An interdisciplinary approach to evaluating native and invasive fish connectivity and spatial ecology in Canada’s historic Rideau Canal Waterway

by

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Jordanna N. Bergman
“Unless someone like you cares a whole awful lot,

nothing is going to get better. It's not.”

The Lorax
Dedication

This thesis is dedicated to the wild, natural places that nurtured my soul in times of darkness and gave me hope, peace, and in working to protect them, a sense of purpose.

I also dedicate this work to my loved ones who, though sometimes questioned my sanity, supported my dreams unconditionally and stood by me. Your love and encouragement have meant the world to me, and I wouldn’t be here if it wasn’t for you.

Finally, I wouldn’t be here if I wasn’t first given the opportunity by Drs. Steven Cooke and Joseph Bennett. They provided a chance to explore research independently and grow as a scientist (and, subsequently, person). They guided me on a wonderful PhD journey and prepared me so well for the future. I dedicate this work to my two advisors, who made it all possible.
Abstract

As global freshwater biodiversity continues to deteriorate rapidly, it is critical that system-specific conservation actions are identified and implemented. In interconnected freshwater systems like waterways and canals, foremost threats include river fragmentation and connectivity loss, and the diffusion of invasive species. However, managing barrier (e.g., locks, dams) connectivity in waterways to selectively allow and restrict passage of native and invasive species, respectively, is a major global challenge. Canada’s historic Rideau Canal Waterway, located in eastern Ontario, is interconnected by 24 operating lockstations and embodies this challenge. To minimize invasive species dispersal, without compromising connectivity to native species, we must first assess if, when, and to what extent native and invasive fishes move throughout the waterway and the potential factors influencing movements. Within each reach (i.e., the waters between two lockstations), connectivity may also seasonally vary due to ice formations and reduced flows and/or water levels, though literature on this topic is currently limited. Here, we blended several fish tracking methods with ecohydraulics and management consultations to evaluate system connectivity and fish movement patterns. Three native fishes, largemouth bass (*Micropterus salmoides*; *N* = 56), muskellunge (*Esox masquinongy*; *N* = 23), and northern pike (*Esox lucius*; *N* = 114), and two invasive fishes, common carp (*Cyprinus carpio*; *N* = 54) and round goby (*Neogobius melanostomus*; *N* = 45), were acoustically tagged and tracked in 2019-2021 across 45 km of the waterway. Additionally, we externally (anchor) tagged 9564 individuals across 15 species, with tags deployed in 2018-2023, to evaluate potential passages and general space use. Movement data suggests that lockstations reduce, but not entirely restrict, connectivity, and that seasonal water-level drawdowns further reduce connectivity within river reaches. We found that most passages were in the direction of flow, a potential issue to native upstream migratory species. Notably, while we documented several native fish species conducting inter-reach movements, no common carp passages were detected and only a single round goby moved upstream through a lock. Results from this research add to the limited, but growing, literature base of native and invasive fish movements in waterways, providing evidence and suggestions for managers and conservation groups to develop selective fish passage strategies or take restorative actions. Given that waterways are pervasive globally, this research informs not only the conservation and management of fish populations in the Rideau Canal Waterway, but of other waterways in Canada and beyond.
Acknowledgements

Although I acted as the “lead” for each of the following chapters, this is the sort of work that takes a village to conduct. I would not have accomplished any of this research if it wasn’t for the many hands (and minds) who provided guidance and support along the way.

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Thesis format and contributions

This thesis is comprised of six chapters, four of which are co-authored manuscripts that are in various stages of publication with peer-reviewed journals (Chapters 2-5). Please note that I use the pronoun “we” throughout this thesis as the nature of my research is highly collaborative and includes experts across several disciplines; I believe in acknowledging the cooperative efforts involved in making this research possible. For each chapter, supplementary material, online resources, and/or appendices can be found under Appendix E: Additional files. Details of contributions are as follows:

Chapter 1: General introduction


This article was collaboratively written and designed by the team of authors with expertise across several disciplines (social science, ecology, hydraulic engineering, management) and included early-career researchers to produce an interdisciplinary review of canals as social-ecological systems. This project was conceived by Cooke as part of a multi-year program supported by a Natural Sciences and Engineering Research Council of Canada (NSERC) Strategic Partnership Grant, and all co-authors contributed to writing. Bergman led and coordinated writing and publication.


This study was conceived by Bergman, Bennett, and Cooke. Bergman conducted the field work with support from research technicians, waterway managers, and lockstation operators. Neigel and Rennie performed hydraulic field work, provided water-level data, and co-produced figures. Bergman, Raby, and Bennett conducted data analysis. Fisk coordinated and provided acoustic receiver equipment. Bergman wrote the original manuscript and all co-authors reviewed and provided revisions. Bergman was interviewed on this research by CBC and several local news media outlets.

Bergman, Cooke, Glassman, and Landsman conceived and designed the study. Bergman, Glassman, LaRochelle, and Landsman performed field work. Bergman and Bennett analyzed data. Vermaire, Rennie, and Neigel performed substrate field work. Neigel and Rennie performed hydraulic field work, provided and analyzed drawdown and velocity data, and co-developed a figure. Bergman wrote the original draft; review and editing was provided by all co-authors.


Bergman, Bennett, and Cooke conceived the study with management recommendations and suggestions from Minelga and Vis. Bergman and Cooke collected field data. Bergman and Bennett conducted statistical analyses. Fisk coordinated and provided acoustic receiver equipment. Bergman wrote the original manuscript; all co-authors reviewed and provided revisions. We recently received positive feedback from reviewers and are in the process of revising the manuscript to resubmit for publication.

Chapter 6: General discussion, conclusions, and future directions
Chapter 1: General introduction

1.1. The state of fresh waters and wild freshwater fish populations

The rate of global species extinctions continues to accelerate despite growing conservation efforts (Pimm et al. 2014). In particular, biodiversity is rapidly declining in freshwater ecosystems, where the drivers of extinctions are mounting in magnitude and difficult to manage given complexity and synergies with climate change (Arthington et al. 2016; IUCN 2019). Populations of freshwater vertebrate species have declined at more than twice the rate of terrestrial or marine vertebrates, with monitored populations globally declining by 84% on average and approximately one in three freshwater species threatened with extinction (WWF 2020; IUCN 2019). All freshwater taxonomic groups show higher risk of extinction compared to terrestrial systems (Collen et al. 2013). Freshwater systems are experiencing five main threats: 1) habitat degradation, 2) species overexploitation, 3) invasive species and disease, 4) water pollution, and 5) flow modification (Dudgeon et al. 2006). Invasive species pose one of the greatest threats to biological diversity in freshwaters, with potentially adverse socio-economic effects on human welfare (Reid et al. 2019). Additionally, the effects of climate change – an “emerging” threat (Reid et al. 2019) – have become one of the most researched drivers of freshwater biodiversity losses (see Williams-Subiza and Epele 2021).

The longitudinal fragmentation of freshwater systems poses one of the greatest threats to freshwater fish biodiversity; severing connectivity impedes species persistence by disrupting their dispersal and migration, with potential long-term consequences to ecosystem processes (e.g., nutrient transport) and community structure (Gido et al. 2016). The term connectivity is widely used across landscape change and conservation practice literature, and while it generally refers to the “degree to which a landscape enables or restricts movement of organisms among resource patches” (Lindenmayer and Fischer 2007), there are multiple and multifaceted meanings. For example, ecological connectivity refers to the connectedness of ecological (e.g., energy flow) and evolutionary (e.g., gene flow) processes at multiple spatial scales (Soulé et al. 2004; Pulsford et al. 2015). Alternately, landscape connectivity refers to the degree to which a landscape facilitates movement of organisms among resource patches (Taylor et al. 1993; Fahrig et al. 2020) and is commonly divided into (1) structural connectivity, relating to the physical arrangements of disturbance and/or habitat patches, and (2) functional connectivity, relating to the actual movement of individuals across contours of disturbance and/or patches (see Fahrig et al. 2020). A recent global analysis of river connectivity revealed that only 37% of rivers longer than 1000 km remained free flowing, with many rivers in highly-developed North American regions experiencing considerable fragmentation (Grill et al. 2019). Today, dams are the leading driver of river connectivity loss (Grill et al. 2019).
Approximately 50% of freshwater fishes are threatened by global climate change (Darwall and Freyhof 2015) and, additionally, it is generally accepted that migratory fishes (compared to non-migratory) are disproportionately threatened as they traverse long distances and require different habitats to carry out their life history (Robinson et al 2009). As defined by WWF, migrations are “the movements animals undertake between critical habitats to complete their life cycle. Often, this is a seasonal or cyclical movement between breeding and non-breeding areas.” Critical habitat requirements are highly dependent on the species itself and can vary based on the system; however, for migratory species, movement corridors – contiguous areas of natural habitat that organisms can migrate through (Caskenette et al. 2020) – are essential to ensure fishes can reach their destination. There are several different classifications of freshwater migratory species, including those that are diadromous (travel between saltwater and freshwater to carry out their life cycle), amphidromous (travel between saltwater and freshwater, but not to breed), and potamodromous (entirely freshwater migrations to complete their life cycle). Collectively, migratory fish populations have experienced a staggering decline of -76% since 1970 with the key drivers of decline being fragmentation, degradation, and loss of habitat (Deinet et al. 2020).

In response to the identification of threats and a need to determine and implement recovery actions, an Emergency Recovery Plan was developed by the WWF (Tickner et al. 2020). The plan provides six priority actions that can be take to “bend the curve of freshwater biodiversity loss” focusing on accelerating the implementation of environmental flows, improving water quality, protecting and restoring critical habitats, managing the exploitation of freshwater ecosystem resources, preventing and controlling non-native species invasions, and safeguarding and restoring river connectivity. Tickener et al. (2020) recommend framing and planning priority actions coherently such that measures to address one driver of biodiversity loss can simultaneously address others given that causes of biodiversity loss often act synergistically (Craig et al. 2017) so priority actions must work harmoniously to keep up with the pace of extinction rates. This is especially relevant given most freshwater systems are not experiencing just one threat. For example, in freshwater waterways, navigable rivers, and canal systems, human-mediated disturbances like poor water quality and invasions are common and, additionally, most of these systems have experienced connectivity loss (Grill et al. 2019). Free-flowing rivers offer cultural, recreational, and economic services (Deinet et al. 2020), and by ensuring connectivity in these systems we can stem biodiversity losses by enhancing migratory populations, supporting genetic diversity, and providing access to ideal critical habitats (Rahel 2013).
The connectivity of waterways and canals, as experienced by fish species, can be determined by habitat preferences, jumping and swimming abilities, risk perception, and the landscape features fish may encounter like water velocity (Castro-Santos 2005), water temperature (Agostinho and Zalewski 1995), changes in elevation (Adams et al. 2000), and water depth (Lonzarich et al. 1998). The movements of fishes are ecologically important for the transfer of energy, nutrients, and genes between lentic and lotic, upstream and downstream, and main- and side-channel habitats (Lucas and Baras 2001; Flecker et al. 2010). Additionally, the spatial distribution of freshwater fish movements ranges in temporal scales from localized diel movements (e.g., foraging, predator evasion), to seasonal migrations (e.g., overwintering, reproduction), to life history events (e.g., ontogenetic habitat shifts) (Lucas and Baras 2001). From the perspective of canals and waterways with anthropogenic barriers, such as navigation locks, hydropower dams, and water-control structures, the longitudinal fragmentation of these systems is a main concern, as upstream and downstream movements are reduced to some degree depending on infrastructure type and if mitigation efforts are in place (e.g., fishways). Evaluating the use of space through time by fishes will be essential in understanding population distributions and the degree of barrier passability, subsequently supporting the evidence-based management and conservation of wild populations (Whoriskey et al. 2019).

Protecting habitat – critical habitats in particular – plays a key role in biodiversity conservation (Camaclang et al. 2015). In recognition of this, many nations including Australia, Canada, and the United States have enacted endangered or at-risk species legislation that requires the identification and protection of critical habitats for imperiled species. In Canada, the Species at Risk Act (SARA) defines critical habitat as “...the habitat that is necessary for the survival or recovery of a listed wildlife species and that is identified as the species’ critical habitat in a recovery strategy or in an action plan for the species” (SARA 2002, s. 2(1)). Specific to aquatic species, critical habitat includes, “…spawning grounds and nursery, rearing, food supply, migration, and any other areas on which aquatic species depend directly or indirectly [our emphasis] in order to carry out their life processes, or areas where aquatic species formerly occurred and have the potential to be reintroduced…” (SARA 2002, s. 2(1)). Thus, any area that supports a life history process necessary for the survival of a species would therefore be considered critical. Where critical habitats like spawning grounds and food supply areas are explicitly listed, overwintering habitats are not, though by default any habitat which supports the survival of overwintering aquatic organisms should consequently be considered critical. Additionally, travel to and from critical habitats is essential and must also be considered for migratory species. The lack of explicit inclusion of migratory-corridor and overwintering areas as critical habitats is a management “loophole” that may be contributing to population declines.
In temperate freshwater systems, connectivity can also change seasonally, and freshwater fishes may face an additional layer to existing interacting threats during the winter season. Habitats may become fragmented naturally during winter due to lower winter flows that increase ice formations and dewater habitats, thereby reducing and fragmenting accessible habitat (Heggenes et al. 2018) in managed waterways, canals, and other engineered ecosystems where water levels may be drawn down intentionally. For example, water levels are reduced in many managed systems prior to the winter season and refilled the subsequent spring to protect infrastructure and in preparation for spring freshet and flooding. Drawdowns may reduce water levels to such a degree that shallow-water regions become barriers to connectivity, resulting in a concentration of threats into a smaller area and pressuring the species within. In some cases, these pressures may become too great, resulting in skip spawning (i.e., when sexually-mature fish skip reproduction, usually in response to poor physiological condition, to direct time and energy into growth and survival to increase future success rather than exacerbate already-low energy reserves by spawning in the current year; Jørgensen et al. 2006; Fernandes and McMeans 2019). In more severe cases, it may lead to winterkill events (Shuter et al. 2012). In the spring, barriers may instead be present in the form of high velocities that prevent fish access to other areas.

1.2. Selective fragmentation

Interconnected, freshwater systems like navigable waterways and canals have been described as “ecological paradoxes” because they embody a unique challenge – the novel connection they provide may offer new and potentially better habitat to the biodiverse native species they host, yet they can also facilitate invasions. For example, the Laurentian Great Lakes are home to notorious examples of canals that enable invasions (e.g., sea lamprey [Petromyzon marinus] via the Welland Canal; Lawrie 1970) and today the Great Lakes’ basins are at risk of an invasive carp invasion, which includes grass (Ctenopharyngodon idella), bighead (Hypothalmichthys nobilis), silver (Hypothalmichthys molitrix), and black (Mylopharyngodon piceus) carps, likely via the Chicago Area Waterways System (Cudmore et al. 2017). In cases where preventing an invasion is more important than providing connectivity to native species, an intentional and/or complete fragmentation strategy at barriers may be applied (Rahel 2013), whereby structures are permanently closed. In navigable systems where locks acts as a connectivity pathway, permanent lock closures are usually not supported by recreational and commercial users (Hinterthuer 2012), however examples do exist (e.g., the Rapide Croche boat lock in the Fox River, Wisconsin, USA was permanently closed to block invasive sea lamprey from entering the Lake Winnebago system; Lavis et al. 2003). More often, managers and researchers focus on developing non-structural and species-specific deterrents, like chemosensory stimuli, underwater acoustics, and electric barriers, that could be implemented at navigation barriers with no effect on waterway operations and, ideally, only negatively affect the target invasive species (Jones et al. 2021).
Many waterways are linked by anthropogenic barriers (e.g., navigation locks, dams), offering some degree of connectivity to aquatic species; however, managing barrier connectivity to simultaneously allow and restrict passage of native and invasive species, respectively, is a major and global challenge (Rahel and McLaughlin 2018). Connecting previously disconnected habitats can encourage biotic homogenization, defined as the “increased similarity of biotas over time caused by the replacement of native species with nonindigenous species, usually as a result of introductions by humans” (Rahel 2002). Waterway managers are therefore challenged with addressing two key threats in freshwater riverine systems: 1) mitigating effects of habitat fragmentation by instream structures that disrupt migrations and movements, and restrict species distributions and 2) managing invasive species dispersal and impacts on ecological processes. As waterways with anthropogenic barriers have been described as “invasion highways” for aquatic species (Leuven et al. 2009), it is vital to consider how infrastructure and/or operations could be refined to reduce invasive species spread. To do so, and without compromising connectivity to native species, we must first assess if, when, and to what extent native and invasive fishes move throughout a system and the potential factors influencing movements.

