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PRIMARY RESEARCH PAPER

Multi-year evaluation of muskellunge (*Esox masquinongy*) spatial ecology during winter drawdowns in a regulated, urban waterway in Canada

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Abstract Winter is an ecologically challenging time for freshwater fishes in temperate regions. In aquatic systems that experience annual winter water-level drawdowns, the pressures that fish already face during winter can be exacerbated. The Rideau Canal, a 202 km waterway located in eastern Ontario, Canada, is one such freshwater system that encounters these challenges. The 8.3 km "Eccolands Reach," near Ottawa, experiences a considerable annual drawdown from mid-October to mid-May of 1.79–2.13 m and is home to a self-sustaining, urban muskellunge population. Because the Eccolands Reach is relatively shallow and narrow, the drawdown may significantly reduce overwintering habitat. We used acoustic telemetry and hydraulic measurements to evaluate connectivity, critical winter habitats, and residency patterns of muskellunge ($N=23$) over two drawdown seasons (2020–2021; 2021–2022) in the Eccolands Reach. Our results revealed that most muskellunge overwinter in a central portion of the reach with distinct, contiguous deeper sections and that the drawdown functionally fragments the river in several areas, eliminating connectivity to adjacent habitats, by creating shallow-water barriers and high-velocity currents in riverine constrictions. Additionally, we documented potential spring spawning movements and discuss implications of reproduction prior to system refill. Our work provides insights into connectivity and winter habitats of muskellunge in a regulated waterway.

Keywords Ecohydraulics · Esocidae · Conservation · Connectivity · Regulated rivers

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Introduction

Winter in temperate and boreal areas is an ecologically challenging season for freshwater fishes, with survival and population sizes pressured by low or freezing temperatures, reduced habitat and food, and ice phenomena like ice dams and frazil ice (Helland et al., 2011; Brown et al., 2011; Nafziger et al., 2017; Heggenes et al., 2018). In northern regions, the annual reduction of water levels through dam operations each fall (hereafter, "drawdowns") and subsequent spring refills are a common management practice for various anthropogenic reasons including invasive species management, flood control, and/or to protect infrastructure (e.g., retaining walls, docks; Carmignani & Roy, 2017). These drawdowns, however, can exacerbate the pressures fishes already experience during winter by limiting the availability of winter habitat, including refugia from lethal dissolved oxygen levels (which larger fish like *Esox* sp. are more susceptible to; Gaboury & Patalas, 1984; Cott et al., 2008), and minimizing connectivity between suitable overwintering habitats (Cunjak, 1996; Cott et al., 2008). Additionally, drawdowns can be a major threat for aquatic species that use littoral areas as critical habitat to carry out their life history (Winfield, 2004; Strayer & Findlay, 2010).

One such freshwater system that experiences considerable annual winter drawdowns is Canada's historic Rideau Canal. The Rideau Canal is a 202 km continuous navigable waterway located in eastern Ontario that forms a hydrological connection between the Ottawa River at Canada's capital city of Ottawa and Lake Ontario at the city of Kingston. Although the waterway was originally constructed in the 1830s for commercial shipping and national defence (Bumsted, 2003), today it is primarily operated for recreation by the federal agency Parks Canada. The Rideau Canal is a National Historic Site of Canada, a Canadian Heritage River, and was inscribed as a UNESCO World Heritage Site in 2007 (https://whc.unesco.org/en/list/1221/) as one of the greatest engineering feats of the nineteenth century. Because of the system's global importance and its inherent nature as an engineered ecosystem, it is highly regulated. During the navigation season (mid-May to mid-October), a navigation channel (minimum depth 1.5 m) is maintained within the waterway for boaters to safely travel. Outside of the navigation season, however, water levels in many reaches are lowered to mitigate the effects of spring flooding (i.e., freshet) and to prioritize water supplies, infrastructure, navigation, recreation, and hydro-generation (Parks Canada, 2022). While most of the waterway experiences some degree of water-level lowering in autumn, a northern reach of the Rideau Canal, the 8.3 km "Eccolands Reach" (Fig. 1), experiences one of the most substantial drawdowns. The Eccolands Reach is also unique in that it is home to one of North America's few unstocked, self-sustaining urban muskellunge (*Esox masquinongy* Mitchill, 1824) fisheries (Gillis et al., 2010; Walker et al., 2010). Similar to most freshwater ecosystems, muskellunge in the Rideau Canal are ecologically important as apex predators and recreationally important as iconic sportfish pursued by primarily catch-and-release anglers (Margenau & Petchenik, 2004; Kerr, 2007; Landsman et al., 2011).

Biotelemetry has been a valuable tool in providing information on winter habitat use and movement patterns relevant to conservation actions of fishes (see Marsden et al., 2021). In regulated rivers, the integration of hydraulic modelling with biological (fish) responses is key in holistic ecological interpretation of spatial ecology (Murchie et al., 2008). The combined use of hydraulic and ecological data has been valuable in mitigation efforts in regulated rivers (Sundt et al., 2022), with researchers further calling for increased integration of hydraulics and ecology into conservation and management settings (Petts et al., 2006; Murchie et al., 2008). Although previous work has evaluated muskellunge spatial ecology in the Rideau Canal (Gillis et al., 2010; Pankhurst et al., 2016), movements were evaluated via manual radio tracking and lacked collaborations with engineers to associate movement patterns with hydraulic measurements.

Identifying—and subsequently protecting—critical habitats, like overwintering areas, is important to freshwater fish population conservation (Rosenfeld & Hatfield, 2006). Because drawdown conditions in the Eccolands Reach may be limiting muskellunge production and/or threatening population health, identifying, protecting, and potentially enhancing critical winter habitats will be crucial to ensure muskellunge are conserved and protected. While muskellunge populations in Ontario are not listed as decreasing or of concern (Ontario's *Endangered Species Act*, 2007; see https://www.ontario.ca/laws/regulation/080230), there is suggestion that the Rideau Canal population may be in decline (Supplementary Material A). Muskellunge, along with most aquatic species in the system, are indeed facing substantial persistent and interactive pressures from pollution, invasive species, and fragmentation (Bergman et al., 2021); drawdowns

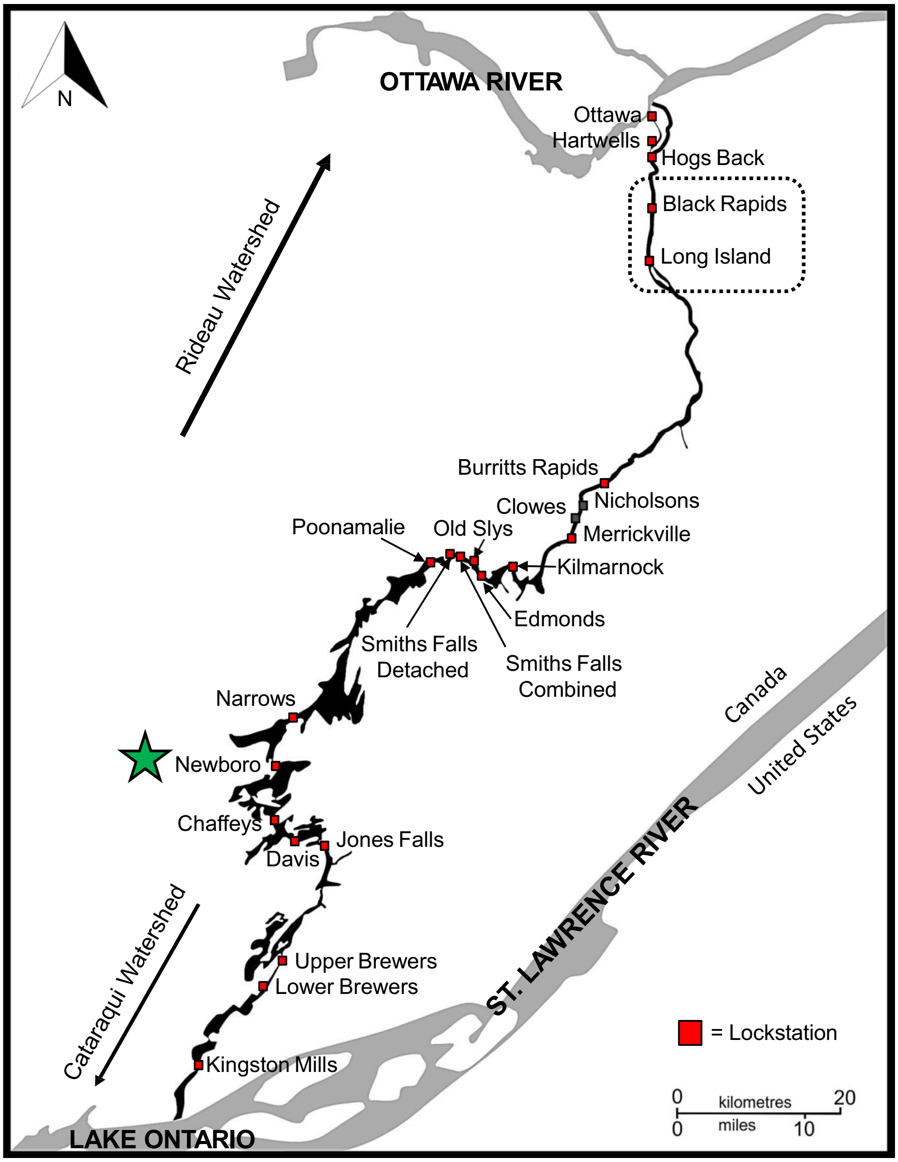

Fig. 1 Overview map of Canada's historic Rideau Canal. The black channel represents the 202 km navigable waterway, and the gray channels represent hydrologically-connected waters (Lake Ontario and the St. Lawrence River in the south; the Ottawa River in the north). Red boxes indicate lockstations that interconnect the system. Newboro Lockstation, indicated by the green star, represents the highest elevation on the Rideau Canal and delineates the Rideau Watershed (flowing north) and the Cataraqui Watershed (flowing south). Lake Ontario and the St. Lawrence River act as a natural border between Canada and the United States. Our study took place within the black-dashed lines between Black Rapids Lockstation and Long Island Lockstation, the "Eccolands Reach." This map is adapted from Bergman et al. (2021, 2022)

