk et al. 2021). Given poaching can greatly influence the success or failure of FPAs (Acreman et al. 2020), it will be critical that OMNR, Parks Canada, and other conservation agencies work together on outreach, education, and enforcement to ensure an effective FPA that provides biodiversity benefits.

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

#### **Declarations**

**Conflict of interest** The authors declare no competing interests.

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