The need to promote river connectivity for native fishes while concurrently preventing (or, at least, reducing) invasions has led to a growing need to develop selective fish passage technologies. Rahel and McLaughlin (2018) reviewed the topic of selective fragmentation and the (selective) management of fish movement across barriers; briefly, the overall goal of selective fragmentation is to create additional filters that will permit the passage of desirable (usually native) species while preventing the passage of undesirable (usually invasive) species. Selective fragmentation builds on the concept of ecological filters, proposed first by Smith and Powell (1971) and expanded on by Lake et al. (2007). Essentially, the local fish assemblage is the result of having passed through an ecological filter or series of filters. These filters can be biogeographic (e.g., rapids, waterfalls), physical (e.g., high velocities, shallow waters), physiological (e.g., cold water temperatures), or biotic (e.g., presence of predatory species) (Rahel 2007). The objective of selective fragmentation is to establish new or additional barriers based on the above-listed filters to selectively permit and/or restrict movement. There are five biological traits that can be exploited for the basis of selective fish passage and are as follows:

1) Physical ability
   a. Swimming ability: differences in swimming speed and endurance used to filter species passage through fishways (e.g., Starrs et al. 2015)
   b. Jumping ability: barrier height could act as a filter to upstream movements based on fish jumping capacity (e.g., Ficke et al. 2011)
   c. Climbing ability: some species have poor swimming abilities but can climb slanted and vertical surfaces (e.g., Moser et al. 2011)
2) Body morphology: in-water barriers with size-specific grates or gates could exclude larger- or wider-bodied species while allowing passage to smaller- or laterally-compressed species (e.g., Hillyard et al. 2010)

3) Sensory capability
   a. Electrical: fishes avoid electrical fields; as such, electricity could block fish passage and guide undesirable species into traps. Note that electrical fields would also likely block native species (e.g., Weber et al. 2016)
   b. Acoustic: species-specific hearing abilities, whereby certain species (or families) are more sensitive to certain sounds, could be used to prevent passage (e.g., Linke et al. 2018)
   c. Visual: species respond differently to strobe lights, light levels, or light types (e.g., light color) which could be used as a movement barrier (e.g., Richards et al. 2007)
   d. Olfactory: repellant and attractant odors could be used to deter or entice nonnative and native species, respectively, for passage (e.g., Imre et al. 2014)
   e. Magnetic field: specific to elasmobranchs, which use their electroreceptors for navigation and movement, could be used to deter entry into specific areas (e.g., O'Connell et al. 2018)
   f. Carbon dioxide (CO₂): CO₂ is a metabolic poison and fish therefore avoid regions that have high levels of this gas (e.g., Treanor et al. 2017)

4) Behaviour
   a. Depth orientation: depending on where fish orient themselves in the water column during migrations, the location of fishway entrances could be positioned to either allow or restrict entry to fishes (e.g., Schultz et al. 2007)
   b. Schooling: fishes that school may be averse to fish passage entries that are narrow or require individuals to break from the school (i.e., only allow one individual to pass at a time) (e.g., Mallen-Cooper and Stuart 2007)

5) Phenology
   a. Diel activity patterns: barriers are implemented at specific times of day to allow or restrict species (i.e., those that are active during the day versus night) (e.g., Noonan et al. 2012)
   b. Seasonal migration patterns: barriers can be applied based on the timing of migrations (e.g., Johnson et al. 2016)

To develop effective selective fragmentation strategies, an understanding of species-specific movement and/or spatial ecology is necessary (i.e., we first need to know where, when, and how species interact with and/or pass through “filters” to then fragment them selectively). Movement ecology and spatial ecology, while often complementary in biodiversity conservation, are distinctly different fields that
generate different information; where movement ecology focuses on the how, why, when, and where of organismal dispersal and migration (see Nathan et al. 2008), spatial ecology aims to understand the processes influencing species distributions and dynamics across space (Fletcher and Fortin 2018). A popular tool for evaluating fish movement and spatial ecology is acoustic telemetry, a method that involves the surgical implantation of acoustic transmitters that emit a sonic pulse and can then be detected and logged by acoustic receivers. Acoustic telemetry can be used in both freshwater and marine environments and provides valuable movement data on aquatic animals across taxa and life stages (Donaldson et al. 2014). Passive acoustic telemetry evolved in the 1980s and involves the deployment of stand-alone acoustic receiver stations that record detections and can later be retrieved and processed, resulting in 24-hour monitoring and a less labour-intensive process compared to active tracking of individuals (e.g., radio telemetry; Kessel et al. 2014). Hereafter, any “acoustic telemetry” method or study referenced used a passive acoustic array. Acoustic telemetry can reveal important movement data to evaluate species- and individual-specific spatial ecology (Brownscombe et al. 2019) and movement ecology (Matley et al. 2023) across time and space.

Movement data has been used to provide the necessary evidence for selective fragmentation strategies. For example, in the Laurentian Great Lakes, the Sea Lamprey Control Program operates barriers to be fully closed during sea lamprey spawning migrations (i.e., a seasonal barrier), but opens the barriers before and after their migration to allow native species passage (Klinger et al. 2003; Velez-Espino et al. 2011). Another Laurentian Great Lakes example is the Cootes Paradise Marsh Fishway which is a physical barrier that uses narrow vertical bars to exclude large-bodied nonnative common carp (Cyprinus carpio) while permitting passage to slimmer, native species (Boston et al. 2016). The barrier is highly effective at eliminating common carp entry into the Cootes Paradise Marsh, Ontario, Canada with a population reduction of >95% (Boston et al. 2016). Movement data has also been used elsewhere, for example in the Murray River, Australia where nonnative common carp were successfully excluded via a Williams’ Carp Separation Cage. The cage was installed to separate common carp from native fishes that use the fishway by exploiting the jumping and migratory behaviours of common carp (Stuart and Conallin 2018). Notably, captured common carp were marketed and sold for a total return of >AU$0.90 million, which far exceeded setup costs. Piczak et al. (2023) suggest the most effective selective fragmentation methods for common carp in navigation waterways will involve exploiting their sensory capabilities (e.g., visual, auditory, olfactory), as sensory barriers would not physically restrict navigation or water flow. These researchers showed how an evidence-based selective fragmentation strategy, that exploited biological traits of an invasive species, not only resulted in an ecological benefit to the native fish community but also an economic profit.
The monitoring of native and invasive fish movements across barriers is beginning to gain traction. Many studies on passage through navigation locks report low percentages of fish navigating lock chambers to move up- and/or down-stream (i.e., average of 14%; JN Bergman unpublished data), supporting the long-held perception that lock chambers lack the necessary attractant flow below the lock, and within the chamber once the upper gates have opened, to facilitate fish passage (Coker 1929; Wilcox et al. 2004; Lubejko et al. 2017). However, some studies report >60% of their tagged fishes moving through locks. For example, Smith and Hightower (2012) found that 85% and 75% of American shad (Alosa sapidissima) and striped bass (Morone saxatilis), respectively, passed through a lock chamber in the Cape Fear River, United States. Fritts et al. (2021) documented fish using a navigation lock in the Mississippi River, United States, recording both native fish (10 passages) and invasive carp (14 passages) passages, and noting that opportunities for passage occurred during large-vessel lockages and by season. Their phenology data suggests that if a deterrent at the lock is deployed in summer and fall, invasive carps would be more affected than native species, because native species passages occurred primarily in the spring. Additionally, in the River Murray, Australia, Bice et al. (2018) monitored the downstream catadromous spawning migration of adult congolli (Pseudaphritis urvillii) through the Goolwa Barrage Navigation Lock using acoustic telemetry, finding that when the lock was operated to facilitate fish passage, 60% of their tagged fish successfully located and passed through the lock.

In many cases, an interdisciplinary approach may be needed whereby hydraulic engineers and infrastructure managers work together to understand how flows and operations, respectively, influence fish passage and movements. Studies blending multiple fish tracking methods (e.g., satellite telemetry, radio telemetry, mark-recapture) with data from other disciplines (e.g., environmental, hydraulic, and/or infrastructure operation data), though rare, can yield a more complete understanding of fish movement (Verhelst et al. 2023). In addition, most research that monitored the use of navigation locks as a fish connectivity pathway focused on evaluating the timing and frequency of passages at specific sites or by select species, with limited evidence of multi-species work or the subsequent selective fragmentation at those sites (though see Wilcox et al. 2004, Kim and Mandrak 2016, Fritts et al. 2021).

1.3. Introduction to Canada’s historic Rideau Canal Waterway

The Rideau Canal Waterway (hereafter, “RCW”), located in eastern Ontario, Canada, is a 202 km navigable route that connects the Laurentian Great Lake Ontario at the city of Kingston and the Ottawa River at Canada’s capital city of Ottawa. The waterway is interconnected by 23 operating lockstations (i.e., lock-and-dam structures; hereafter, “LDs”) to facilitate navigation and for water-level management, linking together a medley of large and small lakes, riverine stretches, and constructed channel habitats. Patrons of the RCW, including boaters, anglers, and other recreationists, have reported fish passing
through locks alongside watercraft. However, the extent of fish movements through navigation structures in the RCW has yet to be quantified and, additionally, it is unknown if fish passages are species-specific or seasonally driven. The passage of fish through navigation locks is believed to be mostly unintentional as these structures are placed in calm, low-flow areas for the primary purpose of boat navigation and not to attract fishes (Larinier and Marmulla 2004). As such, if fish migrations and movements are being blocked by LDs, the effects would be considerable for species whose life history includes obligate migrations (e.g., to reach spawning or overwintering habitats; Larinier 2001). Various freshwater fish in the RCW exhibit migratory behaviours, including northern pike (Esox lucius), smallmouth bass (Micropterus dolomieu), white sucker (Catostomus commersonii), and yellow perch (Perca flavescens) (Meixler et al. 2009).

The RCW is a biodiverse freshwater system and has a diverse fish assemblage of 34 species belonging to 10 families (two of which are introduced; Phelps et al. unpublished). The waterway supports one of the few naturally-reproducing, urban muskellunge (Esox masquinongy) fisheries in North America (Gillis et al. 2010) and other gamefish (e.g., largemouth bass [Micropterus salmoides], northern pike), as well as federally-listed at-risk species like bridle shiner (Notropis bifrenatus; COSEWIC 2013). Yet, the stability of native fish populations in the RCW is threatened by ecologically-destructive invasive species.

Two invasive fishes are of concern in the RCW: common carp, native to Eurasia, and round goby (Neogobius melanostomus), native to the Black and Caspian Seas. Common carp are a large, deep-bodied species of light gold to dark brown color with reddish fins that, today, have a wide (nonnative) distribution throughout North America. They were introduced for aquaculture and recreational fisheries purposes and have now established as a predominant species in numerous freshwater environments (Bajer and Sorensen 2010). Common carp spawn in shallow, vegetated wetland habitats and floodplains in the spring and early summer when water temperatures are between 17-28°C (Panek 1987). Each female can carry up to three million eggs that when released will stick to submerged vegetation (MAISRC 2023). Common carp continue using littoral regions throughout their life cycle as nursery and foraging habitats (Penne and Pierce 2008). A combination of early sexual maturation (at 2-3 years old), rapid growth, and ecological plasticity contributed to the expansion of common carp populations since their introduction to Ontario in the 1800s (Cole 1905; Weber and Brown 2009). They are mechanically destructive, as their reproductive and foraging behaviours involve the uprootal and destruction of aquatic vegetation, resulting in impaired water quality and reduced habitat for native species (Weber and Brown 2011). In high densities, common carp can completely alter shallow-lake systems from a clear state, dominated by submergent vegetation (oligotrophic), to a turbid state, dominated by phytoplankton (eutrophic) (see alternate equilibrium theory by Scheffer et al. 1993; Pearson et al. 2019), with the resultant degraded habitat conditions negatively affecting the abundance and richness of native fishes.
(mostly sight predators and piscivores; Weber and Brown 2011; Vilizzi and Tarkan 2015; Kopf et al. 2018). For example, researchers estimate that over 70% of lakes in southern Minnesota (USA) have lost their plant cover and suffer from resultant algal blooms due to common carp foraging activity (MAISRC 2023). Since their initial introduction 200 years ago, common carp have proliferated throughout the RCW and can be found in most reaches of the system and in abundance in shallower, riverine environments. The habitat needs of many native fish species – in particular, species that are phytophilic – in the RCW overlap with those of common carp. Two recreationally important fish species of particular concern include northern pike and largemouth bass as these species require the same shallow, heavily vegetated habitats that common carp favour (and often disturb/destroy) (Gertzen et al. 2017). Common carp may be driving native gamefish to seek out alternate, potentially less favourable habitats, though the degree of competition for space and resources is unknown.

The round goby is a small (25 cm maximum total length), aggressive, demersal fish that has very successfully invaded the Laurentian Great Lakes and was recently discovered to have colonized a discrete central portion of the RCW in 2019. The first round goby was observed in Lake St. Clair, Michigan, USA in 1990 and thereafter spread throughout the Laurentian Great Lakes and many connected tributaries (Gutowsky and Fox 2012). The pelvic fins of round goby are fused into a suction disk with some adhesion ability and they lack a swim bladder (hence their demersal nature) (Nikolsky 1954; Balážová-L’avrščiňková and Kováč 2007). Although they can be difficult to distinguish from native sculpins and darters in Ontario freshwaters, round goby have a prominent posterior black spot on their first dorsal fin (Kornis et al. 2012). Round goby exhibit sexual dimorphism via their urogenital papilla which in females is broad and blunt and in males is long and triangular (Charlebois et al. 1997), however males specifically may display additional sexually dimorphic features as “guarder males”. Round goby males express an alternative reproductive tactic with two morphs: 1) the guarder male, which are territorial, larger males that invest in secondary sexual traits that support their securement of females via competition, and 2) the sneaker male, also referred to as “parasitic males”, which are smaller, avoid physical competition and do not court females, and instead invest in traits that improve their chance of fertilizing eggs via sexual coercion of sperm competition (Oliveira et al. 2008). The sexual secondary characteristics guarder males display makes them easy to identify and include larger, darker, wider heads and swollen cheek pads (McCallum et al. 2019). Sneaker males are smaller and display a more mottled coloration, use stealthy tactics to sneak into nests and cuckold caring males, and will even adopt female tactics to gain access to spawning events (Gross 1982; Neff and Gross 2001; McCallum et al. 2019). During their extended reproductive season, that occurs at water temperatures from 9-26°C (usually from late April to early September in Ontario; Charlebois et al. 1997; McCallum et al. 2019), females will deposit their adhesive eggs (up to 10,000 eggs in a single batch; MacInnis and Corkum 2011) onto a fixed overhead surface within a cavity and is capable of spawning multiple times within the
season (Miller 1984). Round goby select largely for rocky and boulder substrate habitats that offer complex microhabitats for shelter and nest building (McCallum et al. 2019), however they can be habitat generalists (Henseler et al. 2020). Numerous studies detail the ecological and economic impacts of round goby invasions, ranging from public health concerns as a vector in avian botulism to competitive exclusion and/or predation of native species (Balshine et al. 2005; Krakowiak and Pennuto 2008; Kornis et al. 2012).

The RCW is comprised of various environments, many of which vary within themselves in respect to size and depth (e.g., larger, deeper lakes versus smaller, shallower lakes). It is generally assumed that animals distribute themselves over space and time to maximize fitness (Huey 1991), typically as it relates to acquiring resources (e.g., reproduction, food) and to avoid predation (Peat et al. 2016). Fish that live in aquatic systems, which are multidimensional environments, can additionally distribute themselves laterally and vertically (i.e., depth use) to access resources and seek out suitable habitat and/or thermal regimes. Lockstations in the RCW, which fragment the longitudinal waterway into reaches, are restricting to some degree native and invasive fishes to their resident reach (and the available habitat within) to carry out their life history. Selective fragmentation of lockstations in the RCW may offer a solution in minimizing invasive species with no impact to, and theoretically support, native species. Although telemetry studies of fish related to lock-and-dam infrastructure are uncommon, they show promise in supporting management decisions (e.g., Wilcox et al. 2004; Kim and Mandrak 2016). Research has promisingly shown that movement ecology data compounded with lockstation operations, for both common carp (Raboin et al. 2023) and goby (Bergman et al. 2022), can support targeted control and/or preventative efforts. Though few studies have undertaken large-scale tracking of invasive and native fishes to provide the evidence necessary for selective fragmentation strategies in waterways, the work that does exist (Tripp et al. 2014; Finger et al. 2020; Fritts et al. 2021) suggests credible potential in mitigating the introduction and dispersal of invasions.

1.4. Thesis purpose and objectives

In collaboration with Parks Canada (the primary stewards of the RCW), my doctoral research combines two fish tracking methods (acoustic telemetry and mark-recapture) with ecohydraulics and management consultations to examine system connectivity and movements of native and invasive fishes in the RCW. Specifically, we investigated species- and season-specific barrier passability and seasonal movements, and, when possible, combined these data with hydraulic measurements, environmental data, and lockstation operations. Our ultimate goal is to produce the necessary evidence for managers to use in conservation actions and management strategies, whether that be protecting native fish critical habitat(s) or a selective fish passage model. We used acoustic telemetry to determine finer-scale
movements related to habitat use, connectivity, and residency, while mark-recapture data offered broader-scale insights into inter-reach movements. Fish movements were monitored over five years (2018-2023), which includes the anthropause (i.e., the global lockdown in 2020; Rutz et al. 2020) during the COVID-19 pandemic. Thus, we additionally sought to evaluate potential effects of the anthropause on fish behaviour and connectivity.