collate and likely intensify these pressures into a smaller area during winter. As such, the main objective of this study was to determine muskellunge critical overwintering habitats in the Eccolands Reach. We acoustically tagged 23 muskellunge and blended telemetry data with hydraulic measurements during two drawdown seasons in 2020–2021 and 2021–2022 to: (1) identify overwintering areas, (2) evaluate movement patterns relative to site fidelity, residency, habitat distribution, and connectivity, and (3) investigate size-specific habitat use.

Materials and methods

Study area

This study took place in the 8.3 km Eccolands Reach, spanning from the Black Rapids Lockstation (45° 19′ 18.0″ N 75° 41′ 54.0″ W) to the Long Island Lockstation (45° 15′ 03.0″ N 75° 42′ 06.9″ W). The Eccolands Reach is part of the 100 km, north-easterly flowing Rideau River, comprising the northern portion of the Rideau Canal (north of Poonamalie Lockstation; Fig. 1). The Black Rapids Lockstation consists of a single-flight lock that connects to two stop-log weirs and a concrete spillway dam (3.3 m high and 139.9 m wide; Parks Canada Dam Safety Engineering Inspection, 2011). The Black Rapids dam stretches across the Rideau River and creates a slackwater section to the upstream triple-flight Long Island Lockstation, which is connected to a large stone arch dam (9.7 m high and 76.2 m wide; Parks Canada Dam Safety Engineering Inspection, 2007) that spans the eastern Rideau River channel. At the southern (upstream) terminus of the Eccolands Reach, the Rideau River diverges into two channels around Long Island with the main (navigable) Rideau River channel on the eastern side and the smaller, narrow West Branch Rideau River on the western side (note that the West Branch Rideau River is simply a bifurcated channel of the main Rideau River). The Rideau River and the West Branch Rideau River remain as two distinct channels for ~ 6 km before reconnecting. Approximately 4 km upstream within the West Branch Rideau River is the Watson's Mill Historic Site and Dam that extends across the channel.

Two main tributaries flow into the Eccolands Reach: Mosquito Creek and the Jock River. Much of the 41 km^2 Mosquito Creek watershed runs through agricultural lands with only 7% of the catchment being wetland habitat. Though the Mosquito Creek catchment has experienced increasing anthropogenic development since the 1990s, it remains an important spawning habitat for baitfish and gamefish, including muskellunge (Rideau Valley Conservation Authority (RVCA), 2015). The Jock River watershed is considerably larger at 556 km^2 (Rideau Valley Conservation Authority (RVCA), 2016). In the middle and upper reaches of the Jock River, shorelines are typically natural, forests and wetlands are numerous and connected, and water quality is better compared to its lower reach near the Rideau River (Rideau Valley Conservation Authority (RVCA), 2016). Significant efforts have been conducted to support muskellunge and other fishes in the Jock River in response to concern over increased development activities reducing fish habitat (e.g., see https://www.rvca.ca/jock-river-fish-habitat-embayment-creation-project). The Eccolands Reach has a third small tributary near the Black Rapids Lockstation, the "Black Rapids Creek," a 5.7 km creek also known to have high-quality fish habitat (Canadian Environmental Assessment Agency, 2012).

Acoustic 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 29 July to 27 October 2020 and 07–09 June 2021 during daylight hours between 0700 and 2000. Muskellunge were captured using standard hook-and-line angling and boat electrofishing (~ 70% via hook-and-line in 2020 and 100% via hook-and-line in 2021; we expect no difference in behaviour or survival between capture methods, see Landsman et al., 2011, 2015). Specialized volunteer muskellunge anglers, many from the Muskies Canada Inc. Ottawa Chapter and the Ottawa River Musky Factory, aided in capturing fish. When anglers captured a muskellunge, they were directed to keep the fish in water and phone in their capture site. Our designated "surgery" boat would motor to their location to acoustically tag and release the fish at the capture site. Because of the length of the Eccolands Reach and the surgery boat's slow speed, anglers stated they sometimes held fish in water for several minutes before the surgery boat arrived. Fish that appeared in distress (e.g., equilibrium imbalance, change in ventilation rate, lack of movement when gently prodded; Tsitrin et al., 2020) were immediately released and not used in this study. For electrofishing, we used a Smith-Root electrofishing boat (2.5 Generator Powered Pulser; Smith-Root Inc., Vancouver, WA, USA) to sample littoral areas. Pulsed direct-current (rate: 60 pulses/second) was used to reduce the risk of injuring muskellunge within proximity of the electrical field (Snyder, 2003). The electrical current ranged from 4 to 6 A (low range) and maximum output voltage was 500 V. Two people netted fish from the bow while the boat moved slowly forward at idle speed.

Upon capture, muskellunge were transferred to a foam-lined V-tray filled with fresh river water and placed supine such that the head and gills were submerged in water but the incision site was left dry. Twenty-three muskellunge were implanted with a small ($N = 4$) or large ($N = 19$) disinfected (betadine) Lotek Juvenile Salmon Acoustic Telemetry System (JSATS) Acoustic Micro Transmitter (AMT) (hereafter, "tag"), set to transmit a signal at a 20 s interval, into the coelom (small tag: L-AMT-8.2, 3.5-g in air, 23 × 9 × 9 mm, expected battery life = 1,522 days;

large tag: L-AMT-14-12, 8.0-g in air, 45 × 14 × 14 mm, expected battery life = 3,114 days). Total length (TL) of each fish was measured, ranging from 270 to 1,143 mm (mean ± SD = 715.78 ± 221.73 mm). If the fish was smaller than 500 mm, we used a small tag. All fish longer than 500 mm were surgically implanted with a large tag except one individual (TL: 676 mm, muskellunge ID #0069). Mass measurements were not taken in the field; instead, they were generated using models from Harrison & Hadley (1979) and Casselman & Crossman (1986). Tag burden (tag:body-mass ratio) was low and therefore likely had no negative effect on fish behaviour or survival (range: 0.07–3.27%, average: 0.65%; Table 1) (Bridger & Booth, 2003; Jepsen et al., 2005). To immobilize fish for surgery, Smith-Root electric fish-handling gloves were positioned on the head and caudal peduncle. Gloves were set to the lowest current setting (4 mA) to immobilize the fish but allow continuous opercular respiration. 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 body cavity with 1–2 simple, interrupted sutures (PDS II

Table 1 Tracking and biological data for acoustically tagged muskellunge ($N = 23$)

Detection category	Release date	Release date water temperature (°C)	Fish ID	Total length (mm)	Tag burden (%)	Drawdown season 1: 2020–2021 ($N = 13$)		Drawdown season 2: 2021–2022 ($N = 15$)	
						TDD	Overwintering area	TDD	Overwintering area
U	2020-10-14	12.94	6DA8	275	3.18				
	2020-10-14	12.94	CE85	290	2.96				
	2021-06-07	23.35	08DD	709	0.31				
	2021-06-09	24.91	0069	676	0.17				
	2021-06-09	24.91	A253	1080	0.09				
D1	2020-07-29	26.68	EC9A	775	0.25	16	Segment 3		
	2020-10-15	12.92	127F	901	0.15	42	Segment 3		
	2020-10-16	12.65	F9B5*	845	0.20	19	NA		
D2	2021-06-07	23.35	E4A7	798	0.24			39	Segment 2
	2021-06-07	23.35	398C	840	0.20			76	Segment 2
	2021-06-07	23.35	453A	855	0.19			104	Segment 1
	2021-06-07	23.35	6216	1143	0.07			125	Segment 1
	2021-06-09	24.91	C20E	711	0.31			85	Segment 1
D1/2-X	2020-10-27	9.37	623E*	270	3.27	4	NA	1	NA
	2020-10-14	12.94	E718*	707	0.31	7	NA	113	Segment 3
	2020-10-15	12.92	D3EE*	685	0.37	8	NA	83	Segment 2
D1/2	2020-08-07	25.05	54FD	611	0.47	44	Segment 2	61	Segment 2
	2020-08-07	25.05	4155	748	0.29	126	Segment 2	95	Segment 2
	2020-08-11	25.73	D3FF	639	0.44	115	Segment 2	93	Segment 2
	2020-10-14	12.94	4421	685	0.37	42	Segment 2	41	Segment 2
	2020-10-16	12.65	ADDE	540	0.79	34	Segment 2	79	Segment 2
	2020-10-16	12.65	4487	920	0.15	79	Segment 2	74	Segment 2
	2020-10-27	9.37	638D	760	0.25	21	Segment 2	50	Segment 2