Notably, this research could proactively defend against future invasions and inform strategies to manage existing invasions. If invasive carps do enter the Laurentian Great Lakes, the spread may be rapid for Lakes Michigan, Huron, and Erie; however, given the St. Mary’s Lock & Dam Complex and Welland Canal separates Lakes Huron and Superior and Lakes Erie and Ontario, respectively, managers could employ preventative and intentional fragmentation strategies at those barriers. Our goal is for common carp to serve as at least a partial analogue to invasive carps, and thus as a proxy for mitigation against a future invasion. Additionally, limited research exists on the fine-scale movement patterns of round goby; as pioneers researching their spatial ecology in the RCW, we not only work to close a knowledge gap, but additionally use telemetry results to inform potential management actions that can prevent further dispersion. Information generated from this work offers management recommendations to the Government of Canada to protect the interconnected cultural, natural, and social values of Canada’s Rideau Canal Waterway. Finally, this work is topical at a global scale given that inland waters are now explicitly included in the new Global Biodiversity Framework (Targets 2 & 3; see https://www.cbd.int/gbf/targets/).

Chapter 2: Historical, contemporary, and future perspectives on a coupled social-ecological system in a changing world: Canada’s historic Rideau Canal

2.1. Abstract

Anthropogenic waterways and canal systems have been part of the cultural and natural landscape for thousands of years. As of the late 20th century, more than 63 000 km of canals exist worldwide as transport routes for navigation, many with barriers (e.g., locks, dams) that fragment the system and decrease connectivity. Fragmentation alone can have negative implications for freshwater biodiversity; by isolating populations and communities, other human-mediated disturbances associated with canals like poor water quality and invasive species can exacerbate these negative effects. As such, the capacity of these interconnected freshwater systems to support biodiversity is continuously degrading at a global level. One critical, highly complex issue that unites canals worldwide is the challenge of governing these systems in a holistic, unified way to both protect biodiversity and preserve historical elements. Managing historic canals involves multiple objectives across many agencies and stakeholders, often with different or conflicting objectives. Here, we use the Rideau Canal, a UNESCO World Heritage Site and National
Historic Site of Canada, as a case study to demonstrate the importance of considering canals as social-ecological systems for effective and efficient governance. Historic canals are integrated systems of both humans (social) and the environment (ecological), linked by mutual feedbacks and coevolution, and must be managed as such to achieve conservation goals while maintaining commemorative integrity. We discuss the history of the Rideau Canal and its current governance, biodiversity in the waterway, different threats and issues (user conflicts, aquatic pollution, shoreline development, water management, species at risk, and invasive species), and conclude by outlining ways to address the challenges of managing it as a coupled social-ecological system. We present different research needs and opportunities that would enable better management, though above all, we propose a shift from the current governance structure – which at best can be considered “patchwork” – to a coordinated, multi-scalar and multi-stakeholder governance regime such that the Rideau Canal can be maintained for its historical integrity without compromising biodiversity conservation. Given that canals are now pervasive worldwide, this article is not only topical to the Rideau Canal, but also to other waterways in Canada and beyond.

2.2. Introduction

For thousands of years, humans have modified natural waterways (e.g., lakes, rivers) and created others where they did not exist. The first canals constructed were done so by Mesopotamians around 4000 BC, where waters from the Tigris-Euphrates river system were diverted for irrigation, drainage, household water supply, and navigation (Bjornlund and Bjornlund 2010; Geyer and Monchambert 2015). Canals were commonly built by various ancient empires across the globe, primarily for urban and agricultural water consumption and for transportation, extending from ancient times to British “canal mania” (Hadfield 1986; Lin et al. 2020). To this day, canals continue to be constructed to support human development in both rural and urban areas (Lin et al. 2020). Beyond these uses, canals also provide cultural, aesthetic, and economic values through historical heritage, cultural identity, and recreational opportunities (Walker et al. 2010; Hijdra et al. 2014; Guo et al. 2016). Though some canals still serve their original purpose, many historic canals have been either abandoned, partially buried or drained, or are now used and managed for other purposes. Managing historic canals today often includes objectives like conservation of heritage value and protecting ecosystem services and biodiversity, which are beyond their original development and economic functions and services (Arlinghaus et al. 2002; Walker et al. 2010; Guo et al. 2016). Many canals are now used in ways that were not envisioned when they were built and thus are not always optimally designed to fulfil their new roles.

The Rideau Canal in Ontario, Canada, exemplifies the social-ecological challenges facing many canals and waterways today. In the Rideau Canal, there is a legal requirement to maintain navigation and
protect the commemorative integrity of the system, including historical infrastructure and associated landscapes, and contemporary issues related to biodiversity. The Rideau Canal is also faced with competing user interests, external development pressures, and complex governance. Waterways like the Rideau Canal are coupled social-ecological systems (Gunderson et al. 2017; Llausàs et al. 2020) – that is, complex adaptive systems where social and biophysical agents interact at multiple temporal and spatial scales (Ostrom 1990; McGinnis and Ostrom 2014). Recognizing that canals are coupled social-ecological systems is intuitive because the natural environment – and how humans use it – is inherently linked to the built environment, and because it acknowledges that these are difficult systems to govern, particularly in the face of change. Changes can come in many forms, though relevant to the Rideau Canal is the fact that human behaviour (e.g., increased development in watersheds, continued use of canals for recreation) and climate change (e.g., Perry et al. 2010) are major drivers that will shape the complex interactions in social-ecological systems in the coming years. The challenge lies within the need to strike a balance between conservation of heritage value and supporting the ecosystems within; for the Rideau Canal, protection of ecosystem services and biodiversity is more an inadvertent consequence of this waterway being protected for navigation over the past 100 years. It is not the current primary management focus, nor was conservation considered by engineers during canal construction in the 1830s.

The environmental status and capacity of canals and other artificial waterbodies depend on their history (e.g., original landscape, design/structure, purpose, and associated management) and ongoing management (Clifford and Heffernan 2018; Lin et al. 2020). Thus, we use the Rideau Canal as a case study and explore its history, current state, and future as a prime example of a coupled social-ecological system. This article is a narrative synthesis; its purpose is to detail ongoing social-ecological issues relevant to conservation and management of the system, and serve as a template for other canal managers worldwide. We describe the system and its interconnected components, consider challenges and opportunities for the future, and identify research needs. To conclude, we provide information to managers on ways to improve the Rideau Canal’s resilience for its continued benefit to users and the environment. Although each canal system has its own unique set of conditions and history, many aspects of the Rideau Canal are analogous to other waterways globally, and thus the information detailed below is useful to managers not only in Canada but worldwide.
Figure 2.1. Overview map of the Rideau Canal. The black channel represents the Rideau Canal, 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 the 23 operating lockstations that interconnect the system. Newboro Lockstation, indicated by the green star, is the “isthmus”, representing 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. Base map source: Government of Canada 1:250 000 NTS
maps — 31B (Ogdensburg), 31C (Kingston), and 31G (Ottawa). Locations of lockstations were plotted from the relevant 1:50 000 NTS maps (31B/13, 31C/8, 31C/9, 31C/16, 31G/4, and 31G/5).

2.3. History of the Rideau Canal

2.3.1. Purpose and construction

The Rideau Canal was conceived and designed by the Ordinance Department of the British military and opened in 1832. Prior to the start of the railway era in the 1840s, waterways and canals were a key method of transportation in North America. The Rideau Canal is located in eastern Ontario and is a 202 km continuous route that connects the Ottawa River at Canada’s capital city of Ottawa to Lake Ontario at the city of Kingston (Fig. 1). It was originally built to enable trade and military defence by the British in the face of military pressures from the United States (Fig. 2E; Tulloch 1981). By the late 1800s, the Rideau Canal began to transform into a recreational waterway (Acres 1994; Forrest et al. 2002). Today, in addition to its purpose as a recreational waterway, the Rideau Canal serves as a heritage tribute to Canada’s early history.

Colonel John By of the British Royal Engineers led the construction efforts (Fig. 2D). The first step involved extensive surveying of the region, conducted on foot and by canoe, and began as early as 1783 to identify navigation impediments (Passfield 1983). The Rideau Canal was constructed largely by hand, with the use of small tools and stock animals to haul heavy materials. The completed Rideau Canal includes a series of rivers, lakes, and constructed channels connected by lockstations that form the continuous waterway. The route includes ~19 km of human-built canal cuts with 45 locks at 23 lockstations, many of which have adjacent water-control dams (Legget 1986). Many lockstations included mills (lumber, grist, and carding), which were later replaced by hydroelectric facilities (https://www.pc.gc.ca/en/lhn-nhs/on/rideau/histoire-history/histoire-decluse-lock-history). Even today, most lockstations are operated by hand and do not rely on automated systems to drain and fill locks for navigation. From Lake Ontario at Kingston, the Rideau Canal rises 50.6 m to the summit at Newboro Lockstation and then descends 83.8 m to the Ottawa River at Ottawa (Fig. 1). Although most of the canal system is shallow (several metres deep), there are deeper areas within some of the larger lakes (e.g., Big Rideau Lake, maximum depth 91 m). The system operates based on the use of European slackwater technology (see https://www.pc.gc.ca/en/docs/r/on/rideau/wlh-lhm/chap3/chap3C), which exploits the existing natural lake and river reaches and relies comparatively little on constructed reaches (only 9% of total canal distance). Using the natural local environment and its waters to develop a canal system for human use only emphasizes the interconnectedness of the social and ecological components in the Rideau Canal. Extensive investments have been made to preserve heritage components of the
system via restoration of masonry and wooden construction materials (Narduzzo and Naudts 1994; Parks Canada 2012). See Fig. 2 for present-day and historical images of the Rideau Canal.

2.3.2. Historical governance and management

From 1856 to 1936, various jurisdictions were responsible for the Rideau Canal as a commercial transportation corridor. In 1925, the Rideau Canal was recognized by the (Canadian) federal government as a National Historic Site of Canada (Charron et al. 1982). The federal agency Transport Canada held primary responsibility for managing the Rideau Canal from 1936 to 1972 (Charron et al. 1982). In 1972, Parks Canada (which was then part of the Department of Indian and Northern Affairs) became the primary stewards of the Rideau Canal, after which there was a marked shift towards recreational use (Charron et al. 1982). Parks Canada promoted the unique engineering of the Rideau Canal and its connectivity between Ottawa and Kingston as a tourism and recreational boating destination (Charron et al. 1982). The Canadian (federal) and Ontarian (provincial) governments signed an agreement in 1975 outlining a plan for development and land use, and established jurisdictional responsibilities (Charron et al. 1982). The federal government was to manage navigation, water flows, recreation, historical and cultural heritage, while responsibilities pertaining to natural resource management were divided among municipal, provincial, and federal organizations (Fig. 3). Below, in the “Current governance and management” section, we describe the different governing bodies managing the Rideau Canal and their responsibilities.
Figure 2.2. Historical and present-day images of the Rideau Canal. Images on the left (A-C) illustrate modern day usage of the Rideau Canal; images on the right (D-F) illustrate historical use. (A) The multi-flight lockstation in Canada’s capital city, Ottawa, represents the northern terminus of the Rideau Canal and consists of 8 locks in flight. (B) Edmonds Lockstation, located in Smiths Falls, Ontario, and most other Rideau Canal lockstations are still manually operated. Note the hand crank in the far left and right corners, which lockmasters use to open and close gates and fill and empty the lock chamber. Additionally, this lockstation marks the location of the recently discovered invasive round goby (Neogobius melanostomus). (C) Each winter, the National Capital Commission transforms the canal into the Rideau Canal Skateway. Known as the “world’s largest skating rink”, the Skateway extends for 7.8 km through downtown Ottawa and can bring in over one million visitors in a single season. (D) Colonel John By of the British Royal Engineers (on far right) led construction of the Rideau Canal. Here, he watches over building efforts in 1826. (E) This 1838 painting by Philip John Bainbrigge displays military use of the Rideau Canal as a company of Royal Marines passes through Jones Falls on their way to
Kingston. (F) Image of a steamboat docked at the wharf at Entrance Bay, just outside of the Ottawa Lockstation, sketched between 1850 and 1855. Image credits: (A) Swanee Payne, distributed under a CC BY-SA 3.0 license; (B) Photo taken by Kate Neigel; (C) Saffron Blaze via http://www.mackenzie.co, available from Wikimedia Commons; (D) Charles William Jefferys, Imperial Oil Collection series, Library and Archives Canada, accession number 1972-26-795, C-073703; (E) Philip John Bainbrigge fonds, Library and Archives Canada, accession number 1983-47-44, C-011835; (F) John Henry Walker, available from the McCord Museum under access number M930.50.7.868.

2.3.3. Ecological implications of construction and operation

Prior to construction, the area surrounding the Rideau Canal was composed of mixed woodland and wetland (Karst and Smol 2000), with original inhabitants in the area including Anishinaabe, Omàmiwinini (Algonquin), Haudenosaunee (Iroquoian Confederacy), and Huron-Wendat peoples (Native Land 2020). The lakes and rivers in the region were used as important traveling and trading routes by Indigenous peoples, and construction of the Rideau Canal had a significant impact on their unique relationship with the land by disrupting these routes. The initial expansion of European colonization in the 1780s was accompanied by ecosystem alteration, including the construction of small dams and mill ponds (Karst and Smol 2000). Construction of the Rideau Canal incurred profound changes to the local environment. System-wide flooding is clearly delineated in sedimentary records via changes in sediment physical characteristics (Sonnenburg et al. 2009), as well as changes in aquatic organism and pollen assemblages (Karst and Smol 2000; Forrest et al. 2002). Prior to construction of the Rideau Canal, the “Rideau Route” existed across three watersheds: Rideau River, Gananoque River, and Cataraqui River. The latter two – the Gananoque and Cataraqui – were heavily altered, transforming a delta-like wetland into a constructed river, and forming a new connection between the upper (Rideau) and lower (Cataraqui) watershed (see Watson 2006). Additionally, the construction of dams and mills further fragmented the Rideau and Cataraqui rivers, creating barriers to passage and increasing the possibility of blade strike for migratory species (e.g., American eel (Anguilla rostrata), which have not been observed in the Rideau Canal since 2000; D.A. Algera, K. Neigel, K. Kosziwka, A. Abrams, D. Glassman, J. Bennett, S. Cooke, and N. Lapointe, unpublished data). Several lakes were created (e.g., Colonel By Lake) or greatly expanded (e.g., Bobs Lake, Opinicon Lake) during construction. The magnitude of ecological change appears to have differed across lakes, with biological indicators in deeper lakes, like Big Rideau Lake, suggesting less change compared to shallower lakes, like Lower Rideau Lake (Forrest et al. 2002). Indicators of terrestrial change suggest strong local human impacts: pine (presumably white pine, Pinus strobus) pollen diminished in the system during the construction period, while ragweed (Ambrosia), an indicator of open land, greatly increased (Karst and Smol 2000). Post-construction sedimentary records suggest gradual increases in nutrients, corresponding with increased housing.
development in the region during the early 20th century (Forrest et al. 2002), while terrestrial indicators suggest increased growth of secondary forest (Karst and Smol 2000).

Canal systems worldwide are widely recognized as conduits for invasive species (Kim and Mandrak 2016; Lin et al. 2020), and the Rideau Canal is no exception (see “Invasive species” section under “Threats and issues”). Key invasive species include Eurasian water-milfoil (Myriophyllum spicatum), which was first observed in the Great Lakes in the 1960s and has spread rapidly through connected waterways (Borrowman et al. 2014). Zebra mussels (Dreissena polymorpha) have also expanded rapidly, colonizing most of the Rideau Canal by 2015 (Martel and Madill 2018). More recently, the round goby (Neogobius melanostomus) was discovered to have colonized portions of the Rideau Canal, having first been observed in the system in 2019, and are now dispersing rapidly (Fig. 2B; J.N. Bergman, personal observations; McIntosh Perry Consulting Engineers Ltd. 2019). Connecting the watersheds facilitated new corridors and habitats, which results not only in new invasions, but also encourages biotic homogenization (i.e., the replacement of local biotas with non-indigenous species, resulting in increased genetic, taxonomic, and (or) functional similarities over time across regions; McKinney and Lockwood 1999; Olden and Rooney 2006). Biotic homogenization is not unique to the Rideau Canal (Rahel 2007); this ecological concept impacts canal systems worldwide including but not limited to the Nicaragua Canal (Nicaragua; Härer et al. 2017), the Chicago Sanitary and Shipping Canal (United States; Kolar and Lodge 2000), the Suez Canal (Egypt; Galil 2000), and the Rhine-Main-Danube Canal (Europe; Leuven et al. 2009). Herein lies the ecological paradox of artificial waterways; they provide a novel connection between previously separated ecoregions or watersheds, therefore offering new (and potentially more suitable) habitat for native species, yet they also facilitate the introduction of non-native species and exotic pathogens (Leuven et al. 2009; Rahel 2013; Lin et al. 2020). In the Rideau Canal, the level of ecological and landscape connectedness is unknown and understudied, making successful conservation actions difficult to develop and apply.

2.4. The Rideau Canal today

2.4.1. Tourism and use patterns

The primary use patterns and associated management of the Rideau Canal changed over time from defense and development to recreational activities and heritage preservation (Parks Canada 2017a), similar to many historic canals around the world (Lin et al. 2020). Beyond today’s management of navigation and water levels along the entire corridor, the Rideau Canal is used for recreation by local residents and tourists. Parks Canada estimates that more than one million people visit the lockstations annually, while another 1.4 million people visit Ottawa in the winter to recreate on the Rideau Canal Skateway (which is promoted as the largest outdoor skating rink in the world; Fig. 2C) each winter (Parks
Common activities on the Rideau Canal include both nonmotorized (e.g., canoe, kayak, stand-up paddleboard, windsurfing, sailboats) and motorized vessel use (e.g., fishing boats, water ski and wakeboard boats, seadoos), and land-based activities along the shores like hiking (e.g., Rideau Trail and Cataraqui Trail), picnicking, camping, swimming, fishing, and wildlife viewing (Donohoe 2012). There are several resorts and fishing camps along the Rideau Canal, as well as housing developments.

Not only does the history and culture of the Rideau Canal attract visitors, but the natural landscape and environmental features do as well. This contributes to the social-ecological nature of a system whose marketing successes rely not only on local partnerships, but also on sustaining a healthy freshwater ecosystem (Donohoe 2012).

In 2005, an economic analysis revealed that the Rideau Canal itself contributes more than $24 million to Canada’s national GDP and sustains over 600 full-time jobs (Parks Canada 2005). One method of quantifying and monitoring canal use is through the number of boats locked on a daily and annual basis. In 2019, there were 61,145 total vessel passages through locks; in 2020, only 44,141 vessel passages occurred likely as a result of COVID-19 restrictions that decreased tourism (see http://www.rideau-info.com/canal/statistics.html). Nevertheless, lockages alone do not provide a full picture of use or boating pressures facing the Rideau Canal given that many reaches can be accessed by boat ramps (i.e., lockages not required). Ottawa’s population in 2021 is estimated at 1.4 million people and is expected to continue growing (World Population Review 2021), which will presumably lead to increases in use and urban development pressures in the watershed. Investigating demographic changes will be important to target the right people with policies and programs. While tourism activities may be economically profitable, and in some ways socially desirable, they can have negative or positive environmental impacts depending on how they are organized. There is a need to better understand the various use patterns, tourism priorities, and stakeholder perspectives on these patterns and priorities to balance social and ecological needs in the system. Surveying the public and conducting interviews could help better understand the diversity of interests and values among stakeholders like community groups, businesses, and environmental organizations.

2.4.2. Current governance and management

Water resource management is recognized globally as challenging, especially when governance regimes are not cooperative or collaborative, and most notably in the context of urban waterways that have ecological importance and are also sources of human welfare (Naustdalslid 2015; Chikozho and Mapedza 2017; Cooper et al. 2017; Muneepeerakul and Anderies 2017; Schweizer 2017; Kattel et al. 2021). Managers of the Rideau Canal (and other Ontario waterways) are tasked with water management, navigation, and the maintenance of aging infrastructure, with development and
construction on a mix of private and public properties. They must additionally consider energy generation (hydropower), fisheries, water quality, and tourism and economic activities while ensuring the protection of cultural, historical, and environmental heritage. Governance of the Rideau Canal is complex because it encompasses not only the actions of different levels of government, but also other actors like community groups, nongovernmental organizations, and businesses (Lemos and Agrawal 2006) (Fig. 3). Parks Canada has ownership and jurisdiction over all in-water (i.e., the bed of the Rideau Canal including its lakes and rivers) and shoreline works built in, on, or over the system (Parks Canada 2017b), while adjacent lands and the watersheds are privately owned or under other jurisdictions like municipalities or the provincial government. The Rideau Canal spans 13 municipalities and counties, and two watersheds (the Cataraqui River watershed and the Rideau River watershed), with their respective Conservation Authorities (the Cataraqui Conservation Authority (CC) and the Rideau Valley Conservation Authority (RVCA)), and is regulated by a variety of legislative acts, regulations, and policies from multiple provincial and federal authorities. As such, the governance structure of the Rideau Canal can be described as “patchwork”, as it is complex and at times unclear, characterized by overlapping jurisdictions and coupled with many stake-holders that may have competing interests (Van Tatenhove 2013). We outline the various governing bodies, associated management organizations, relevant legislation, and tasks of each governing body in Fig. 3 and in the online Supplementary material, Table S11. Similar governance circumstances (i.e., jurisdictional fragmentation and multi-layered governance) can be found in other historic canals, such as the Grand Canal in China (Wang 2012).

Governance of the waterway also includes several First Nations. Parks Canada engages with the Algonquins of Ontario, the Haudenosaune (Mohawks of Bay of Quinte, and the Mohawk Council of Akwesasne), Alderville First Nation, and the Williams Treaties First Nations Signatories, whose territories intersects with the Rideau Canal. Parks Canada has stated its commitment to growing their relationship with Indigenous communities and recognition of the significant pressures that communities may have due to limited resources and external pressures. Engagement and consultation activities undertaken by Parks Canada with these First Nation groups includes management planning, advisory committees, project input, and operational interactions (see https://www.pc.gc.ca/en/agency-agency/aaia; Fig. 3).

As the primary stewards of the waterway, Parks Canada also engages with stakeholders at different levels ranging from full and occasional engagement to “one-way” information-sharing. The Rideau Canal National Historic Site Management Plan produced by Parks Canada in 2005 was due to be updated in 2015; it is currently being reviewed in a multi-year process which includes nonmandated engagements with key stakeholders and mandated (i.e., required by law) consultations with the public and Indigenous rights-holders. The new plan aims to establish a vision for the waterway with clear, measurable targets.
that would facilitate progress-tracking and keep the agency accountable. Parks Canada operates under the Parks Canada Agency Act and Historic Canals Regulations whereby their main management focus is to maintain the commemorative integrity of the Rideau Canal and manage visitor use and tourism – this focus aligns with some stakeholders, while others have different priorities. For example, the town of Smiths Falls embraces tourism and there are partnerships with “Le Boat”, a cruising company that arrived in the town in 2018. Because of fragmented and multi-layered governance, the Rideau Canal is difficult to manage in a unified way, with consequences for both environmental governance and ecological health (Bakker and Cook 2011). We describe this situation, which can undermine natural resource management of the Rideau Canal, as a social-ecological mismatch between (1) the connected ecosystem and watershed boundaries and (2) the fragmented social-political structure that governs the system (Sayles 2018).

Research on the various perspectives and interests of stakeholders involved in management is necessary to better understand this complex social-ecological system and improve governance and management (see examples of historic canal management in the Netherlands (Hijdra et al. 2014) and Spain (Llausàs et al. 2020)). Considering stakeholders’ passion and enthusiasm for the Rideau Canal, and their involvement in community science (see section that follows: “Case study - lake associations”), research on how to best engage the plurality of actors involved and mobilize their knowledge about the system in decision-making and policy processes is crucial. Research findings indicate that stakeholders want more opportunities to participate in governance and inform environmental policy (Mistry 2020). Upcoming research should help identify opportunities to improve governance through social-ecological alignment that allows for holistic management of the system.

Case study - lake associations

Volunteer residents and cottage owners around the Rideau Canal unite through their love of the water to create lake associations. These local groups play various roles as stewards in communities along the waterway by educating residents through newsletters and conferences, participating in community science, monitoring the state of their lakes, contributing to recreational programming, and promoting environmental awareness (Rees 2014). Lake associations also foster relationships among lake residents, users, and partners. They work with each other as well as other community groups, scientists, regional groups (e.g., Federation of Ontario Cottagers’ Associations), and governmental entities like municipalities, Parks Canada, and Conservation Authorities. While lake associations are well placed to support and participate in ecological research, more could be known about their role in communities and collaborative governance initiatives.

2.4.3. Biodiversity in the Rideau Canal
Despite comprising only <1% of the water on Earth, freshwater ecosystems host remarkable biodiversity. A global inventory revealed that freshwater ecosystems hold approximately 10% of Earth’s described species, including one-third of all vertebrates (Balian et al. 2007; Strayer and Dudgeon 2010). The Rideau Canal is a biodiverse freshwater system, and has been described as having one of the most diverse fish assemblages (107 documented fish species; Coad 2011) in Canada (Poulin 2001; Parks Canada 2005). Although local fish communities in most regions are characterized by warm-water species (e.g., pumpkinseed (Lepomis gibbosus), bluegill (Lepomis macrochirus), largemouth bass (Micropterus salmoides); Walker et al. 2010), the canal system is also home to cool-water (e.g., smallmouth bass (Micropterus dolomieu), northern pike (Esox lucius)) and cold-water (e.g., lake trout (Salvelinus namaycush)) species (thermal guild assignment as per Gertzen et al. (2017)). The Rideau Canal also supports one of the few wild urban muskellunge (Esox masquinongy) fisheries in North America (Gillis et al. 2010), as well as species at risk across several taxa (e.g., bridle shiner (Notropis bifrenatus) (special concern); eastern milksnake (Lampropeltis triangulum) (special concern), least bittern (Ixobrychus exilis) (threatened); COSEWIC 2020; see “Species at risk” section). Similarly, high biodiversity has been noted in other canal systems (Lin et al. 2020). For example, Dorotovicová (2013) found canals in Slovakia to be macrophyte biodiversity hotspots, and Smith et al. (2004) discovered that the Panama Canal, which connected isolated freshwater communities in Pacific and Caribbean watersheds, resulted in a local increase in freshwater fish species richness with no species extinctions.

In 2001, the Canadian Museum of Nature partnered with government agencies, educational institutions, and community groups to conduct a three-year multidisciplinary study, the Rideau River Biodiversity Project, to evaluate biodiversity in the Rideau River (Poulin 2001). Although the project solely examined the Rideau River (the northern 100 km portion of the Rideau Canal), researchers identified close to 600 species, including the discovery of several species previously unknown to inhabit the Rideau Canal (e.g., freshwater drum (Aplodinotus grunniens); Phelps et al. 2000). Their results illustrate a high diversity across taxonomic groups: 314 phytoplankton species, 59 aquatic plant species, nine mussel species, 128 invertebrate species, 35 fish species, 19 amphibian and reptile species, and 20 waterfowl species. It should, however, be noted that several of the species identified in the Rideau River Biodiversity Project are considered invasive (see “Invasive species” section). This project is an example of a successful collaborative initiative that could guide future efforts in the Rideau Canal, as it brought together various social actors to attend to ecological components of the system.
Figure 2.3. Horrendogram of the Rideau Canal governance structure. A “horrendogram” is a visual tool used to map and describe complex relationships. Here, we present the many organizations governing the biotic and abiotic elements of the Rideau Canal. The Rideau Canal is governed by six different “governing bodies”: (1) the Parks Canada Agency (a federal Canadian organization), (2) other federal departments (Transport Canada (TC), Environment and Climate Change Canada (ECCC), the Canadian Council of Ministers of the Environment (CCME), Fisheries and Oceans Canada (DFO), the Impact Assessment Agency of Canada, and the Canadian Food Inspection Agency (CFIA)), (3)
provincial groups (the Ministry of Environment, Conservation, and Parks (MOECP), the Ontario Ministry of Natural Resources and Forestry (MNR), Public Health Units, the Ministry of Heritage, Sport, Tourism, and Culture Industries (MHSTCI), the Ministry of Agriculture, Food, and Rural Affairs (OMAFRA), and the Ontario Provincial Police (OPP)), (4) Conservation Authorities (the Rideau Valley Conservation Authority (RVCA) and the Cataraqui Region Conservation Authority (CC)), (5) municipalities (including the Municipal Engineers Association (MEA), and often working with provincial groups like OMAFRA, MOECP, the Ministry of Municipal Affairs and Housing (MMAH), and the Ministry of Health and Long-Term Care (MOHLTC)), and (6) First Nations. The different organization(s) that manage the same element under each governing body is written in white font inside of the ring. This horrendogram is meant to visually describe the six governing bodies and associated organizations regulating different elements of the system, whether legally mandated to or not. Each circular ring represents a biotic or abiotic element of the Rideau Canal. Elements have been color-coded to clarify themes: blue indicates Management of Waters (Water Management, Hydroelectricity, Navigation, Riverbed Administration), red indicates Wildlife Management (Fish Habitat & Sanctuaries, Aquatic Vegetation Management, Species at Risk, Invasive Species), yellow indicates Outreach (Engagement & Consultation, Tourism & Recreation, Environmental Education), purple indicates Fisheries (Recreational Fisheries, Commercial Fisheries), teal indicates Law Enforcement & Safety, gray indicates Reserve Lands, and green indicates Impact Assessments (Environmental Assessment, Land Use Planning). Dotted lines do not indicate that governing body manages that element; it is to simply make clear the continued path of the elements’ ring. See Supplementary Table S11 for a detailed list of each figure element, governing bodies, organizations, legislation and documents, and the actions and (or) purpose of each governing organization. *The CCME is an intergovernmental organization in Canada with members from the federal, provincial, and territorial governments. **OMAFRA is a provincial group; however, municipalities work with OMAFRA for permitting.

2.5. Threats and issues

2.5.1. User conflicts

Conflict can be common in social-ecological systems like historic canals, and often arises because of the various interests and users (Wang 2012; Lin et al. 2020; Llausàs et al. 2020). Conflicts are magnified with increasing numbers of users, and when users become more specialized and polarized in their specific outdoor pursuits (Jones 1996). In some reaches of the Rideau Canal, conflict arises in periods of high use during which the activities of some groups impede the activities or enjoyment of others (Gramann and Burdge 1981; see “Case study - bass fishing tournaments”). These issues can be magnified when some users are also landowners (e.g., cottagers), who may feel that their property rights
outweigh the access rights of occasional users (e.g., day visitors). Conflict can also occur within groups. For example, research has shown that recreational anglers are a heterogeneous group and that there is often more conflict within that sector than between it and other sectors (Arlinghaus 2005). Differences in environmental values and individual behaviours among recreational fishers can lead to conflict (Arlinghaus 2005). Such conflicts can be mitigated by increasing opportunities for shared understanding via communication, mediated by government or independent parties (Graefe and Thapa 2004; Bruckmeier 2005). Further research on the environmental values and governance expectations of stakeholders could help inform the design of communication mechanisms and help determine common values and objectives among users.

Case study - bass fishing tournaments

Big Rideau is the largest lake within the Rideau Canal and is among the most heavily fished water bodies in eastern Ontario (OMNRF 2020). The OMNRF, a provincial government agency, sets fishing regulations and manages fisheries (excluding species at risk) for the Rideau Canal. Bass fishing tournaments occur regularly throughout the open fishing season and sometimes multiple events take place on the same day. Tournaments tend to start and finish within close proximity to publicly accessible boat launches on the Rideau Canal. Shared space and resources associated with bass fishing tournaments (e.g., congestion at boat launches, large-scale fish displacement, noise, speed of bass boats), as well as the conspicuous nature of these events, fuels intergroup conflict that persists today (Kerr and Kamke 2003). Conflict has existed for decades (Schramm et al. 1991); however, there remains a need to better understand polarizing opinions. Research is required to examine user perspectives of bass populations and management in Big Rideau Lake. This information would be beneficial to strengthening consensus among user groups and thus diffuse intergroup conflict (Nguyen et al. 2016).

2.5.2. Aquatic pollution

Managing pollution, specifically from nonpoint sources, in freshwater systems is a “wicked problem” (Rittel and Webber 1973) that threatens water quality and security, ecosystem health and biodiversity, and consequently affects human livelihoods and wellbeing ranging from local to global scales (Patterson et al. 2013). Poor water quality in canals is a consistent theme worldwide and has been documented in New York canal systems (includes 12 major canals; Daniels 2001) and the Everglades canal system in the United States (Wan and Li 2018), the Mak Khaeng canal in Thailand (Wongaree 2019), the Cai Sao canal in Vietnam (Lan and Long 2011), the Taladanda Canal in India (Prusty and Biswal 2020), and the Kennet and Avon Canal in England (Neal et al. 2006), to name a few. In the Rideau Canal, water quality is largely impacted by chemical pollutants (Hamilton et al. 2011) and falls under the jurisdiction of municipal, provincial, and federal levels of government (Fig. 3; Charron et al. 1982). Chemical pollution
is most often the result of anthropogenic factors like wastewater inflow and surface runoff from agricultural and urban land, as well as older infrastructure and leaky septic systems (Forrest et al. 2002; Mistry et al. 2021). Water quality in the Rideau Canal varies spatially and is closely monitored by municipalities, public health units, lake associations, citizen science groups, Conservation Authorities, the Ontario Ministry of the Environment, Conservation, and Parks (MOECP), and Parks Canada, all who use a combination of biological and chemical indicators to monitor water quality and ensure the safety of its users (Fig. 3 and Supplementary Table S11; see Acknowledgements section for list of contributors). The example of water quality showcases the many overlapping jurisdictions that make social-ecological alignment a challenge in the Rideau Canal system. The Rideau Canal’s two Conservation Authorities, the RVCA and CC, use the community composition of benthic invertebrates as biological indicators of water quality, following the Ontario Benthos Biomonitoring Network protocol, which identifies certain groups of benthic invertebrates as being pollutant-tolerant or pollutant-sensitive (Jones et al. 2006). Phosphorus concentrations are another key indicator of water quality, where high levels of phosphorus are indicative of poor water quality (Schindler 1974, 2006). Its presence in excess quantities causes the system to become eutrophic, leading to algal blooms (i.e., noticeable accruals of algae; Reynolds and Walsby 1975). Harmful algal blooms are often formed by cyanobacteria algae, which are potentially harmful to users as some strains can produce toxic substances (Anderson et al. 2002; see “Case study - cyanobacteria blooms”). The use of recreational waterways relies on both indicators of water quality and the user’s perception of water quality (Steinwender et al. 2008; Artell et al. 2013). Users form perceptions of water quality based on physical characteristics like water clarity, smell, and general aesthetic of the waterfront which can be impacted by high nutrient levels and harmful algal blooms (Steinwender et al. 2008). In fact, residents and cottagers in the Cataraqui region (the lower portion of the Rideau Canal) have formed a group to better understand possible sources of nutrients and stakeholder perceptions of water quality (Mistry et al. 2021), and community science programs have been used to track the abundance of filamentous green algae. Maintaining good water quality in the Rideau Canal is a win-win situation that encourages tourism and economic activity in the region, while simultaneously supporting the health of the ecosystem (Smith et al. 2006). Further research on how to incorporate the results of community efforts in environmental management could help support a more collaborative form of governance.