Total length (mm) and acoustic tag burden for each fish is included. Note the four fish (*) that were not detected for full drawdown seasons and therefore could not have overwintering areas assigned. The total number of (non-consecutive) days individuals were detected (TDD) during the 175-day study periods (drawdown season 1: 30 October 2020 to 23 April 2021; drawdown season 2: 29 October 2021 to 22 April 2022). The number of individuals detected each drawdown season and their corresponding overwintering area is provided. The order of the table is divided into detection categories: undetected fish (U); fish only detected during drawdown season 1 (D1); fish only detected during drawdown season 2 (D2); fish detected during both drawdown seasons but not for the full study period (D1/2-X); fish detected during both drawdown seasons for the full study period (D1/2) polydioxanone suture, violet monofilament, 2-0) used to close the incision. All acoustically tagged fish were marked with an external anchor tag (FLOY TAG & Mfg., Inc., Seattle, Washington, USA), inserted into the epaxial muscle ventral to the dorsal fin (Supplementary Material B, Fig. 1). The entire procedure took 2–4 min. Fish were monitored for post-surgical behaviour changes and distress (Tsitrin et al., 2020). No fish showed any apparent deleterious effects from surgery and were released as soon as equilibrium was gained and strong swimming actions were observed (which occurred in all cases within a few minutes post-surgery; Davis, 2010; Landsman et al., 2015). We recorded water temperature for each acoustically tagged muskellunge, and provide tracking and biological information in Table 1.

Acoustic receiver array

In October 2020, eleven acoustic receivers (Lotek Wireless, WHS 4250, 416.7 kHz) were deployed in the Eccolands Reach in strategic locations to track tagged fish movements during the 2020–2021 drawdown season. We also deployed two receivers downstream of the Black Rapids Lockstation (i.e., in the Mooney's Bay Reach; not shown on map) to evaluate potential downstream movements between the two adjacent reaches. Although the Long Island Lockstation is a complete barrier to upstream movement during the drawdown season when locks are not in operation, muskellunge could move upstream into the West Branch Rideau River, so we deployed one receiver 200 m into that channel. Receivers were deployed relatively evenly throughout the Eccolands Reach, in both deeper and shallower areas, to investigate general space use and movement patterns. Receivers were programmed to log on a continuous cycle and were deployed in the Eccolands and Mooney's Bay Reaches on 29 October 2020 and 04 November 2020, respectively, and retrieved 24 April 2021.

On 29 October 2021, we re-deployed the same acoustic telemetry array to monitor muskellunge movements for a second drawdown season. In 2021, we purchased four upgraded receivers (Lotek Wireless, WHS 4350, 416.7 kHz) that have integrated temperature loggers and deployed them at four stations (E1, E5, E8, and E11). WHS 4250 receivers were deployed at all other stations. We found that ~ 50% of receivers during the first drawdown season were non-functional by early April; thus, to better conserve battery life, we re-programmed receivers during the second drawdown season to log on a non-continuous schedule whereby they were "on" for 45 s and "off" for 15 s each minute. Receivers were anchored to the riverbed with the hydrophone positioned ≥ 0.5 m off the riverbed. Each receiver location was recorded using a handheld GPS unit.

Two separate range and detection efficiency tests were conducted over 72-h periods to evaluate the performance of each receiver model. The WHS 4250 receiver model was assessed in June 2020 in a central portion of the Rideau Canal near Edmonds Lockstation (Fig. 1; Supplementary Material B, Figs. 2, 3, and Table 1) and the WHS 4350 receiver model in June 2021 in the Eccolands Reach near Mosquito Creek (Supplementary Material B, Fig. 4, Table 2). Range and detection testing of the WHS 4250 receiver model revealed low detection ranges, especially in vegetated riverine environments (i.e., < 25 m) with higher detection ranges in more open areas (i.e., up to 13% efficiency at 100 m). The upgraded WHS 4350 receiver model had a farther detection range of 18% at 200 m. Based on these findings, detection ranges of WHS 4250 receivers would not span the width of the river, except at receivers E4, E9, and E11 (river widths < 100 m; see Table 2). Detection range of WHS 4350 receivers should span the width of the river. The coverage of our telemetry array was therefore greater during the second drawdown season with the inclusion of the upgraded receivers (coverage of river width at E1, E4, E5, E8, E9, and E11). Due to the winding nature of the river and considerable distance between receivers, we believe the detection ranges of receivers in the Eccolands Reach did not overlap. Results from range testing were not formally integrated into our analyses; instead, we use results descriptively to provide context for our interpretation.

Environmental variables and hydraulic surveying

Five environmental variables were evaluated at each receiver to determine their potential influence on muskellunge spatial ecology: (1) drawdown (metres), (2) average receiver depth (hereafter "receiver depth"; within a 25 m radius of the receiver), (3) river width (metres), (4) velocity (metres/second), and (5) benthic structure. An Onset HOBO U20-001-01 Water Level Logger (Bourne,

Table 2 Environmental characteristics and residency index (RI) of river segments & acoustic receivers in the Eccolands Reach for the 2020–2021 and 2021–2022 drawdown seasons

River segment	Thalweg (m)	Acoustic receiver	Mean velocity (m/s)	Mean RI ± SE			Benthic structure*	Mean drawdown (m)	Mean receiver depth (m)	River width (m)
				Drawdown season 2020–2021	Drawdown season 2021–2022	Overall				
1	3.06	E1	0.17	0	0.037 ± 0.033**	0.020 ± 0.018	Medium	2.15	2.31	116
		E2	0.15	0	0.009 ± 0.007	0.005 ± 0.004	Medium	2.13	2.34	125
		E3	0.07	0.040 ± 0.019	0.167 ± 0.087	0.108 ± 0.048	Low	2.12	5.59	159
2	4.75	E4	0.11	0.256 ± 0.096	0.152 ± 0.072	0.200 ± 0.059	Low	2.11	5.05	84
		E5	0.15	0.177 ± 0.063	0.170 ± 0.060**	0.173 ± 0.043	Low	2.09	3.06	122
		E6	0.12	0.138 ± 0.048	0.218 ± 0.068	0.181 ± 0.043	Low	2.08	3.13	108
		E7	0.15	0.225 ± 0.099	0.181 ± 0.077	0.201 ± 0.061	Low	2.05	2.50	117
3	2.24	E8	0.34	0.058 ± 0.034	0.067 ± 0.067**	0.063 ± 0.038	High	1.84	3.43	186
		E9	0.38	0.121 ± 0.064	0.011 ± 0.009	0.062 ± 0.032	High	1.80	1.07	70
		E10	0	/	0.056 ± 0.056	0.056 ± 0.056	Low	1.75	2.61	144
		E11	0.37	0.137 ± 0.086	0.002 ± 0.002**	0.064 ± 0.041	High	1.77	1.54	51

The velocity at receiver E10 is approximately zero for the entire winter as it is located in a protected backwater area under the Long Island Dam, which is non-operational during drawdown. Receiver E10 malfunctioned during the first drawdown season and was excluded from analysis

*Low structure = silt, clay, sand; medium structure = cobble, gravel; high structure = boulders present

**An upgraded receiver model with a farther detection range was used at receivers E1, E5, E8, and E11 during the 2021–2022 drawdown season

Massachusetts, USA) was installed on the riverbed in the West Branch Rideau River at the Watson's Mill Dam in May 2019 to measure pressure and water temperature. An additional logger was installed on shore at the Long Island Lockstation to measure barometric pressure and air temperature to calculate depth using Onset Hoboware Pro software (Onset Computer Corporation, 2021). Water elevations were surveyed in 2021 at four locations using a Stonex S800A Hemisphere (Gatineau, Québec, Canada) real-time kinematic global positioning system (RTK GPS) on 12 October (pre-drawdown) and 01 December (post-drawdown). Drawdown-season water elevations were subtracted from navigation-season water elevations to determine receiver-specific drawdown. To validate results, we compared water elevations measured in 2021 against daily discharge values and dam operations from 2020 (protected data, Parks Canada). It is possible there were small, localized changes in water elevations during the study periods in 2020–2021 and 2021–2022 due to ice effects. See Supplementary Material B (Figs. 5, 6) for survey locations and additional details.