Case study - cyanobacteria blooms

Cyanobacteria (also known as blue-green algae) are found naturally in all lakes and rivers (Backer et al. 2015). When conditions are favourable for these algae, they can form nuisance or harmful algal blooms (Nwankwegu et al. 2019). Cyanobacteria blooms are of particular concern as some strains produce cyanotoxins that can be harmful, or even fatal, to humans and other animals. Within the Rideau
Canal, cyanobacteria blooms can occur throughout most of the system if conditions are favourable, though blooms are most common in the southern sector of the waterway where historical wetlands were flooded to create lakes during canal construction (Karst and Smol 2000) and phosphorus concentrations are consistently high (>35 μg/L). Research is required to determine what historical water quality conditions were in these sections of the Rideau Canal to set realistic targets for water quality and to determine whether management actions, like increasing waterflow, can reduce cyanobacteria blooms. Setting reasonable expectations and actions may help ease social-ecological tensions brought on by blooms that hinder human activities like swimming. Given that the lakes within the Rideau Canal are also experiencing climatic warming (i.e., “longer summers”), the threat of more frequent and intense algal blooms has been heightened (Smol 2019). Collectively, the various organizations independently managing water quality in different portions of the system will need to work together to address and reduce point and non-point sources of pollutants (Fig. 3; see Supplementary Table S11 for list of managers).

2.5.3. Shoreline development

In historic canals close to human settlements, and that provide rich recreational opportunities, there is a social-ecological tension among shoreline development, preservation of commemorative integrity, and conservation of local biodiversity and ecological systems (e.g., the case of Grand Canal, China; Wang 2012). This is particularly the case in the Rideau Canal where Parks Canada has a suite of regulatory tools for guiding in-water and shoreline works; many factors are weighed when making decisions such as respecting the designation of the Rideau Canal as a National Historic Site, protecting heritage landscapes, minimizing environmental impacts, facilitating the permitting process, and providing clear coordinated guidelines, among others. These tools are meant to work in conjunction with land-use planning guidelines and permits from Conservation Authorities and municipalities that guide riparian and upland development. In rural areas, most development is from waterfront landowners that are usually seasonal users (e.g., cottagers). Typical waterfront development includes docks, boathouses, erosion controls, and aquatic vegetation management. Most development along shorelines in urban areas is historical, but there are several redevelopment projects and other changes in waterfront infrastructure that can have negative social-ecological impacts. Issues with shoreline development range from the aesthetic value and interest in maintaining historic character, through to concerns about freshwater biodiversity and ecosystem health. Parks Canada works closely with landowners and other development proponents to identify development practices that are most consistent with their regulatory framework and guiding principles (e.g., using natural materials, minimizing use of concrete and other hardened structures). Other agencies (especially Conservation Authorities) and organizations (e.g., Love Your Lakes Program co-led by Watersheds Canada and the Canadian Wildlife Federation) engage with
landowners and other partners in their collective goal to protect and enhance shoreline habitats. Watersheds Canada also uses homeowners that make efforts to naturalize their shorelines as champions of stewardship to encourage others to follow suit. In this manner, they are addressing the social values that intersect with ecological health. Further research is required to better understand how alteration of shoreline habitats affects water quality and other ecosystems services and how to use this knowledge to address conflicting social and ecological values of aquatic vegetation (e.g., approaching shoreline property owners who view weeds as undesirable to inform them on this vegetation’s ecological purposes; see “Case study - aquatic vegetation management”).

Case study - aquatic vegetation management

Macrophytes provide refuge to many species of invertebrates and fishes, and offer a wide array of ecosystem services (Jeppesen et al. 2012; O’Hare et al. 2018). The Rideau Canal and its associated lakes, wetlands, and tributaries host a wide variety of macrophytes, including both native and invasive species. Despite the ecological importance of vegetation, large dense beds of macrophytes, particularly canopy-forming native and, in the case of the Rideau Canal, invasive species like Myriophyllum spicatum, can be a nuisance to human activities such as boating, swimming, and angling. Macrophytes are subsequently managed by a variety of methods (Madsen 2000). On the Rideau Canal, Parks Canada directly removes macrophyte biomass by mechanical harvest when and where it impedes navigation, and indirectly by issuing permits allowing property owners to remove macrophytes over a 10 m x 30 m area adjacent to their shoreline (Parks Canada 2017c). Macrophytes may only be removed with a permit, following guidelines set out by Parks Canada (2017c) and in accordance with the Historic Canals Regulations (Minister of Justice 2017), as well as the Canadian Fisheries Act (1985). It is important that landowners and users of the waterway comprehend the positive role that macrophytes play in aquatic ecosystems so that they do not simply view them as weeds to be removed. It is critical we determine how shoreline alteration may be impacting water quality and local fauna, and provide outreach and educational programs for locals and stakeholders to share this knowledge and its social-ecological implications.

2.5.4. Water management

Managing water levels and flows to fulfil the requirements of multiple objectives is a challenge for canals and regulated rivers. Parks Canada manages and monitors water level and flow operations throughout the Rideau Canal to mitigate flooding, meet navigation requirements, fulfil fish and wildlife habitat objectives set out by provincial and federal regulations, and make various recreational activities possible (Parks Canada 2020a). They work closely with Conservation Authorities and the OMNRF (Parks Canada 2020a) to balance these interconnected social and ecological needs. There are numerous
regulated and unregulated channels and reservoirs that feed into the Rideau Canal, making water management challenging (e.g., the Tay River regulated by Bobs Lake Dam and Kemptville Creek regulated by Oxford Mills Dam; unregulated inflows including but not limited to the Jock River, Cranberry Creek, and Mosquito Creek).

Parks Canada water managers specify dam operations daily based on monitored water levels and river flow (both in the Rideau Canal and its tributaries), temperature and precipitation, and future weather forecasts (Parks Canada 2020a). To aid in operations, water level measurements were recorded manually by lock masters; however, in the last five years automated gauges, including 28 real-time water level, four real-time discharge, seven rain, five temperature, and four snow gauges, were set in place with manual measurements ongoing at four lock stations and three snow depth areas. In addition, there are Water Survey of Canada water level and flow gauges located near Ottawa and in various tributaries, maintained by federal agency Environment and Climate Change Canada (Water Survey of Canada 2020).

Weir and gate elevations are set at dams, and water allowances are regulated by working with hydroelectric proponents at the Rideau Falls, Merrickville, Jones Falls, Brewer’s Mills, Washburn, and Kingston Mills generating stations (Ontario Power Generation Inc. 2020; Portage Power 2020). Drawdown (the lowering of water levels throughout the system) is completed each fall to create volume for precipitation and snow-melt run-off (spring freshet) and to mitigate flooding with minimal impact to fish spawning. Although efforts are made to minimally affect fish spawning in the spring, it is unclear how drawdown procedures impact overwintering. For example, in portions of the Rideau River, which is generally 5 m deep, with max depths of 10 m (Navionics 2020), water levels are dropped by ~3 m in the late fall prior to winter, potentially reducing available overwintering habitat for species by a significant amount. In addition to “rule curves” (see http://www.rideau-info.com/canal/water-rulecurves.html), water management in the northern and central sector is supported by an extensive 1D hydrologic and hydraulic model created by the RVCA, extending from Upper Rideau Lake to the City of Ottawa (Ahmed 2010).

Water level and flow operations are determined on a system-wide basis, as operation of hydraulic structures can affect the upstream, downstream, and adjacent water levels, flows, and velocities in the Rideau Canal (Parks Canada 2020b). Currently, water level management attends to both social (e.g., navigation, historic flour grinding demonstrations, Ottawa’s winter Skateway – Fig. 2C) and environmental (e.g., climate) pressures in the system. It should be noted however that Parks Canada has legal mandates to prioritize public safety, navigation requirements, and federally listed species at risk. Parks Canada must also comply with the federal Fisheries Act (regulated by Fisheries and Oceans Canada), which includes protecting fish and fish habitat, although Parks Canada itself is not a delegated
authority under the act (V. Minelga, personal communication; see Fig. 3 and Supplementary Table S11). To examine region- or site-specific research questions around freshwater connectivity from an ecological context, there is a need for hydraulic modelling at specific reaches to better understand the role of structures (locks and dams) on native and invasive fish movement and functional habitat, shoreline erosion and deposition, and flood levels and velocities. This ecological information coupled with information on human activities and values could provide useful scenarios to substantiate past and current water management strategies and understand the sustainability of the current and future ecosystem under climate change. Water management involves complex decision making, often with conflicting priorities; as such, combined social and ecological research (e.g., investigating fish interactions in and around lockstations) could support conservation actions and further inform the meeting of legislative requirements of Parks Canada.

Case study - understanding current water level management of separately controlled channels

Managing water levels in the Rideau Canal is extensive and difficult, particularly given that most structures are operated manually. In the town of Manotick, Ontario there is a complex flow split around an island creating two separately operated channels with dams at different downstream locations, orientations, and elevations (Fig. 4). The eastern channel is the primary navigation channel with a flight of locks, while the western channel is steeper and often has swift water conditions. Though a 1D hydraulic model exists for this reach, 1D models can have poor performance at flow splits and confluences due to the 2D (or 3D) velocities (Ghostine et al. 2012, 2013). In addition, calibration of roughness can be challenging without known calibration flow, velocity, and water level data in each channel prior to modelling (Knight et al. 2018). Due to the complexity of flow and dam operations in this region (i.e., Long Island), future multi-dimensional hydraulic modelling would be helpful for water managers to optimize water level and velocities through the reach, particularly under freshet conditions.
2.5.5. Species at risk

We are living amid a planetary wave of anthropogenically driven biodiversity loss: the sixth mass extinction (Ceballos et al. 2017). In respect to freshwater ecosystems, like those within the Rideau Canal, habitat destruction and connectivity loss (fragmentation) is a leading and persistent cause of the catastrophic declines in freshwater biodiversity (WWF 2018). Currently, the anthropogenic barriers (i.e., locks, dams) throughout the Rideau Canal appear to offer some level of connectivity to wildlife. Reports by anglers, boaters, and lockmasters of fishes and turtles in locks is common; however, to what extent animals are able to successfully move between reaches (i.e., the waterbodies separated by a lockstation) to potentially more suitable habitat is unknown. Interestingly, some canal systems can act as refuges for endangered species. For instance, Sousa et al. (2019) found that irrigation canals in Morocco supported a significantly higher density and condition of the critically endangered freshwater mussel *Pseudunio marocanus* compared to a natural river. The Rideau Canal, too, offers stable habitat to many at-risk species.

Canada has national legislation to protect species at risk and provide for their recovery (the federal Species at Risk Act), which generally applies to lands under federal government jurisdiction. If a species leaves federal land and enters provincial land, then species protection would fall under provincial species at risk legislation (i.e., Ontario’s Endangered Species Act). Sixty species at risk are currently listed as being historically and (or) currently present in the Rideau Canal (many freshwater-dependent

Figure 2.4. Complex flow split and confluence around Long Island, through the town of Manotick, Ontario, Canada. The flow arrows plotted resulted from velocities surveyed with an aDcp, and dam and lock locations are plotted from locations surveyed using RTK GPS. Orthoimagery provided by the City of Ottawa (2015).
terrestrial species), across a range of taxa (protected information provided by Parks Canada). More importantly, several species at risk in the Rideau Canal are migratory (e.g., American eel (*Anguilla rostrata*), snapping turtle (*Chelydra serpentina*)); as the level of ecological and landscape connectedness is currently unknown in the Rideau Canal, it is difficult to develop and apply conservation actions to support their populations. Although management by Parks Canada of the Rideau Canal is not primarily focused on wildlife conservation, continued operation of the system has indeed allowed biodiversity to persist. Reviewing the many different species-specific recovery strategies and conservation actions for species at risk in the Rideau Canal is outside the scope of this article; however, Parks Canada is currently drafting a Multi-Species Action Plan for the canal to update current conservation actions and develop new ones that will be available online (V. Minelga, Parks Canada, personal communication).

**Case study - turtles**

Turtles are among the most threatened vertebrates worldwide (Lovich et al. 2018). The Rideau Canal is home to several at-risk turtle species, including the northern map turtle (*Graptemys geographica*), Blanding’s turtle (*Emydoidea blandingii*), eastern musk turtle (*Sternotherus odoratus*), midland painted turtle (*Chrysemys picta*), snapping turtle (*Chelydra serpentina*), and spotted turtle (*Clemmys guttata*). It is unclear whether locks act as barriers to movement or migration of turtle species for feeding, reproduction, or over-wintering. Although genetic assessments of turtles in the Trent-Severn Waterway (an Ontarian waterway similar to the Rideau Canal) revealed little evidence of connectivity loss (Bennett et al. 2010), the Rideau Canal is an older waterway for which no connectivity assessments have been conducted. The Rideau Canal’s social-ecological nature entails several recreational and economic activities like boat-induced injuries, small-scale commercial fishing, and anthropogenic noise from watercraft and lock infrastructure that may be negatively impacting turtle populations; thus, it is important we determine ways to promote population connectivity and persistence. In addition to investigating how lock infrastructure and operations may be impacting turtle connectivity, collaborations can be fostered with local community groups to protect key habitat features (e.g., basking and nesting sites) and share information about turtle conservation.

2.5.6. **Invasive species**

In 2006, Dudgeon et al. (2006) identified “invasion by exotic species” as a leading cause of population declines and range reductions of freshwater organisms globally; since then, researchers have confirmed that the threat of invasive species has evolved and escalated (Reid et al. 2019; Tickner et al. 2020). Invasive species pose one of the greatest threats to the biotic integrity of freshwater ecosystems, with potentially adverse socioeconomic effects (Reid et al. 2019). The ecological impacts of invasive species
range from behavioural shifts of native species, to restructuring of food webs, to species extinctions (Gallardo et al. 2016), all of which negatively impact resource users. Additionally, the economic costs of managing invasive species are significant – estimated at $1.4 trillion in damages worldwide (Pimentel et al. 2001). With the continued construction of canals and regional and global trade intensifying connectivity, the potential for aquatic invasive species to expand their range and distributions has only increased (Panov et al. 2009).

The Rideau Canal hosts numerous invasive species across fish, invertebrate, and plant taxa. For example, the common carp (Cyprinus carpio), one of the world’s most widespread and “worst” invasive fish species (Lowe et al. 2004), can be found throughout the system, and has caused economic, ecological, and social impacts on several continents (e.g., Australia and North America; Stuart et al. 2006; Kulhanek et al. 2011). The invasive aquatic plant Eurasian watermilfoil (Myriophyllum spicatum) has also proliferated throughout much of the system and can be a major hindrance to boat traffic in deeper regions of the waterway (e.g., navigation channel; Poulin 2001). Perhaps the most infamous invasive species found in the Rideau Canal is the zebra mussel (Dreissena polymorpha), which has incurred negative impacts both ecologically and economically (Martel and Madill 2018). The Welland Canal, a shipping channel that connects Lake Ontario and Lake Erie, has similarly facilitated biological invasions of sea lamprey (Petromyzon marinus) from Lake Ontario to the upper Great Lakes as well as other non-native species (Sullivan et al. 2003; Siefkes 2017). Anthropogenic waterways and canals with barriers (e.g., navigation locks, dams) can act as “invasion highways” and efficiently transport biological invaders (Leuven et al. 2009). Boaters visiting from other water systems can also facilitate invasive species transmission (e.g., zebra mussels can attach to the hulls or motors of boats and be transported to new waters; Timar 2008). If the variety of invasion routes and movement patterns of invasive species could be evaluated, the same barriers that may be enabling passage could instead be used to restrict movement and act as a complete barrier, minimizing population movement and (or) expansion. Research and modelling on connectivity, and how and when locks and dams can act as barriers or facilitate movement, would be required to help prevent the spread of invasive species and enhance native species movement. This research could help adjust lock and dam operations, and guide the development of effective education programs.