Bathymetries (i.e., riverbed elevation) were surveyed May to August 2019 and March to April 2020 using a remote-control Teledyne Marine Q-Boat 1800 (Poway, California, USA) equipped with a NovAtel RTK GPS (Calgary, Alberta, Canada) and SonTek M9 RiverSurveyor (San Diego, California, USA) acoustic Doppler current profiler (aDcp). Bathymetric data were post-processed using MATLAB (script by Rennie & Church, 2010) and combined with bare-earth light detection and ranging (LiDAR) data obtained from the City of Ottawa (flown in 2015) (MathWorks, 2018). A bathymetric grid was interpolated using Surfer v23.1.162 (Golden Software, 2022). A depth grid was then calculated for the navigation and drawdown seasons by subtracting bathymetries from the water elevations surveyed in October and December, respectively. An average depth was calculated for the entire reach pre- and post-drawdown by averaging the wetted cells and at each receiver within a 25 m radius. We set 25 m as the radius boundary because 50 m extended onto dry shoreline at several receiver sites and additionally this is the maximum distance the WHS 4250 receiver model could detect tagged fish in shallow, vegetated environments. The wetted top width of the river (i.e., river width) at each receiver was calculated by measuring perpendicular to flow.

Cross-sectionally averaged velocity was calculated at each receiver on a weekly basis by taking discharge data (protected data, Parks Canada) and dividing it by the cross-sectional wetted area (i.e., river width) measured using the depth grid (via Surfer v23.1.162). Because receiver E8 was located at the confluence of the Jock River and the main Rideau River channel, velocities within the detection range of the receiver varied; accordingly, the maximum velocity located closest to the receiver (50 m upstream) was selected. The velocity within the detection range of all other receivers did not vary since the channel is uniform and there is minimal outfall from other tributaries. Additionally, velocity was calculated between receivers E7 and E8 at the river constriction to evaluate this area as a potential velocity barrier (see Supplementary Material B, Fig. 7). Weekly velocity data can be viewed in Supplementary Material C. Usable habitat was defined as water depths ≥ 0.5 m (we expect muskellunge rarely use waters shallower than 0.5 m; Zorn et al., 1998). Usable habitat lost was determined by subtracting total available winter area from total available summer area (via Surfer v23.1.162).

Benthic substrate was sampled 02–16 September 2020 using an Ekman dredge and/or grab-sampling via shovel. Samples were obtained along transects every 250 m throughout the Eccolands Reach with a sample collected from the left, middle, and right side of the channel(s). Substrate samples were processed in the University of Ottawa Geotechnical Laboratory following American Society for Testing and Materials (ASTM) C136/C136M–19 (ASTM International, 2019). If 50% of the sample was < 75 mm (i.e., gravel and smaller), it was classified following ASTM D2487-17e1 (ASTM International, 2017). If 50% of the sample was > 75 mm, it was classified based on approximate percentages of boulders, cobbles, and/or alluvium observed. Grains smaller than 0.075 mm (i.e., fines) were not differentiated; we refer to them collectively as "silt/clay." The following is our classification scheme: boulder: > 300 mm, cobble: 75–300 mm, gravel: 4.75–75 mm, sand: 0.075–4.75 mm, silt/clay: < 0.075 mm. Boulders 0.5–1 m in diameter were visually observed near the Jock River, with boulders as large as 2 m in diameter observed in the area between receivers E7 and E8.

To match the resolution of substrate mapping (finer-scale) to our telemetry data (coarser-scale), we reclassified "substrate" as "structure" and assigned it as a categorical variable with three discrete levels: silt, clay, and sand as "low structure," cobble and gravel as "medium structure," and if boulders were present a classification of "high structure" was designated. Only the transect closest to each receiver was used in benthic-structure classification for subsequent analytical models.

Data analysis

Raw detection filtering

All telemetry data processing and statistical analyses were conducted using R version 3.6.2 (R Core Team, 2019). When ice is thick (0.02–0.12 m) and stable, detection range and efficiency of acoustic receivers can be high; however, ambient noise generated during ice formation and break-up can interfere with the detection of acoustic transmissions and result in a high level of false positives in the dataset (Klinard et al., 2019). Thus, several filters, specifically a minimum lag-interval filter and a minimum power requirement filter, were employed to identify and remove likely false positives. Detection filtering followed methods by Bergman et al. (2022) and a detailed explanation can be found in Supplementary Material B (Appendix 1). We applied a "detection event" filter (Holbrook et al., 2019) to our final dataset, which groups individual detections into discrete events defined by movements between receivers and sequential detections at the same receiver separated by a predefined time frame. Detections that occurred 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 started a new event. Individual fish abacus plots (Supplementary Material D) were inspected to verify that detection event timestamps and locations were logically and biologically plausible. We filtered out detection events with < 1 detection to eliminate implausible detections (e.g., fish moving large distances rapidly) and applied a distance filter that required ≤ 3,000 m between events. We selected 3,000 m as this was the maximum distance between active receivers during the study periods. We carefully inspected the final dataset and found all events appeared plausible, resulting in a final dataset of 3688 detection events from 18 muskellunge (five muskellunge were not detected post-filtering). Note that the minimum lag-interval filter was responsible for excluding the five muskellunge (designated as "U" in Table 1). If an individual was detected on (1) multiple receivers or (2) on different receivers across the two drawdown seasons, we assumed the fish was alive. As such, abacus plots did not indicate any mortality events.

Individual and receiver Residency Index

A Residency Index (RI) was calculated to quantify site residency as a measure of muskellunge space use. 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). The residency index formula is as follows:

$$\text{Residency Index} = \frac{\text{Distinct number of days detected at a receiver}}{\text{Distinct number of days detected at any receiver}}$$

We used RI because it reduces the potential bias of a large number of detections at a given receiver generated by only a few individuals (Kessel et al., 2016) and additionally it provides a visual and statistical way to assess fish habitat selection (e.g., Algera et al., 2022). RI values are proportional, ranging from 0 to 1, with a value of 1 indicating the highest possible residency at a receiver in the array. RI values were adjusted whereby values of "0" and "1" were modified to "0.0001" and "0.9999" because our modeling framework (beta regression; see below) is incompatible with "0" or "1" as a response. From an ecological perspective, an RI value of 0 versus 0.0001, or 1 versus 0.9999, does not affect our ability to interpret important overwintering areas. RI values were generated separately for each drawdown season: (1) for each individual muskellunge (hereafter "individual RI") and (2) averaged across all fish to produce a mean RI ± SE value for each receiver (hereafter "receiver RI"). The two final datasets, individual RI and receiver RI, encompassed the 2020–2021 and 2021–2022 drawdown seasons and were used for subsequent analysis.

Statistical analysis

For all statistical analyses the significance threshold was set to $\alpha = 0.05$. For each of the following models, detailed information and a summary of statistical test outputs can be found in Table 3. The main objective of this study was to identify which areas in the Eccolands Reach provide critical overwintering habitat to muskellunge, regardless of fish size; as such, residency analysis models are based on receiver RI and therefore do not include fish size as a predictor variable (see later *Size-specific winter habitat analysis*). We assessed the distribution of receiver RI values using the descdistr function in the *fitdistrplus* package to confirm that a beta error distribution was the most appropriate for our dataset (Supplementary Material B, Fig. 8; Delignette-Muller & Dutang, 2014). We then fit a generalized linear mixed model (GLMM) using the glmmTMB function (package *glmmTMB*; Douma & Weedon, 2019; Brooks et al., 2022) with receiver RI as the (continuous) response variable and the following as predictor variables: benthic structure (categorical), receiver depth (continuous), velocity (continuous), river width (continuous), and drawdown season (2020–2021 & 2021–2022; categorical). Velocity was square-root transformed to meet normality assumptions for this model and all following models. A random intercept of "location" (i.e., the receiver station) was included in the GLMM because the likelihood of movement between receivers decreases as a function of distance (Whoriskey et al., 2019; Jacoby et al., 2020; Williamson et al., 2021). We ran residual diagnostics using the *DHARMa* package (Hartig, 2022) to test model assumptions (Supplementary Material B, Fig. 9). Additionally, we used the check_autocorrelation function to evaluate autocorrelation ($P = 0.948$) and the check_collinearity function to assess collinearity (low correlation, VIF < 5) (both from the *performance* package). Akaike's Information Criterion, corrected for small sample sizes (AICc), was used (Burnham & Anderson, 2014; Anderson et al., 2021) via the dredge function from the *MuMIn* package to confirm best model fit. The model with the lowest AICc value was designated as our final, reduced receiver RI model (residual diagnostic results for the reduced model provided in Supplementary Material B, Fig. 10). Note that "drawdown" was not included in these models as we found drawdown to be collinear with benthic structure (via Pearson's product-moment correlation: $P = 0.007$, cor = 0.755). Instead, we evaluated effects of drawdown on muskellunge residency in a later model (see "River segment-drawdown model").

Visual inspection of abacus plots (Supplementary Material D) revealed areas that appear to functionally fragment the Eccolands Reach into three distinct river segments during several months of the drawdown season (denoted by X-symbols in Fig. 2). Come mid-December, muskellunge appear unable to move across these areas and are restricted to their respective river segment until early-mid-April. Most muskellunge were detected consistently at multiple receivers during winter, suggesting "segments" of the river—not individual receiver sites—are important to consider from an overwintering habitat perspective. Therefore, to determine which portions of the river are most ecologically preferable during the drawdown season, we grouped receivers into three geographic river segments and developed an additional GLMM to evaluate residency by river segment. River segment 1 includes receivers E1, E2, and E3; river segment 2 includes receivers E4, E5, E6, and E7; river segment 3 includes receivers E8, E9, E10, and E11. Similar to above, we fit this GLMM with a beta distribution to test for differences in receiver RI by river segment (categorical) and drawdown season (categorical) with a random intercept of location (for DHARMa residual diagnostics see Supplementary Material B, Fig. 11). To assess the relationship between muskellunge residency and segment depth, we measured the average thalweg depth (i.e., the line of continuously deepest soundings; Guo, 2021) extending 100 m north and south of the terminus receivers of each segment (using Surfer v23.1.162). Benthic structure, velocity, and river width were visually inspected for potential patterns unique to each river segment. Finally, we fit a linear regression model evaluating drawdown in each river

Table 3 Summary of statistical test outputs

Generalized linear mixed models using template model builder (*glmmTMB*)

Global receiver RI model: receiver RI ~ velocity + structure + receiver depth + river width + drawdown season + (1 | location), family = beta

Predictor variable	Estimate	SE	*z*-value	*P*-value
(Intercept)	− 6.088	1.363	− 4.467	**< 0.001**
$\sqrt{}$Velocity	3.857	2.225	1.734	0.083*
Benthic structure: low	3.114	0.590	5.274	**< 0.001**
Benthic structure: high	0.747	0.761	0.981	0.326
Receiver depth (m)	− 0.006	0.110	− 0.051	0.960
River width (m)	0.001	0.005	− 0.266	0.790
Drawdown season 2020–2021	− 0.054	0.291	− 0.186	0.852

AICc: − 51.83 | Number of observations: 21 | Marginal R^2: 0.804

Note that the intercept is benthic structure: medium

Reduced receiver RI model: receiver RI ~ velocity + structure + (1 | location), family = beta

Predictor variable	Estimate	SE	*z*-value	*P*-value
(Intercept)	− 5.871	0.957	− 6.133	**< 0.001**
Benthic structure: low	3.073	0.564	5.446	**< 0.001**
Benthic structure: high	0.695	0.704	0.988	0.323
$\sqrt{}$Velocity	3.682	1.931	1.906	0.057*

AICc: − 68.06 | Number of observations: 21 | Marginal R^2: 0.802

Note that the intercept is benthic structure: medium

River segment-residency model: receiver RI ~ river segment + drawdown season + (1 | location), family = beta

Predictor variable	Estimate	SE	*z*-value	*P*-value
(Intercept)	− 3.750	0.440	− 8.532	**< 0.001**
River segment 2	2.454	0.485	5.057	**< 0.001**
River segment 3	1.076	0.545	1.974	**0.048**
Drawdown season 2020–2021	−0.155	0.324	−0.480	0.631

Number of observations: 21 | Marginal R^2: 0.733

Note that the intercept is river segment 1

Size-specific habitat use model: presence ~ total length × benthic structure + total length × velocity + (1 | muskellunge ID), family = binomial

Predictor variable	Estimate	SE	*z*-value	*P*-value
(Intercept)	−9.066	5.460	− 1.660	0.097*
Total length (mm)	0.004	0.007	0.533	0.594
Benthic structure: low	5.987	3.670	1.633	0.102
Benthic structure: high	4.860	4.120	1.157	0.247
$\sqrt{}$Velocity	1.071	10.063	0.106	0.915
Total length × benthic structure: low	−0.003	0.004	−0.588	0.557
Total length × benthic structure: high	−0.006	0.005	− 1.198	0.231
Total length × $\sqrt{}$velocity	0.009	0.013	0.701	0.483

Number of observations: 295 | Conditional R^2: 0.500 | Marginal R^2: 0.427

Note that the intercept is TL × benthic structure: medium

Table 3 (continued)

General linear model (*lm*)				
River segment-drawdown model: drawdown ~ river segment				
Predictor variable	Estimate	SE	*z*-value	*P*-value
(Intercept)	2.134	0.017	124.638	**< 0.001**
River segment 2	− 0.053	0.023	− 2.331	**0.048**
River segment 3	− 0.344	0.023	− 15.207	**< 0.001**

Significant terms are reported in bold. An asterisk (*) indicates the term approached significance (i.e., $P \leq 0.10$). *RI* residency index. "Location" refers to the receivers' deployment location. Continuous variables include: receiver RI, velocity, total length, receiver depth, and river width; categorical variables include: structure, river segment, and drawdown season. Velocity (m/s) was square-root transformed for each model

Multiple R^2: 0.973 | Adjusted R^2: 0.967 | $F_{2,8} = 145.6$ | *P*-value < 0.001

Shapiro–Wilk normality test: $W = 0.967$, *P*-value = 0.849

Breusch-Pagan non-constant variance score test: $\chi^2 = 3.172$, $df = 1$, *P*-value = 0.075

Note that the intercept is river segment 1

segment to determine if water-level lowering was longitudinally distinct and relate that information to muskellunge residency. Linear regression model residuals were visually inspected and validated for normality (Shapiro–Wilk test) and heteroscedasticity (Breusch–Pagan test).

Size-specific winter habitat analysis

We evaluated potential interactive effects of fish size on habitat preferences in the Eccolands Reach during drawdown. We selected benthic structure and velocity as our habitat variables post-hoc as a proxy for drawdown, river width, and receiver depth because of multicollinearity among variables (i.e., the river is narrowest in river segment 2 which is also entirely characterized by low-structure habitat) and because these were the only significant or near-significant predictors of muskellunge residency. We created a presence/absence response variable to test if fish of certain sizes selected for or against ("1" or "0," respectively) different habitat types. Because the response data were binomial, a GLMM with a binomial distribution was used to investigate the potential interactive relationship between total length (mm; continuous) and benthic structure (categorical) and velocity (continuous; square-root transformed as above). A random intercept for individual fish (muskellunge ID) was included in the GLMM because there were multiple observations from each individual fish. Model assumptions were tested as described above (for *DHARMa* residual diagnostics see Supplementary Material B, Fig. 12).

Results

Over the duration of our study, 78% (18/23) of tagged muskellunge were detected in the array. For the first (2020–2021) and second (2021–2022) drawdown seasons, 87% (13/15) and 65% (15/23) were detected, respectively. We determined overwintering sites for 16 muskellunge (seven individuals were excluded because they either were undetected or not detected for a full drawdown season). Seven individuals were detected during both drawdown seasons, all showing site fidelity to river segment 2. Table 1 provides information about total days detected (TDD) and overwintering location for each tagged muskellunge.

Residency index and environmental variables

The Eccolands Reach drawdown decreases the average depth from 3.2 to 2.0 m during the navigation and drawdown seasons, respectively, reducing usable area by 37% from 1,345,577 to 854,686 m^2. No muskellunge were detected on the two receivers outside the study system in the Mooney's Bay Reach, so those receivers were excluded from analysis. Receiver E10 malfunctioned during the first drawdown season and therefore was also excluded. Although no