Case study — preparing for a potential future Asian carp invasion in the Rideau Canal

As a hydrological connection between Lake Ontario and the Ottawa River, the Rideau Canal faces potential biological invasions from both the Laurentian Great Lakes and the St. Lawrence River (Fig. 1). One group of invasive species of serious concern are Asian carps which have received extensive attention from both Canadian and American authorities throughout the Great Lakes basin because of
their ability to negatively impact and modify native ecosystems and associated socio-economic activities (Cudmore et al. 2012, 2017). Although the Rideau Canal’s lockstations may hinder movement to some extent, Asian carps have been documented to successfully pass upstream through dams and lock chambers (Lubejko et al. 2017; Zielinski et al. 2018; Fritts et al. 2021). The Rideau Canal has not yet been identified as a system suitable for establishment (Mandrak et al. 2020; Heer et al. 2019, 2021), although there is indeed suitable habitat (e.g., wetlands, eutrophic lakes) present through the system. If Asian carps do enter the waterway via the Kingston Mills locks (Fig. 1), they could negatively influence the local ecosystem through competition, consumption of plankton and macrophytes, and alter turbidity and dissolved oxygen (Cudmore et al. 2012, 2017). To determine the capability of Asian carps invading the Rideau Canal, expert elicitation and system-specific mechanistic invasion models are needed, as currently there is a lack of empirical data for the system (Chenery et al. 2020). Conceptualizing the Rideau Canal as a social-ecological system could also help build resilience and adaptive capacity in the system (Folke et al. 2003). As a still-functioning historic heritage canal, any changes to infrastructure or operation scheme to reduce the risk of biological invasion must consider the mandates for other management objectives (e.g., maintaining aesthetic sceneries, conserving historic structures, protecting threatened species, providing recreational and economic functions). Future research that incorporates different social and ecological objectives, and examines the trade-offs among objectives, will be needed.

2.6. The future

As anthropogenic pressures in the Rideau Canal corridor continue to increase, we can expect more social-ecological disturbances (e.g., potential social conflicts, loss of habitat and biodiversity, toxic algal blooms, water management with aging infrastructure). These pressures may also be exacerbated by global trends like climate change and the sixth mass extinction, which increase uncertainty about natural phenomena and environmental variations like water levels, erosion, and invasive species (Woodward et al. 2010; Nichols et al. 2011; Ceballos et al. 2017). Other potential climate impacts could include warming waters, extreme weather events, and habitat transformation (Woodward et al. 2010; Nichols et al. 2011). As revealed by the case studies presented here, individual and collective human practices (e.g., bass tournaments, shoreline development, macrophyte removal) can reduce system resilience to these stressors. There are, however, opportunities for research and restoration actions, community science, and government coordination to increase resilience and promote positive environmental change in the Rideau Canal. Additionally, population growth and changing demographics along the Rideau Canal corridor could influence the diversity of interests and environmental values of stakeholders. For example, the generational gap between year-round residents, many of whom are retirees, and seasonal residents, often younger generations, could lead to tensions that should be investigated prior to additional conflict occurring. Finding a balance between preserving the natural
environment and heritage character of the Rideau Canal with the recreation and leisure opportunities of various user groups is a challenging task for a fragmented governance regime.

2.6.1. The challenge of managing the Rideau Canal as a coupled social-ecological system

The Rideau Canal is best conceptualized as a coupled social-ecological system – humans and their activities influence system properties (e.g., invasive species, algal blooms, loss of biodiversity, etc.) – while the physical and ecological properties of the waterway provide a rich environment for human actors to engage with (e.g., for recreation, income, food), thus shaping behaviour and institutions. Using a transdisciplinary social-ecological approach (Angelstam et al. 2013), whereby experts from multiple disciplines (e.g., biology, engineering, social science) work together to understand and manage freshwater systems as a whole, or certain specific aspects like pollution or invasive species could be adopted to canals and waterways worldwide. For example, biological invasions (Ferreira-Rodríguez et al. 2019) are inherently and often explicitly social-ecological in nature, both directly and indirectly linked to human activities, and must be managed as such; developing strategies to manage either the humans or the animals, instead of both simultaneously as one unit, is illogical. In the Rideau Canal, managing invasive species will require knowledge on how and when organisms move (i.e., the ecological aspect) and how operations of infrastructure and the infrastructure itself influences movements (the social aspect); effective management actions will then need to be developed by canal managers, biologists, and hydraulic engineers. Canals are fundamentally anthropogenic ecosystems and accordingly should be managed as the complex social-ecological systems they are. With more than 60,000 km of canals with anthropogenic barriers worldwide (Revenga et al. 2000), and their implications in biodiversity reductions having a global reach, it is critical that managers shift from single disciplinary management to evidence-based, transdisciplinary governance.

A multitude of linkages and feedback loops exist in the Rideau Canal among specific resource systems and units (e.g., fish and turtle populations, habitat, water composition, macrophyte expansion), actors and governance systems (e.g., locals, decision-makers, community groups), and technologies (e.g., locks and dams, built canal sections) (McGinnis and Ostrom 2014). As a highly managed system, the Rideau Canal presents interesting and rare opportunities to influence management and address several social-ecological challenges; for instance, Parks Canada could manage barriers to promote or restrict movements of native or invasive species, respectively, or manipulate water levels to satisfy recreational activities and navigation while still offering critical habitats to fish and turtles for spawning and nesting, respectively. Social-ecological factors external to the Rideau Canal can also influence the system like the Ottawa River and the Laurentian Great Lakes, public attitudes towards climate change, and international recommendations for environmental policy. Such connectivity and complexity underline the
need for reliable transdisciplinary environmental and social sciences (Perz 2019) about the state of the Rideau Canal’s interdependent natural conditions and social dynamics. Transdisciplinary research can involve strategic collaboration among researchers from many disciplines, as well as stakeholders, members of the public, and Indigenous groups, so that various forms of knowledge can be considered to tackle the complex challenges of the Rideau Canal (Perz 2019). Here, we have included a team of authors with expertise across several disciplines, as well as several early-career researchers, to increase the diversity of perspectives represented and produce a meaningful, transdisciplinary review of the Rideau Canal as a social-ecological system.

As we noted previously, water systems are uniquely difficult to govern because of their geographic variability, large numbers of stakeholders, and the involvement of multiple levels of government with different jurisdictional authority, frequently leading to a social-ecological mismatch (Fig. 3; Sayles 2018). Successful governance of the Rideau Canal system in a time of social-ecological change will require governance innovations. Some of these innovations are “easy wins” that can be undertaken quickly with broad support—for instance, findings from interviews with Rideau Canal stakeholders indicated a strong desire for increased participation in decision-making and co-governance (Mistry 2020). This would require an extension and expansion of current stakeholder engagement and consultation practices, but models exist in other parts of Canada (e.g., Fraser River salmon fisheries in British Columbia) that could be adopted. Other innovations may, however, be more difficult to implement. For example, stakeholders have shown interest in the creation of a single regulatory board that could coordinate leadership at the various local, regional, Indigenous, provincial, and federal governing levels to consider cross-jurisdictional questions like engagement practices, development proposals, zoning issues, fishing regulations, and others (Mistry 2020). This holistic type of management is seen as more desirable than the current reality of fragmented authority in which proposals must be tabled to multiple authorities, and feedback or approvals from one authority (for instance, a municipality) may conflict with those offered by others. While the establishment and operation of such a coordinating body would be difficult for the Rideau Canal, examples do exist (e.g., the National Capital Commission in the Cities of Ottawa and Gatineau). Future research about collaborative governance opportunities, and specifically participatory processes, could also help support social-ecological resilience in the Rideau Canal while considering environmental justice (Moran et al. 2019).

2.6.2. Needs and opportunities

The most immediate opportunity is to work towards building resilience in the Rideau Canal and formally acknowledging and managing it as a social-ecological system. Doing so means thinking about resilience in terms of adaptive co-governance (Berkes 2017), social systems, and the ecology of the system, as
well as the ways in which those domains interact. Revisiting relationships among governmental and nongovernmental actors is essential to facilitate the development of adaptive and collaborative capacity. The history of the Rideau Canal, its contemporary complexities, and the threats and issues presented in this article can guide future research about the various bidirectional interactions between social and ecological components in the system. Additionally, if management of the system could be conducted successfully and cooperatively across the different governing bodies, it could serve as a model for other waterways within Canada and beyond.

There are opportunities to engage in philosophical discussions about modified ecosystems composed of historical built infrastructure within natural reaches, and how our conceptualizations of the “natural” and the “human-made” shape worldviews, behaviours, and social-ecological linkages (e.g., natural versus artificial water bodies; Clifford and Heffernan 2018). Considering which values (e.g., social, environmental) society wants to collectively sustain in the future will be necessary so that we can use appropriate strategies to protect those values. This rethinking of our conceptualizations of, and relationships with, the environment can help us shift from fragmentation and misalignment towards inclusion, coordination, and ecosystem health. Such processes must engage stake- and Rights-holders, especially Indigenous peoples who have stewarded this land since time immemorial, in meaningful and sustained ways. There is an opportunity for greater collaboration with Indigenous nations whose traditional territory includes the Rideau Canal to inform transdisciplinary research.

There are also opportunities to address specific social-ecological issues through use of creative management and policy options. Opportunities exist for thinking about aquatic plant management beyond simply navigation and incorporating more ecological knowledge into plant management (both at the individual shore-line scale and harvesting scale) to enhance habitat for fish and threatened species. There is also much opportunity for continued work on improving water quality throughout the system by reducing nutrient loading into the waterway, especially in the middle (Rideau Lakes region) and southern (Cataraqui watershed) portions where lakes are prevalent and there are engaged stakeholders willing to change their behaviour. Located in the central region of the Rideau Canal, Newboro Lockstation represents the highest point of elevation (i.e., the “isthmus”; Fig. 1), and as such, ecosystems downstream in both the northern and southern directions would also benefit from reduced nutrients and associated harmful algal blooms. Many sections of the waterway have undergone transition from agricultural landscapes to urbanization, resulting in increased runoff and alterations to water chemistry and flows. As land-use change is expected to continue, it is essential we consider how these impacts can be mitigated. Determining the level of connectivity at both individual locks and across the Rideau Canal is vital to support native species migrations, and there is opportunity to use connectivity evidence to minimize invasive species dispersal as well. Finally, there are opportunities to mobilize existing efforts
and programs (e.g., Love Your Lake program, lake associations, bass fishing tournaments) as starting points to collectively work toward common objectives.

2.7. Conclusion

Historic canals occur worldwide, and a common feature is that their history both constrains and defines current uses. This is exemplified in the Rideau Canal, a National Historic Site of Canada and UNESCO World Heritage Site. Here, the federal management agency and primary steward, Parks Canada, focuses on preserving the systems’ commemorative integrity while simultaneously creating contemporary recreational opportunities and considering certain aspects of ecosystem integrity. This creates an inherent tension, but also yields fascinating governance challenges, particularly when one considers that environmental change and other drivers of change can be synergistic and (or) dynamic. Though it is difficult to plan for the future when we do not precisely know what it holds, there is an opportunity for Parks Canada, stakeholders, and other jurisdictional management organizations to develop actionable plans to protect and restore biodiversity throughout the waterway. Engaging visitors and residents in community science efforts could serve as a steppingstone for social-ecological change while building meaningful relationships. Most importantly, the current governance structure must shift from “patchwork” governance that is punctuated by periods of consultation towards consistent, coordinated multi-scalar and multi-stakeholder governance. Parks Canada and the Ontario provincial government move on long and slow cycles (the 2010 consultation is still ongoing with a plan yet to be seen), whereas municipal governments and Conservation Authorities move at a faster pace. This mismatch does not always generate conflict, especially if it can be coordinated with appropriate communication. Further research on how we could envision this coordination would clarify confusion about the current governance regime and help identify a common goal to which actors can align their agendas. The social-cultural features of the Rideau Canal create a rich foundation for re-envisioning waterways of the future – waterways that respect and celebrate the past while simultaneously recognizing that the world is changing and our systems must benefit future users and the environment.
3.1. Abstract

The round goby (*Neogobius melanostomus*), native to the Black and Caspian Seas, is one of the most wide-ranging invasive fishes, having established in much of Europe and North America. In 2019, round goby were discovered to have colonized a central portion of the Rideau Canal, a 202 km historic waterway in Ontario, Canada. Round goby were found in low densities and had not been previously reported in any adjacent sections of the waterway, implying a newly-established source population. Passage through locks is the most likely means by which round goby can naturally disperse throughout the system, so modifying lock operations and infrastructure to minimize passages could reduce their spread. Additionally, understanding the range expansion and habitat preferences of pioneering individuals can help inform control efforts. We combined acoustic telemetry with hydraulic data to (1) characterize sex- and size-specific movements, (2) identify entry and exit pathways through a lock, and (3) assess dispersal rates and probability. We tracked 45 adult round goby downstream of Edmonds Lockstation during the navigation season from July to October, during which nine were detected inside the lock, with one fish successfully passing upstream. Most fish remained near the release site, though 26% of tagged individuals dispersed. The farthest distance a fish moved was 500 m (downstream) after 27 days, generating a maximum dispersal rate of 18.5 m/day. Although we lacked sufficient statistical power to detect size- or sex-specific movements, males were more commonly detected further from the release site. Our results suggest possible modifications to lock operations and infrastructure that managers could consider to reduce round goby expansion upstream from the invasion site.

3.2. Introduction

The round goby (*Neogobius melanostomus*), native to the Ponto-Caspian region of Europe, is a small (<25 cm), benthic fish that is one of the most prominent aquatic invasive species in North America and Europe, with introduced populations in the Laurentian Great Lakes, the Baltic Sea, and several European rivers (Kornis et al. 2012; Brandner et al. 2015; Adrian-Kalchhauser et al. 2020). Rapid range expansion, explosive population growth, and life history trait plasticity have contributed to their success as an invader (Cerwenka et al. 2014; Brandner et al. 2015). Although numerous studies have reported the ecological and economic impacts of round goby invasions (see Balshine et al. 2005; Bergstrom and Mensinger 2009; Kornis et al. 2012; Oesterwind et al. 2017), few eradication or control attempts have been made (though see Dimond et al. 2010; Ojaveer et al. 2015; Dorenbosch et al. 2017). Biological invasions are complex and consist of different stages, including introduction, establishment, spread, and impact, each with an independent probability of success (Kolar and Lodge 2002); once a non-native
species reaches the point of ‘established’ (is reproducing and forms a self-sustaining population; Gozlan et al. 2010), there is usually little hope for eradication. However, density and dispersion control, or functional eradication (suppressing invader populations below levels that cause unacceptable ecological effects; Green and Grosholz 2021), may be possible, especially if the invasion front is managed aggressively to stop further spread (Rytwinski et al. 2019).

In January 2019, 17 round goby were discovered near Edmonds Lockstation in the Rideau Canal Waterway, a National Historic Site of Canada, Canadian Heritage River, and UNESCO World Heritage Site, located in eastern Ontario, Canada (hereafter referred to as “Rideau Canal”; Parks Canada 2005). The Rideau Canal forms a 202 km continuous navigable route between Lake Ontario and the Ottawa River, and is interconnected by 47 locks and 24 lockstations, most of which have adjacent water-control dams (Fig. 1). When this waterway was constructed in the 1820s, three previously disconnected watersheds were connected (the Rideau River, Gananoque River, and Cataraqui River watersheds; Watson 2021). Located in the central region of the Rideau Canal, Newboro Lockstation represents the highest point of elevation (i.e., the “isthmus”; Fig. 1), with waters in the Rideau Watershed flowing downstream (northward) towards the Ottawa River and waters in the Cataraqui Watershed flowing downstream (southward) towards Lake Ontario. Large sections of the system at similar elevations (e.g., the Rideau Lakes) have negligible flows between adjacent reaches. Although connecting the watersheds offered new and potentially more suitable habitat to native species, it also enabled access to new geographic areas for non-native species and exotic pathogens (Leuven et al. 2009; Lin et al. 2020). The Rideau Canal is not unique in this sense; as of the late twentieth century, more than 63,000 km of canals exist worldwide (Revenga et al. 2000), forming convenient transport routes for supply transfer and facilitating countless biological invasions (Kelly et al. 2009). For example, the Welland Canal near Niagara Falls facilitated the destructive spread of invasive sea lamprey (Petromyzon marinus) from Lake Ontario to the upper Great Lakes (Sullivan et al. 2003; Siefkes 2017). Given that waterways with extensive anthropogenic modification (e.g., locks, dams) have been described as “invasion highways” for aquatic species (Leuven et al. 2009), it would be useful to better understand how infrastructure and/or operations in these systems could be refined to control the spread of invasive species.