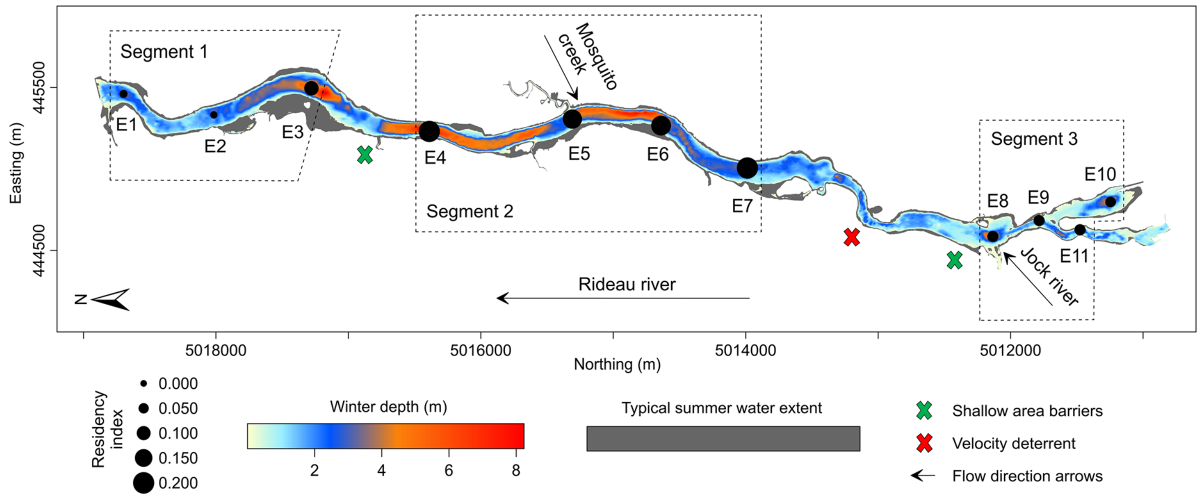

Fig. 2 Overlay of depth mapping and muskellunge residency index (RI) analysis. The Rideau River flows northwards: receiver E1 is the downstream terminus, with receivers E10 and E11 the most upstream sites. Four km upstream the West Branch Rideau River is the Watson's Mill Historic Site and Dam (not shown on map; see Supplementary Material B, Fig. 6). Deeper areas are indicated by orange and red colors whereas cream and blue colors indicate shallower regions. The grey portion of the river represents air-exposed riverbed due to drawdown. Each circle reflects combined mean RI at a receiver for the two drawdown seasons (2020–2021 & 2021–2022). Circles are graduated such that larger circles denote more time and/or more muskellunge detected at that receiver. The green (✖) and red (✖) X-symbols mark likely shallow-water barriers and a velocity deterrent, respectively, reducing river connectivity for most of the drawdown season and fragmenting the system into three river segments. River segments are denoted by dashed-black lines. Note that RI values were overall low, with the highest RI value being 0.201. Two important muskellunge spawning tributaries, Mosquito Creek and the Jock River, are referenced with arrows indicating tributary flow direction

fish were detected on receivers E1 or E2 during the first drawdown season, muskellunge were detected on all receivers during the second drawdown season. Combined mean receiver RI ± SE for the two drawdown seasons was relatively low, ranging from 0.005 ± 0.004 to 0.201 ± 0.061. This indicates most muskellunge did not have a strong preference for a specific receiver, or they may have spent time (undetected) between receivers, supporting our strategy of grouping receivers into river segments for habitat-selection analysis.

Our global receiver RI model revealed benthic structure significantly influenced muskellunge residency (low structure: $P < 0.001$; medium structure: $P < 0.001$; high structure: $P = 0.326$). All other variables, including velocity, river width, receiver depth, and drawdown season, did not have a significant effect on muskellunge residency though velocity approached significance ($P = 0.083$) (Table 3). The reduced model, with only benthic structure and velocity as predictor variables of residency, had the best fit (i.e., global receiver RI model AICc: − 51.83, reduced receiver RI model AICc: − 68.06; Table 3). The reduced receiver RI model indeed showed that benthic structure had an effect on residency whereby muskellunge displayed significantly higher residency in areas with low benthic structure ($P < 0.001$; Fig. 3) and preferred slower-velocity regions ($P = 0.057$).

Results from the river segment-residency GLMM illustrated muskellunge residency was highest in river segment 2 ($P < 0.001$; Fig. 2; Table 2), with residency values significantly higher (mean RI ± SE = 0.189 ± 0.026) compared to river segments 1 (mean RI ± SE = 0.044 ± 0.018) and 3 (mean RI ± SE = 0.062 ± 0.020). The river is deepest (via average thalweg depth) in river segment 2 at 4.75 m, with river segments 1 and 3 being shallower at 3.06 m and 2.24 m, respectively. River segment 2 is structurally unique as it is entirely composed of low-complexity (structure) habitat (Fig. 3). Our linear regression model revealed that drawdown was distinct in each segment ($F_{2,8} = 145.6$; $P < 0.001$; Adjusted R^2: 0.967; Table 3), with the mean drawdown in river segment 3 (1.79 m) less than in river segment 1 (2.13 m) and

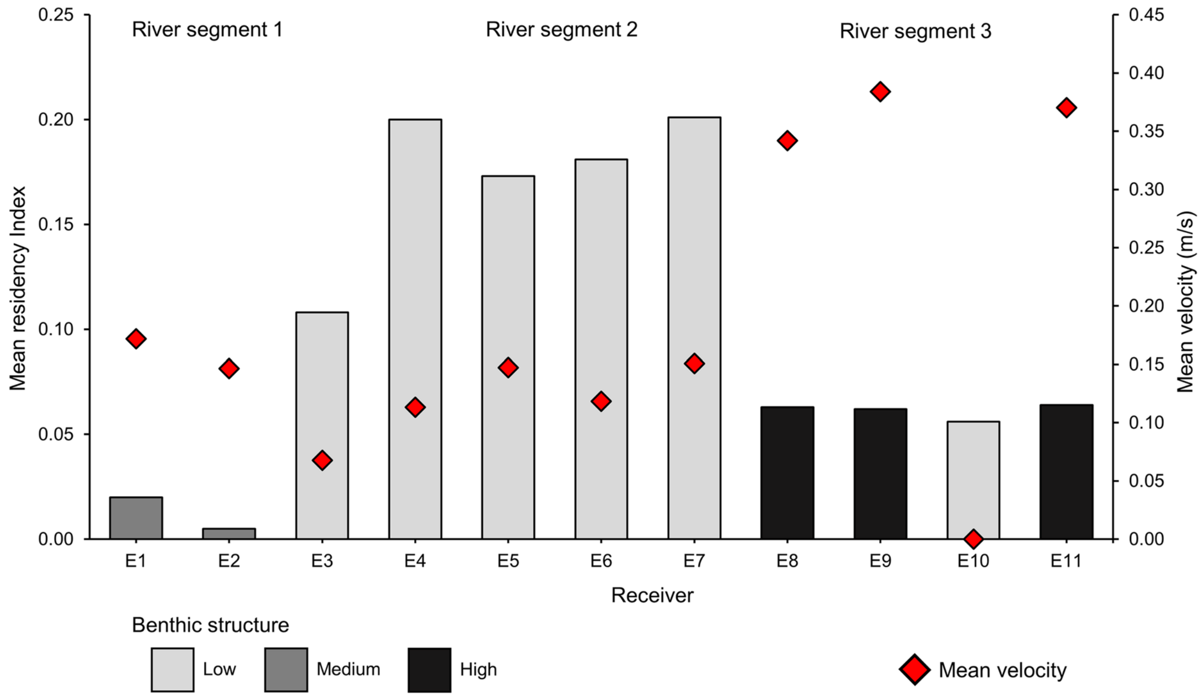

Fig. 3 Relationship between mean receiver residency index (RI) for both drawdown seasons, mean velocity, and benthic structure across the full acoustic array. The Eccolands Reach was partitioned into three river segments based on connectivity analysis: river segment 1 includes receivers E1–E3, river segment 2 includes receivers E4–E7, and river segment 3 includes receivers E8–E11. Structure was categorized into three classes: low (silt, sand, clay), medium (gravel, cobble), or high (boulders present). Velocity (m/s) was averaged across the two drawdown seasons to produce a single representative value for each receiver. Receivers E1 and E2 were the only sites assigned "medium" structure; receivers E8, E9, and E11 were the only sites assigned "high" structure. The middle portion of the Eccolands Reach is composed entirely of low-structure habitat. Velocity was considerably higher in river segment 3, except at receiver E10 which was deployed in a protected backwater area with no flow. See *Environmental variables and hydraulic surveying* for a detailed explanation of riverbed substrate mapping and processing

river segment 2 (2.08 m) (Fig. 4). Mean velocity was highest in river segment 3 (0.274 m/s) with river segments 1 and 2 experiencing lower mean velocities of 0.129 m/s and 0.133 m/s, respectively, though we documented somewhat higher velocities near the Black Rapids dam at receivers E1 and E2. Note that velocity is zero at receiver E10 as it is located in a protected backwater area. Velocity in the constricted portion of the river between receivers E7 and E8 was considerably higher, averaging 0.693 m/s with a peak velocity during spring freshet of 1.68 m/s. We use Fig. 2 to illustrate variation in river width whereby the river is narrowest in central portions of the Eccolands Reach with several larger pools near receivers E8 and E10, and Fig. 3 to visually describe the relationship between benthic structure, residency, velocity, and river segment.