To develop and implement a successful management strategy for invasive species, it is essential to understand how the species interacts with the environment, and the environment itself (i.e., how conducive the new environment is to that species). Biotelemetry is a valuable tool that can provide evidence and information on dispersal and movement patterns relevant to control efforts. Acoustic telemetry has been used to identify key habitats, activity times, and home ranges of invasive species worldwide, and can be highly relevant to management interventions which aim to control invasions.
(Lennox et al. 2016; Crossin et al. 2017). For example, Holbrook et al. (2014) used acoustic telemetry to evaluate if the lock and dam in Cheboygan River, Michigan, a tributary of Lake Huron, serves as a barrier to upstream passage of invasive sea lamprey. Although no tagged lamprey were detected above the Cheboygan Dam, they estimated that 0-2% of the untagged population could have escaped upstream, most likely exploiting the vessel lock and passing upstream during lock operation (Holbrook et al. 2014). Indeed, conservation actions are less likely to be effective when animal movements are not considered (e.g., the scale or timing of movements; Allen and Singh 2016).

Numerous efforts have been made to evaluate movement patterns of round goby, but only one published study has used telemetry tracking to quantify their movements (see Christoffersen et al. (2019) who examined diel and seasonal patterns in a Baltic Sea estuary). Although researchers have conducted field experiments to provide information on round goby dispersal patterns (e.g., see Lynch and Mensinger 2012; Marentette et al. 2011, 2012; Šlapanský et al. 2020), the mark-recapture methods used do not provide fine-scale, round-the-clock movement data like those that telemetry does. Collectively, those articles offer a deeper understanding of round goby spatial ecology, though it would be inappropriate to apply results from those studies to the Rideau Canal population given individual variability and incomparable regions and ecotypes. As such, the main goal of this study was to characterize the establishment and spread of the recent biological invasion of round goby in the Rideau Canal, and specifically (1) to evaluate the passability of locks as potential upstream dispersal pathways, (2) to characterize round goby space use and overall dispersal, and (3) as the first researchers to acoustically tag round goby this small, to identify potential impacts of acoustic tagging.
Figure 3.1. Overview map of the historic Rideau Canal. The black channel represents the Rideau Canal 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, is the “isthmus,” representing the highest elevation on the Rideau Canal and delineates the Rideau Watershed (flowing north) and the Cataracti Watershed (flowing south). Lake Ontario and the St. Lawrence River act as a natural border between Canada and the United States. Note that this map does not include the lockstation that connects the main waterway to the Tay Canal. Although round goby are present...
throughout Lake Ontario and the St. Lawrence River, they were unknown to have invaded the Rideau Canal until 17 fish were discovered near Edmonds Lockstation in January 2019. Our acoustic telemetry array \((N = 29)\) focused on an 8.7 km portion of the Rideau Canal between Old Slys Lockstation and Kilmarnock Lockstation.

3.3. Materials and methods

3.3.1. Study area

This study took place in an 8.7 km section of the Rideau Canal spanning from Old Slys Lockstation (N 44°53.590' W 76°00.250') to Kilmarnock Lockstation (N 44°53.075' W 75°55.825') (Fig. 1; Online Resource 1, Fig. S1). In this article, a “lock” refers to a chamber with gates (i.e., doors) at both ends that allows water to be let in or let out to raise or lower a vessel from one water elevation to another (i.e., to move upstream or downstream), whereas a “lockstation” describes an entire site, including land and associated buildings, the lock(s), the water-control dam and weir, and any other navigation or water-management structures. Though many lockstations in the Rideau Canal are single locks (i.e., only one lock chamber), several are composed of multiple locks in close proximity, ranging from two to eight locks in flight (i.e., connected to each other by gates). Construction of the Rideau Canal was completed in 1832, primarily for commercial shipping and national Canadian defence (Forrest et al. 2002), to provide a direct route from Lake Ontario at Kingston, Ontario to the Ottawa River at Ottawa, Ontario. Today, it is mostly used for recreational purposes and is maintained by the federal agency Parks Canada primarily for navigation and to preserve commemorative integrity of the waterway (Acres 1994; Parks Canada 2005; Bergman et al. 2021). Many shorelines in the area are stabilized with rocky riprap, though several regions are stabilized instead by shoreline vegetation or concrete vertical retaining walls (RVCA 2019). Lakes, rivers, and constructed channels in the study area have bottom substrate consisting of clay-bed, sand, rocks, gravel, and pebbles, with some areas being heavily vegetated. The Rideau Canal is a biodiverse freshwater system and has been described as having one of the most diverse fish assemblages (107 documented fish species; Coad 2011) in Canada (Poulin 2001; Parks Canada 2005). This system supports both recreationally important gamefish, like largemouth bass \( (Micropterus salmoides) \) and muskellunge \( (Esox masquinongy) \), as well as at-risk species like bridle shiner \( (Notropis bifrenatus; \) special concern) \( (Poulin 2001; \) COSEWIC 2020). A navigation channel along the entire waterway is maintained (typically \( \leq 1.5 \text{ m} \)) during the navigation season for boaters to travel safely. Aquatic vegetation that impedes boaters is removed within the navigation route, though areas outside of the deeper main channel are shallow (\( \sim 1-2 \text{ m} \) deep) with large expanses of aquatic vegetation and riverine wetlands. In 2019, the navigation season began 17 May and ended 14 October.
Edmonds Lockstation (N 44°52.650’ W 75°59.015’) consists of a 40.8-m-long and 10.5-m-wide lock (see Fig. 2A and 2C for an aerial view of the lock chamber and downstream gates, respectively, and Fig. 3 for a 3-D view). When the downstream and upstream gates are open, the average depth inside the lock chamber is 2.2 m and 5.1 m, respectively. Edmonds Lockstation has a 167-m-long and 4.1-m-high stone arch dam consisting of a 96 m overflow stone weir and a 7.5 m long waste-weir of stacked logs (Wanless 1997). The lock is situated at the east end of a 150 m excavated (navigation) channel. Edmonds Dam spans the width of the Rideau River, creating a 2.7 km slackwater section to the upstream double-flight lockstation, Old Slys. The section from Edmonds Lockstation downstream to Kilmarnock Lockstation is also slackwater (for information on slackwater technology, see https://www.pc.gc.ca/en/docs/r/on/rideau/whl-lhm/chap3/chap3C), spanning 6.0 km and includes extensive wetlands and a lacustrine area of open water with heavy vegetation (Online Resource 1, Fig. S1).

There are several different ways in which fish can enter Edmonds Lock. First, when the upstream or downstream lock gates are open, a 10.5-m-wide channel becomes available for fish to use. Second, on the downstream gates, there are four sluice valves (two on each gate) near the bottom which release water from the lock chamber via a swing-type plate (Fig. 3B). When opened, each valve has two rectangular areas 0.46-m-high and 1.52-m-wide that fish can swim through. Third, there are two sluice tunnels on the upstream end of the lock which are used to fill the chamber (Fig. 3C). The sluice tunnels are approximately 1.4-m-high, 0.9-m-wide, and 10.5-m-long (Government of Canada 1987). The tunnel entrance is divided into four rectangular areas for fish to enter, ranging in height from 0.19 to 0.37 m with a width of 0.85 m. Hereafter, we refer to downstream gate valves as “valves” and upstream sluice tunnels as “tunnels.” Depths in the areas surrounding Edmonds Lockstation are relatively shallow during average summer flows, mostly 1-2.5 m deep, with a deeper 4.0 m pool located upstream of the dam (Online Resource 1, Fig. S2). During non-operational hours (i.e., night), water levels in the lock chamber are lowered to minimum depth (i.e., 2.2 m) for safety purposes and to relieve pressure on infrastructure. During non-operational hours, lockmasters leave 1-2 valves open on the western downstream gate to ensure water levels remain low (Parks Canada, personal communication).

3.3.2. Acoustic tagging

As this is a new invasion, we expected round goby densities to potentially be low; thus, snorkel and free diving surveys were conducted downstream of Edmonds Lockstation to determine where sampling efforts should be focused. We surveyed the lock channel and the area within ~250 m downstream of the dam, observing round goby only near the dam and along the far eastern shoreline. Round goby were discovered at Edmonds Lockstation only six months prior and this area is one of the few regions
in the reach with rocky substrate that round goby prefer (see below). Based on these observations and our surveys, we assumed that the round goby population was likely to still be close to the dam and we therefore did not conduct additional snorkel surveys throughout the entire reach. Further, we chose not to continue extensive surveys throughout the full 8.7 km study system in order to deploy tags and begin tracking round goby movements swiftly. Fish sampling occurred from 9 to 18 July 2019 during the day between 0900 and 1700. Round goby were collected using a backpack electrofisher (LR-24 electrofisher, Smith Root, Vancouver, Washington, United States). Electrofishing by slow wading upstream along the right bank, as well as immediately downstream, of Edmonds Dam (denoted by areas within the black dashed lines on Fig. 4) was the most effective sampling method for catching a range of sizes of round goby inhabiting the littoral zone (mostly in rocky areas). Several studies have shown round goby prefer hard substrates for spawning and feeding (Charlebois et al. 1997; Ray and Corkum 2001; Bhagat et al. 2015) and the interstitial spaces created by rocks provide refuge from predation (Jude and DeBoe 1996). Other methods (e.g., beach seining, traps, angling) were not used due to inappropriate habitat conditions and low efficiency, and electrofishing nearshore habitats has previously been shown to be a reliable method for sampling round goby (Šlapanský et al. 2020). Due to bathymetric gradients, sampling was restricted to within 3 m of the water’s edge.

All captured round goby were immediately placed in a 19 L plastic bucket filled with fresh river water and brought to shore. Body measurements taken, including total length (TL), standard length (SL), head width (HW), body width (BW), and genital papilla length (GPL, measured with calipers), were measured to the nearest 1 mm and 0.5 mm for GPL. Each round goby was photographed to confirm species identification (e.g., Fig. 2B). Sex was determined by visually examining the urogenital papillae, located between the base of the anal fin and the anus, which in females is broad and blunt and in males is long and triangular (Charlebois et al. 1997). The smallest round goby captured was 52 mm TL; according to size-at-maturity literature values for round goby in North America whereby individuals >50 mm TL are adults (Phillips et al. 2003; Lynch and Mensinger 2012; Blair et al. 2019), all individuals were classified as such. To minimize potential negative impacts of tag burden, only individuals ≥65 mm TL were implanted with acoustic transmitters (hereafter, ‘tags’), with the exception of one round goby that was 61 mm TL. Individuals <65 mm TL captured were donated to the Canadian Museum of Nature as voucher specimens. Thus, we refer to two separate groups of round goby for morphological analysis: the “tagged population” refers only to acoustically tagged individuals, and the “total population” refers to all round goby captured. Mass measurements were not taken in the field; they were instead extrapolated from a least-squares linear regression model using length-weight data (\( N = 1724 \)) from a population of round goby in Hamilton Harbour, Ontario, Canada (\( R^2 = 0.96 \); dataset provided by S. Balshine).
Forty-five round goby were implanted with a ‘small’ \( (N = 26) \) or ‘large’ \( (N = 19) \) sterilised (betadine) mini-acoustic Lotek Wireless Juvenile Salmon Acoustic Telemetry System (JSAT) tag in the coelomic cavity (small: L-AMT-1.416, 0.28 g in air, \( 10.7 \times 5.4 \times 3.1 \) mm, expected battery life = 87 days; large: L-AMT-1.421, 0.32 g in air, \( 11.1 \times 5.5 \times 3.7 \) mm, expected battery life = 131 days). Tag type (i.e., large versus small) was relatively evenly distributed across sexes, with males \( (N = 18) \) implanted with nine large tags and nine small tags, females \( (N = 22) \) implanted with nine large tags and 13 small tags, and the smaller individuals of unknown sex \( (N = 3) \) implanted with small tags. The tags used were the smallest commercially available acoustic transmitters at the time; because of their small size, we inserted them using methods similar to PIT tagging. Fish were individually 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. No anesthetic was needed given that fish remained immobilized while supine and because of the speed and simplicity of the procedure. Tags were inserted through a lateral-ventral incision (\( \leq 5 \) mm) posterior to the pectoral fin using a sterilized No. 21 scalpel. Sutures have been considered unnecessary for small (\( \leq 1 \) cm) incisions in fish tissue (Baras and Jeandrain 1998; Shelton and Mims 2003; Acolas et al. 2007; Raoult et al. 2012), yet, from an ethical perspective, closing the wound after tag insertion may be important in terms of reducing infection (Hegna et al. 2019). Thus, 19 fish were randomly selected to have cyanoacrylate adhesive applied to their incision. Of the males tagged, 66\% had glue applied to their incision. In the field, glue was applied randomly to every second or third fish, resulting in a bias of more males having glue applied to their incisions. Glue was applied to incisions on 50\% of tagged females (equal proportion of females with and without glue applied to their incisions). One of the three individuals of unknown sex had glue applied to its incision. The tag:body-mass ratio (i.e., tag burden) was on average 5.3\% (range: 0.8-10.4\%). The highest tag burden of 10.4\% is on the upper end for electronic tagging of fish, however there is a growing body of literature suggesting there is no universal “rule” for tag burden, and that some fish species do not exhibit significant impairments when tagged with devices as much as 8-12\% of body mass (Brown et al. 1999; Lacroix et al. 2004; Jepsen et al. 2005; Cooke et al. 2011). Tag burden and the application of glue to the incision was recorded to evaluate potential effects of the tagging procedure on apparent survival and short-term movements. All tagged fish were marked (superficially injected) with non-toxic, pink acrylic paint beneath the dorsal fin in case of recapture (O’Brien and Dunn 2018). The entire procedure took 2-4 min. Fish were monitored for post-surgical behaviour changes (e.g., equilibrium imbalance, change in ventilation rate, lack of movement when gently prodded; Tsitrin et al. 2020) in a recovery bucket with fresh river water for a minimum of 30 min post tagging and released thereafter to minimize potential deleterious effects from prolonged confinement (Jepsen et al. 2002). No fish showed any apparent deleterious effects from surgery. We released all acoustically tagged round goby immediately downstream of Edmonds Lock over the site-of-release receiver (Fig. 2C) to (1) ensure we could detect at least initial
tag transmissions and have a single point from which to track movements (i.e., standardizing movements across depth and habitat), (2) evaluate upstream movements into and/or through Edmonds Lock, and (3) determine if round goby have a propensity to return to their site of capture near the dam (i.e., “home”). Although round goby can be habitat generalists (Henseler et al. 2020), as mentioned above literature indicates they prefer rocky, riprap habitat which in our study area is common in both the lock channel and near the dam (J.N. Bergman, personal observations).

3.3.3. Acoustic telemetry array

Twenty-nine acoustic receivers (Lotek Wireless, WHS 4250, 416.7 kHz) were deployed in strategic locations to track tagged fish movements. Receivers were stationed inside the lock chamber and immediately outside (5 m) on the upstream and downstream ends of Edmonds Lock to detect space use and successful passage events, and evenly throughout the reaches upstream and downstream of Edmonds Lock to examine dispersal capacity and overall movements (Online Resource 1, Fig. S1). A higher density of receivers was placed downstream of Edmonds Dam (i.e., the site of capture) to investigate potential homing capability in round goby. Receivers were deployed 17 May 2019 and collected 25 October 2019 and were anchored to the bottom with the hydrophone positioned ~0.6 m above the substrate. Receiver locations were recorded using a handheld GPS unit. Range and detection efficiency tests of our receivers were conducted post hoc in June 2020. For detailed information and results for range and detection efficiency testing, see Online Resource 1: Table S1, Fig. S3, and Fig. S4.

3.3.4. Hydraulic survey and processing

Hydraulic surveying and processing inside Edmonds Lock was conducted to evaluate how fish interact with lock infrastructure and in the surrounding area to determine potential effects of velocities on fish movements. Onset HOBO U20-001-01 Water Level Loggers (Bourne, Massachusetts, United States) were installed adjacent to three receivers on 10 May 2019 to record temperature and pressure: one 120 m upstream Edmonds Lock, one 50 m downstream of Edmonds Lock, and one inside the Edmonds Lock chamber in a downstream corner. An additional logger was installed on shore to record barometric pressure and to calculate depth of the other loggers. A hydraulic survey was conducted in the local area surrounding Edmonds Lock station extending from approximately 200 m upstream to 100 m downstream. Bathymetries and velocities were surveyed over three days from 20-27 August 2019 using a remote-control Teledyne Marine Q-Boat 1800 (Poway, California, United States) equipped with SonTek M9 RiverSurveyor (San Diego, California, United States) acoustic Doppler current profiler (aDcp). Bathymetry and velocity data were processed using MATLAB code developed by Rennie and Church (2010). Ordinary kriging interpolation was applied to the processed bathymetric plus topographical data.
received from Parks Canada, and u- and v-depth-averaged velocity components to determine bathymetry and depth-averaged velocity vectors for the reach. For a more detailed explanation of our hydraulic survey and data processing, see Online Resource 2.