Size-specific habitat use

We found a relationship that approached significance ($P = 0.097$) between fish size and benthic structure whereby the largest muskellunge were detected in medium-structure areas (Fig. 5). There was considerable overlap in detections across fish sizes in high- and low-structure areas, though larger fish appear to associate with rocky habitats (e.g., boulders in high-structure areas, cobbles and pebbles in medium-structure areas) and smaller individuals tending to select regions characterized by low structure (e.g., silt, clay, sand). No relationship between fish size and velocity was found ($P = 0.483$). Note that the smallest fish (270 mm) was detected in both low- and high-structure habitats, though only for four days during the

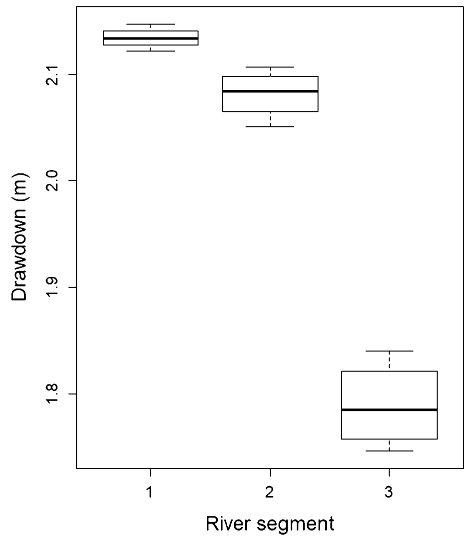

Fig. 4 Drawdown (m) in the Eccolands Reach by river segment. River segments are statistically distinct from one another. Note that river segments 1 and 2 (receivers E1–E7) experience a significantly greater drawdown compared to river segment 3 (receivers E8–E11) due to a backwater effect from the Black Rapids Dam

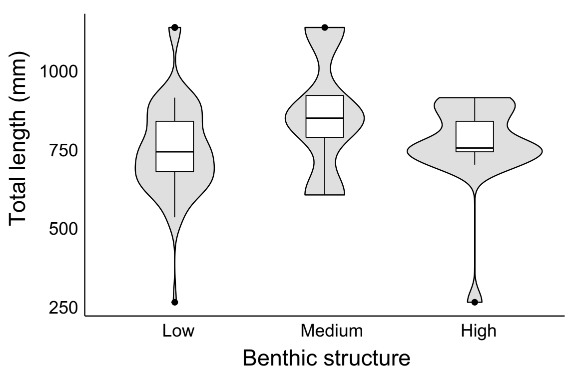

Fig. 5 Violin plots and boxplots illustrate size-specific habitat use of muskellunge in the Eccolands Reach. Our results indicate there is considerable overlap in habitat use by muskellunge across sizes, however smaller muskellunge appear to select for low-structure habitat with larger muskellunge associating with more complex medium- and high-structure areas. We found a relationship that approached significance with the largest muskellunge selecting for medium-structure habitat most downstream near the Black Rapids Lockstation. Violin plots illustrate the probability density. Boxes represent the boundaries of the upper and lower quartiles, thick lines represent medians, and whiskers represent upper and lower adjacent values

first drawdown season and one day during the second drawdown season.

Discussion

Drawdown season space use

Identifying critical muskellunge overwintering habitat in the Eccolands Reach was the key objective of this project and, while we did achieve this, it is likely that several interacting factors are responsible for providing winter refuge. The lowering of water levels for winter does not seem to directly influence muskellunge habitat selection as we found that muskellunge residency was highest in the central region (river segment 2) of the Eccolands Reach during both drawdown seasons, an area that experiences considerable—though not the greatest—drawdowns. River segments 1 and 2 experience the highest system drawdowns as a result of a backwater effect caused by the Black Rapids dam (Pasternack et al., 2008; Liro et al., 2020). Essentially, more logs are placed in the dam waste weirs during the navigation season which increases the surface water elevation, with the effect strongest near the dam. We believe one reason we observed high residency in river segment 2 is likely a function of the segment's unique and uniform deeper channel and lower water velocities. We found no influence of receiver depth on muskellunge residency, potentially because our receiver depth variable averaged depth across a 25 m radius, failing to capture linear (thalweg) depth conditions in the area. Thalweg measurements revealed river segment 2 was approximately 1.69× and 2.51× deeper than river segments 1 and 3, respectively. Because muskellunge roamed often throughout their respective river segment during winter, we believe thalweg measurements better explain overwintering habitat preferences. Indeed, our findings are consistent with those of other studies that documented deeper-water muskellunge overwintering behaviour (e.g., Younk et al., 1996; Gillis et al., 2010).

The seven fish detected across both drawdown seasons showed overwintering site fidelity to river segment 2. River segment 2 receives consistent tributary outfall throughout winter from the upstream West Branch Rideau River and during spring freshet from the Jock River (which collectively flow as the Rideau

River downstream), and potentially from the smaller Mosquito Creek (see Fig. 2). Tributary outfalls can provide important overwintering habitat support for and increase survival of riverine fishes as these regions may minimize frozen areas and/or offer thermal refuge and slower flow velocities (Koizumi et al., 2017). The low-complexity, soft-bottom habitats that characterize river segment 2 are indeed typically associated with areas of slower water velocities in rivers, potentially providing energy refuge during winter (Szalóky et al., 2021). Interestingly, except for two fish, all muskellunge overwintered near their capture/release site; thus, site fidelity could extend to specific areas year-round. However, most of our tagged muskellunge moved to a different river segment once connectivity was restored in April (see section "Reach connectivity"), so it is unlikely muskellunge remain in a single region all year. This is consistent with Pankhurst et al. (2016) who found that most of their tagged muskellunge (a study also conducted in the Rideau Canal) increased activity levels in spring and Schaeffer et al. (2020) documented muskellunge exhibiting seasonal shifts in spatial use. We did not conduct surveys to evaluate persistent (winter) vegetation or woody debris, though these structures may have been present and provided the structural habitat needed for refuge. We did, however, find that fish are capable of overwintering in any of the three river segments, so it is likely that a combination of abiotic factors influence overwintering habitat selection.

Our telemetry data revealed a pattern in habitat selection whereby only the largest muskellunge were detected in medium-structure areas near the Black Rapids dam. Largest muskellunge were detected in rocky habitats (i.e., medium- and high-structure habitats) found in river segments 1 and 3, with smaller individuals selecting for low-structure river segment 2 (Fig. 5). Size-specific use of habitat in fishes is common (i.e., ontogenetic habitat shifts), with smaller conspecifics known to use different habitats as a result of resource competition (Freeman & Stouder, 1989) and/or predation (Harvey & Stewart, 1991). Our finding of larger fish being detected in more structurally-complex areas was unexpected, as other work has documented smaller individuals preferring rocky, high-structure areas as protection against predation in both freshwater (Stuart-Smith et al., 2007) and marine (Heck et al., 2003) environments. The relationship we found is difficult to interpret because of collinearity and complexity in the system. For example, both medium- and high-structure habitats are found in areas with higher velocities near the Black Rapids dam and the mouth of the Jock River, respectively. Additionally, river segment 2 is composed entirely of low-structure habitat, is narrow, and has lower velocities (Table 2). It may be that as fish increase in size, they can overwinter in a greater variety of habitats with more difficult conditions (e.g., like higher flows), though we found no significant relationship between velocity and fish size. Our results suggest some relationship is occurring between larger muskellunge and habitats with greater structural complexity, possibly because these habitats afford better ambush points and/or provide protection from faster water velocities (Brenden et al., 2006).

Reach connectivity

We identified three areas that functionally fragment the Eccolands Reach into three river segments, with barriers to connectivity between receivers E3 and E4 (i.e., division between river segments 1 and 2) and receivers E7 and E8 (i.e., division between river segments 2 and 3). Thus, while our models indicated drawdown itself did not have an effect on muskellunge residency, it did consequentially minimize river connectivity. Our telemetry data suggests complete fragmentation between river segments from mid-December until early-mid-April when barriers seem to dissolve. Of the 16 individuals detected for full drawdown seasons, muskellunge roamed often and were detected on multiple receivers even during ice-on (see Supplementary Material E), further suggesting that the lack of cross-segment movements is not due to muskellunge physiology or energy capabilities during winter but because of physical or abiotic barriers minimizing connectivity.

It is unclear what conditions change that restrict or permit connectivity across the Eccolands Reach. The most likely contributing factor is simply shallow waters (<1.5 m; denoted by green X-symbols, Fig. 2) that fish cannot navigate during drawdown. Fragmentation does not seem to coincide with surface-ice coverage, as the ice-on period for both drawdown seasons spanned from early January to mid-March, whereas fish seem confined to their respective river segment from mid-December until early-mid-April. Satellite imaging (retrieved from https://www.sentinel-hub.

com/explore/sentinelplayground/) revealed that, even when most of the Eccolands Reach was covered in ice, the constricted area between receivers E7 and E8 was rarely iced-over. Higher velocities, especially during spring freshet, in combination with river constriction between receivers E7 and E8, is likely causing a velocity barrier (denoted by the red X-symbol, Fig. 2) to fish until discharges subside (protected data, Parks Canada). To move upstream to river segment 3, fish must navigate at minimum 500 m of constricted river with higher velocities and would then encounter a wider area with very shallow waters (< 1.5 m) before finding deeper refuge at the Jock River confluence. A fish swimming performance tool (see http://www.fishprotectiontools.ca/index.html; Katopodis & Gervais, 2016; Di Rocco & Gervais, 2021) indicates water velocity would have to be ≤ 0.62 m/s for muskellunge ≥ 750 mm TL (our smallest tagged muskellunge to move upstream in April) to navigate the constricted area. In April 2021, the four muskellunge we documented moving upstream across the constricted river area only did so when velocities subsided to 0.61 m/s; however, the one muskellunge we documented to successfully move upstream in April 2022 did so against high currents of approximately 1.28 m/s, suggesting energy refuges exist in eddies, shallow nearshore pools, or behind large boulders. These higher velocities can also minimize the drawdown (i.e., increasing water depth in the area) which also provides shallower, protected areas muskellunge may be able to exploit as they traverse against high velocities upstream. Thus, it appears this area may not be a complete barrier, but at the least is a deterrent to upstream movements. We therefore acknowledge this area as a velocity deterrent, and not barrier, in Fig. 2.

In most temperate freshwater rivers, the winter season typically means low flows, contributing to ice build-up that can reduce habitat availability and fragment connectivity (Cunjak et al., 1998, 2013; Heggenes et al., 2018). Fragmentation in the Eccolands Reach is likely due to a combination of fast currents and shallow waters that prevent (or discourage) winter connectivity. However, the downstream connectivity barrier (between river segments 1 and 2) does indeed experience lower velocities and the formation of surface ice and anchor ice or ice dams (Nafziger et al., 2017; Thellman et al., 2021) may have contributed to fragmentation there, minimizing available waters for fish to navigate. Muskellunge appear to successfully overwinter in all river segments of the Eccolands Reach, so riverbed construction to provide connections is not currently pressing. However, if winterkill (hypoxia) events become an issue, creating corridors could be important to consider. Winterkill has indeed been documented several times in the Rideau Canal. For example, Gillis et al. (2010) found one of their radio-tagged muskellunge dead among “many dead fish” and Walker et al. (2010) also documented a winterkill event in April 2006. Further, most muskellunge selected to overwinter in river segment 2 and were subsequently confined for the duration of winter, potentially rendering them vulnerable to increased exploitation, predation, and/or competition (Bunt et al., 2021).

Potential reproductive movements

Across both drawdown seasons, we saw increased muskellunge activity levels in April. In the first and second drawdown seasons, 67% (6/9) and 71% (10/14), respectively, of muskellunge detected in April were detected on a new receiver or in a new river segment after overwintering. Given muskellunge spawning is expected to occur approximately two weeks post-ice melt (Pankhurst et al., 2016), which occurred both years in late March, it is possible these movements are reproductively driven. Most muskellunge that displayed increased activity were close to (within 100 mm) or longer than 700 mm, which in Ontario is generally considered size-at-first maturity (Casselman, 2007). Larger spring movements by muskellunge, presumably driven by spawning temperatures, have indeed been documented in the Rideau River (e.g., Pankhurst et al. 2016) and in other North American systems (e.g., Schaeffer et al., 2020; Weber & Weber, 2021).

Potential spawning in April is of concern given Parks Canada does not raise water levels in the Eccolands Reach until early May (refill began 06 May 2021 and 03 May 2022). Muskellunge spawning in the Rideau River has occurred as early as 22 April (Pankhurst et al., 2016), often taking place in shallow littoral areas (Farrell, 2011), much of which remain unavailable until refill occurs (gray portions of Fig. 2). Additionally, the Jock River and Mosquito Creek are both important muskellunge spawning tributaries, yet the entry points remain mostly exposed during drawdown and therefore likely cannot be used by muskellunge for reproduction. When water levels remain low before and during spawning, the consequential effects can be most severe, limiting the amount of suitable spawning habitat and affecting recruitment and year-class strength (Gaboury & Patalas, 1984; Carmignani & Roy, 2017). We note, however, other work has suggested that if water levels are restored in early spring prior to spawning, muskellunge populations may benefit from winter drawdowns. For example, high hatching success has been documented when spawning substrate was aerated by a 2 m winter drawdown (Zorn et al., 1998), a drawdown similar to that seen in the Eccolands Reach. It will be important for future work to confirm timing of the muskellunge spawn in the Eccolands Reach and reproduction itself with spawning surveys (e.g., Diana et al., 2015).

Adaptive water-level management of the system, whereby water levels are altered on a seasonal basis to support aquatic species, would be quite complex. Although Parks Canada must comply with the federal *Fisheries Act*, which does require protecting critical (overwintering and spawning) habitats, Parks Canada itself is not a delegated authority (i.e., not designated as a department that can enforce, permit, or regulate under the *Act*; Valerie Minelga, Ontario Waterways, personal communication). Additionally, it is the provincial government (the Ministry of Northern Development, Mines, Natural Resources and Forestry) that manages fisheries in Ontario. This jurisdictional quagmire of several agencies managing different aspects of the same taxa was identified as a key barrier to effective aquatic species conservation in the Rideau Canal (Bergman et al., 2021). Further, Parks Canada could only consider raising water levels once the spring freshet flood risk has passed, irrespective of fragmentation during winter or warmer, earlier water temperatures and fish spawning needs. Earlier spring freshets are indeed being recorded in rivers across Canada, including the nearby Petawawa River (which feeds into the Ottawa River, Fig. 1) (Jones et al., 2015; Kang et al., 2016). Agencies should work collaboratively and determine if current drawdown procedures are negatively impacting muskellunge and if regulations should be altered to reduce drawdown severity and/or refill the river at an earlier or temperature-specific date.

Limitations

Although our study provides an interdisciplinary account of muskellunge winter movements in concert with hydraulic data, as with any telemetry study, there are certain limitations. First, incorporating drawdown, velocity, and bathymetric data into our study was vital in helping us understand fish habitat selection and space use in response to the water-level lowering; however, this was the extent of our hydraulic analysis. Continuous (daily, weekly, etc.) spatially-dense 2D velocity modelling each drawdown season throughout the study system could have offered key insights into connectivity and potential changing (or more severe) drawdown conditions, so this will be valuable for future research to consider. Second, none of the three tagged juvenile (<300 mm TL) muskellunge were detected for a full drawdown season, possibly because they (1) overwintered in littoral areas outside our receivers' detection range, (2) may have been consumed by larger predatory fish that swam outside the array, or (3) died post-surgery in an area they could not be detected. Integrating acoustic tags with predation sensors (Halfyard et al., 2017) into future work to determine if and/or how many juvenile muskellunge are preyed upon would be useful. We therefore acknowledge that while our study does provide evidence of key overwintering areas of muskellunge, we do not know where juveniles overwinter. Third, while detection range and efficiency testing were indeed conducted, the 72-h assessment of both receiver models was done during summer months, though Walton-Rabideau et al. (2020) did confirm similar detection ranges of the 4250 model receivers spanning 30–75 m during fall and winter in the nearby St. Lawrence River. The WHS 4350 receivers had a greater detection range and efficiency, which may have influenced the number of detections at those sites, though we found no significant difference in muskellunge residency between drawdown seasons. Several fish were detected infrequently, indicating muskellunge may be using locations outside the detection range of our telemetry array, suggesting a more comprehensive array may be needed for a finer-scale evaluation of spatial ecology. Fourth, receivers did not have temperature loggers integrated until the second drawdown season, and none had oxygen loggers. Temperature and (dissolved) oxygen are the most important water quality parameters that predict and drive fish movements and space use (Stefan et al., 2001; Missaghi et al., 2017), so we may be missing important abiotic drivers of fine-scale habitat use. Finally, we were unable to include interactions in most of our models due to insufficient statistical power; therefore, it would be useful for future research to include a wider size range and higher sample size of muskellunge to investigate interactions between residency and abiotic system characteristics.

Conclusions

The lack of evidence and science-based management needed to effectively manage freshwater fishes has been a major concern among aquatic conservationists (Bartley et al., 2015) and, additionally, conservation actions are notoriously "too little, too late" whereby they are *reactive*—and not *proactive*—in nature (Groves et al., 2002). Water levels in the Rideau Canal are manipulated to ensure safe navigation for recreationists and to manage flood risks, with some regard to protecting fish habitat; however, little knowledge was known about the effects of winter drawdowns prior to this work. Our findings revealed that all areas of the Eccolands Reach can support muskellunge overwintering, but they are discrete, and the river is fragmented for most of the drawdown season. We additionally, and inadvertently, observed adult muskellunge exhibiting potential spawning activities prior to the system being refilled. Overall, we found that muskellunge preferred overwintering areas with low-structural complexity and slower water velocities but, interestingly, it appears larger individuals may associate with more structurally-complex habitats. It will be important for managers to develop an interdisciplinary plan that addresses both river-regulation requirements and fish spatial ecology to ensure the persistence of muskellunge, and other pressured aquatic species, in Canada's historic Rideau Canal.

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Author contributions JNB, SJC, DMG, and SJL conceived and designed the study. JNB, DMG, LEL, and SJL performed field work. JNB and JRB analyzed data. JCV, CDR, and KLN performed substrate field work. KLN and CDR performed hydraulic field work, provided and analyzed drawdown and velocity data for the study, and co-developed Fig. 2. JNB wrote the original draft; review and editing provided by all co-authors.

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Data availability The datasets generated and/or analysed for the current study are available from the corresponding author (J.N. Bergman) upon reasonable request. Discharge data provided by Parks Canada is federally protected.

Declarations

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

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