To evaluate the path by which round goby may enter or exit the lock chamber, we investigated lock operations and chamber water levels. By determining the rate at which the lock was filled, we could deduce if a boat was inside the chamber: when a boat is present inside of the lock, the lock is filled slowly (with the operators’ intent to prevent vessel damage due to turbulence). As such, if the lock was filled slowly, we assumed the downstream gates were opened for at least a few minutes prior to allow a boat to enter, and for a few minutes the upstream gates would be open post-filling to allow a boat to exit. Lock fill rate was therefore used to help uncover potential routes of entry and exit (e.g., through valves versus through open gates). Drain rate, conversely, could be fast or slow, depending more so on how lockmasters operated the lock (e.g., if only one lockmaster was present, they may have opened 1-2 valves instead of all 4), and not if a boat was present (Parks Canada, personal communication).

3.3.5. Data analysis

3.3.5.1. Raw detection filtering

Telemetry data were processed and statistical analyses were conducted using R version 3.6.2 (R Core Team 2019). Conducting acoustic telemetry research in close proximity to “noisy” structures, like navigation locks and dams, can result in a high number of false positive detections; thus, several filters were employed to identify and remove likely false positives. We identified and removed detections from tag IDs that were not in round goby (i.e., tag IDs implanted in other species in the system; 31,362,391 detections removed; remaining “true” detections: 456,367). Any known tag ID detections recorded by receivers that occurred before that tag ID was deployed in the system were also removed (5900 detections removed; remaining “true” detections: 450,467). We used a ‘min lag’ filter from the GLATOS package (Holbrook et al. 2019; Algera et al. 2020; Tuononen et al. 2020), which uses an a priori determined number of detections within a specified timeframe, to identify potential false positive detections. For our study, we required a minimum of two detections to occur on a given receiver within a 10 min period for either detection to be considered “true” (22,611 detections removed; remaining “true” detections: 427,856). We then applied an “interval method” filter (e.g., Algera et al. 2020) whereby we used the programmed JSAT transmission interval (here, 20 s between signal transmissions) to identify false detections. The first transmitted ID detection was considered “true,” and subsequent detections outside the 20 s interval were removed from the dataset (66,233 detections removed; remaining “true” detections: 361,623). Signal power of each detection was also considered. Power readings reflect the strength of the detected signal, ranging from 0 to 1500 dBm, and can be affected by a variety of factors
like distance between receiver and tag, tag orientation, and ambient environment; false positive detections generated by ambient noise typically have weak power values. We generated and visually inspected a histogram of detection power levels and based on observations of outliers we assumed that detections with power levels less than 20 dBm were likely false; these detections were removed (8682 detections removed; remaining “true” detections: 352,941). Finally, we applied a detection event filter to the dataset (Holbrook et al. 2019). The detection event filter groups individual detections into discrete events, defined by movements between receivers or receiver groups (i.e., stations) and sequential detections at the same station separated by a predefined time frame. Because of their close proximity (9 m), we grouped the two receivers on the upstream end and the two receivers on the downstream end of the lock chamber together, resulting in two distinct lock chamber stations (‘upstream lock chamber receivers’ and ‘downstream lock chamber receivers’). All other receivers were considered unique stations. Detections that occurred in sequence with gaps of <1 h between detections at the same station were considered a detection event; if a full hour passed between sequential detections, the subsequent detection was considered to be the start of a new detection event (352,941 raw detections were reduced to 68,083 detection events). Individual fish abacus plots (Online Resource 3) were visually inspected to verify that detection event timestamps and locations were logically and biologically plausible. To eliminate implausible detections (e.g., fish quickly moving large distances, or moving back and forth across the dam or lock), we filtered out detection events with ≤3 raw detections. After applying this requirement to the detection event filter, we carefully inspected the dataset and found all events appeared plausible, resulting in a final dataset of 14,468 detection events from 43 round goby (two fish were not detected post-filtering). Although detection range and efficiencies were evaluated, receiver detection efficiencies were low (Online Resource 1, Table S1). Consequently, detection efficiency and range testing results were not formally integrated into our data analyses; instead, we use them descriptively to provide context for our interpretation.

To evaluate round goby movements inside the lock chamber, detections were filtered slightly differently. The same initial filtering process was still applied (i.e., interval method, min lag filter, minimum power signal requirement), however the detection event filter was altered. Although beacon devices (acoustic tags inside the receiver that emit a signal) were activated on the four lock chamber receivers for range and detection efficiency testing, the testing failed, likely as a result of high ambient noise inside the lock (Lotek Wireless, personal communication). Thus, to determine a finer resolution of round goby movements inside the lock, we grouped the four lock chamber receivers together into a single station. When multiple receivers are grouped into a station, the detection event filter calculates a single, average position based on the detections heard during the event, offering a way to visually assess where and when round goby spent their time in and near the lock. Abacus plots (Online Resource 3) indicated that detection ranges of the downstream-lock-chamber receivers and the receiver located immediately
outside the lock on the downstream side (i.e., the site-of-release receiver) appeared to overlap; thus, the site-of-release receiver was also included into the station for lock-movement analysis. The event filter does not triangulate fish positions; instead, it produces a relative sense of where fish were detected most among those receivers, comparable to a “centre of activity” evaluation for fish movements near and inside the lock chamber. This analysis assumes roughly similar detection range and efficiency for each of the four lock receivers. The receiver immediately outside the lock on the upstream side was left separate as it was at a higher elevation (+3 m) and did not appear to overlap in detection range with the receivers inside the lock. The final lock detection dataset included 743 detection events.

3.3.5.2. Morphology and movement type analysis

Body measurements (TL, SL, BW, HW, GPL) were evaluated for normality; these variables did not meet assumptions of equal variance and normality (as assessed using Levene’s Test for Equality of Variances) so we evaluated them using permutation tests with 100,000 permutations. To evaluate potential drivers of movements, we used two binomial logistic regression models. The logistic regression models were designed to evaluate the potential effects of body size (TL), sex (categorical variable), if glue was applied to the incision (yes or no, categorical variable), and tag burden on round goby (1) dispersal away from the site of release (i.e., movement type analysis) and (2) entry into the lock chamber (i.e., lock chamber entry and passage analysis). We chose to use logistic regression over other techniques (e.g., linear regression) as our measures of movements were binary; individuals either dispersed away from the site of release (1, designated “roamer”) or remained (0, designated “resident”), and either entered the lock (1) or did not (0). Interactions were not included due to insufficient statistical power. An alpha level of 0.05 was set for analyses.

To map detection events, round goby Residency Index (RI) was calculated by dividing the total number of days detected at each station 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 as it reduces the potential bias of a large number of detections at a given station generated by only a few individuals (Kessel et al. 2016). RI was not analyzed for movement or dispersal patterns as round goby were translocated to the site-of-release station from their site of capture, and sample sizes were low at most stations. Because the tags used have a maximum expected battery life of 131 and 87 days – a relatively short amount of time to assess fish movement patterns – for large and small tags, respectively, we relocated tagged individuals to the site-of-release station to give us the best chance at answering key research questions. Additionally, we know of only one other research group who has successfully tracked round goby using
acoustic telemetry (Christofferson et al. 2019), and those fish were ~70% larger (TL) compared to the round goby captured in this study.

Figure 3.2. Images of the study site, Edmonds Lock, Smiths Falls, Ontario, where round goby were first discovered in the Rideau Canal. A Image of the lock chamber as water levels are being lowered. The gates in the image are the downstream gates. Note that most locks in the Rideau Canal, including Edmonds, are still manually operated by hand. B Each round goby captured and acoustically tagged was photographed to confirm species. C View of the Edmonds Lock downstream gates. The yellow arrow indicates the site-of-release station placed immediately outside and downstream of the chamber to determine if and/or when tagged fish entered and exited the lock, or dispersed from the area. All tagged goby were released at this station. Image credits: (A) and (C) taken by Kate Neigel, and (B) taken by Jordanna Bergman.
Figure 3.3. 3-D images of Edmonds Lock chamber and channel. A A full view of Edmonds Lock and its navigation channel. Note that the upstream gates are at a higher elevation, and therefore shorter, compared to the downstream gates. The Edmonds Lock chamber ranges from 10.06 to 11.58-m-wide and is 41-m-long. Water depth in the lock chamber when downstream and upstream gates are open is 2.2 m and 5.1 m, respectively. When water levels are low (i.e., 2.2 m), the platform (i.e., gate sill) on the upstream side of the lock is exposed. In respect to upstream dispersal, when water levels are low, round goby cannot pass upstream as they would be exposed to air. B A 3-D image of the downstream-lock gates. To empty the lock chamber, lockmasters manually open these valves to release water. These valves are left open during non-operational hours (i.e., night) to maintain low-water levels in the chamber for safety purposes and to minimize unnecessary pressure on infrastructure. Telemetry results indicate these valves provide a path for round goby to enter and exit the lock, even when the downstream gates are closed. C A 3-D view of the upstream portion of Edmonds Lock. The 0.9-m-wide and 1.4-m-high yellow sluice tunnels are used to manually draw water into the lock chamber for filling. Lockmasters
close the intake valves for the tunnels when not in use. These tunnels may also serve as a path for round goby to move upstream and exit the chamber (provided the lock is full, not operating, and the valves have been left open) or enter the lock chamber when water is being pulled in during filling. Photo credits: all images created and provided by Kate Neigel.

3.4. Results

3.4.1. Morphology and sex ratio

3.4.1.1. Total population

In total, 58 round goby were captured and measured (32 females, 22 males, and four individuals of unknown sex). The sex ratio of the total population (female to male) was 1.45:1. The four individuals of unknown sex (genital papilla too small to identify sex) were excluded from size and movement analyses. Males were significantly longer (on average 7.61 mm longer; TL: \( P = 0.04 \); SL: \( P = 0.04 \)) and heavier (on average 2.75 g heavier; mass: \( P = 0.03 \)) than females. No statistical differences were found between males and females for head width (\( P = 0.09 \)), body width (\( P = 0.24 \)), or genital papilla length (\( P = 1 \)). Detailed information of sex-specific size measurements can be found in Online Resource 1, Table S2.

3.4.1.2. Tagged population

Forty-five round goby were acoustically tagged and released at the site-of-release station (Fig. 2C). This included 22 females, 18 males, and three individuals of unknown sex. The sex ratio of the tagged population (female to male) was 1.22:1. The three individuals of unknown sex were excluded from size and movement analyses. Overall, males appeared to be larger than females, though no statistical significance was found when comparing total length (\( P = 0.08 \)), standard length (\( P = 0.10 \)), mass (\( P = 0.10 \)), head width (\( P = 0.15 \)), body width (\( P = 0.34 \)), and genital papilla length (\( P = 0.72 \)). Detailed information of sex-specific size measurements for acoustically tagged round goby can be found in Online Resource 1, Table S3.

3.4.2. Hydraulic survey

Water levels were monitored in the lock chamber to determine the timing of lockages and the number of opportunities fish had to move upstream (to overlay with detection data). We define a “lockage” as an event where a vessel entered the lock chamber and water levels were raised or lowered to allow upstream or downstream passage, respectfully. During the study period, upstream and downstream water levels varied by 8 cm and waste-weir operation remained constant. Average water temperatures in July (9-31 July), August, September, and October (1-11 October) were 26.3 °C, 23.9 °C, 19.4 °C, and
14.2 °C, respectively. A total of 603 complete lockage cycles and 19 partial lock cycles (where the lock only filled or emptied partially) occurred during the study period, with a mean of 6.2 cycles/day. On average, there were 8.5 daily lockage cycles in July (9-31 July), 8.6 in August, 3.7 in September, and 2.2 in October (1-11 October). Velocities upstream of Edmonds Lockstation ranged from 0.0 to 0.15 m/s, increasing near the waste-weir, and velocities downstream of Edmonds Lockstation ranged from 0.0 to 0.4 m/s. The peak velocity in the study reach was 0.6 m/s immediately downstream of the waste-weir (Fig. 5). Depth-averaged velocities measured inside the lock chamber were measured to be up to 1.5 m/s during lockages but <0.05 m/s otherwise. We found that following a lock fill, the lock chamber remained full (with upstream gates open) for an average of 34 min, and up to 244 min. Based on known swimming speeds, round goby would only be restricted by velocities in the area immediately downstream of the waste-weir and within and near the lock during operation (Tierney et al. 2011: sprint = 0.66 ± 0.02 m/s, prolonged = 0.36 ± 0.01 m/s; Egger et al. 2020: sprint = 0.43 ± 0.14 m/s, prolonged = 0.54 ± 0.10 m/s [note that sprint values were lower than prolonged values likely due to forced swimming or substrate holding during sprint tests versus volitional swimming during prolonged tests]).

3.4.3. Movement analysis

Over the duration of the study, 96% (43/45) of the fish tagged were detected in the receiver array. The total time detected for each fish ranged between three hours to 88 days, with an average detection time of 16 days. More than half (53%) of the tagged fish were detected for fewer than seven days (Online Resource 1, Fig. S5). Tag burden did not differ significantly between males and females (P = 0.14). Statistical output for logistic regression models can be viewed in Online Resource 1, Table S4.

3.4.3.1. Roamer versus resident round goby (movement type analysis)

We conducted a series of binomial logistic model analyses to examine which variables might predict movement type (i.e., resident or roamer) in our tagged round goby. Fish size (TL), tag burden, glue application to incision, and sex did not have an obvious effect on movement type. Round goby that were detected only at the release site, the receiver 50 m downstream in the lock channel, or inside the lock were classified as “resident”; most of our tagged round goby (74%) were classified as such and remained near the release site. A total of 26% (11/43) of tagged fish left the lock channel altogether (i.e., roamers) and were detected either back at their original site of capture (N = 4) or in the main Rideau River channel (N = 7) (Fig. 4). Roamers included a fairly even number of both sexes (six males, five females), though three of the four fish that returned to the site of capture were male. Seventy-three percent of roamers did not have glue applied to their incision. The farthest (from the release site) a round goby was detected during the study period was ~500 m downstream, 27 days after being tagged and released. The mean body size (TL) of roamers versus residents was almost equal at
76.73 mm and 76.84 mm, respectively. Mean tag burden of roamers versus residents was also similar at 5.05% and 5.38%, respectively. See Online Resource 1, Table S5 for detailed information on where individual round goby were detected.

3.4.3.2. Lock chamber entry and passage analysis

Nine of the 43 tagged round goby (21%) entered the lock chamber, including three males, five females, and one of unknown sex (Fig. 6; Online Resource 1, Table S5). Because it appeared the downstream lock chamber receivers overlapped in detection range with the site-of-release receiver, we required fish be detected on upstream lock chamber receivers to be considered to have truly entered the lock (see abacus plots: Online Resource 3; Fig. 6). Though none of the predictors we examined (TL, sex, tag burden, application of glue to surgical incision) appeared to be linked to whether round goby entered the lock, larger fish had a tendency to enter the lock, though this relationship was not significant ($P = 0.07$). Four individuals entered the lock and remained there until they stopped being detected (i.e., tag battery died); five round goby entered and exited the lock. Residence time in the lock varied greatly, ranging from 30 min to 87 days. By comparing detection data to water-level data in the lock chamber, and taking into account hours of operation, we were able to determine potential pathway(s) of entry and exit (Online Resource 4). Five fish entered the lock chamber during non-operational hours through open downstream-gate valves. Four fish entered the chamber during operational hours: one fish entered while downstream gates were open to allow entry to a vessel for an upstream lockage, one fish entered while gates were closed through downstream valves, and for two fish it was unclear if they entered via downstream-gate valves or when gates were opened for a lockage. Of the five fish that exited the lock after being detected inside the chamber, three exited during non-operational hours via open downstream valves, and for the other two fish it was unclear if they swam out by their own means through open valves or if they were flushed out when the lock was being drained. Only one round goby was detected upstream of the lock (fish FCA9). This 82 mm female, with a large-size tag and no glue applied to the surgical tagging site, was detected on the receiver immediately outside Edmonds Lock on the upstream side for a 15 min period (Figs. 6 and 7). While this fish did indeed pass upstream through the lock, as it was detected exclusively outside the lock for 15 min, we do not consider it to have dispersed as it returned to the lock chamber and was only detected inside or downstream of the lock thereafter. It is possible that given sufficient time and low velocities, the fish could have truly dispersed. Detailed information on entry and exit pathways for each round goby detected in the lock chamber can be found in Online Resource 4.
Figure 3.4. Round goby Residency Index (RI) by acoustic receiver station. Each circle represents mean RI at that station for all tagged round goby across the entire monitoring period 10 July 2019 to 12 October 2019. Red circles indicate at least one round goby was detected at that station; black circles indicate no fish were detected there. Circles are graduated such that larger circles represent more time and/or more individuals at that location. Note that the size of the site-of-release station is inflated as all tagged round goby were translocated from the site of capture (denoted by areas within the black dashed lines) and released there. Receivers were placed immediately (5 m) outside Edmonds Lock on the upstream (more north) and downstream (more south) sides to detect if and when fish entered and exited the lock. Four receivers were placed inside the lock with one in each corner. To determine if fish entered the lock chamber, the lock-chamber receivers on the upstream ($N = 2$) and downstream ($N = 2$) ends were grouped into distinct stations, respectively, such that there are two lock-chamber stations. Only one individual was detected at the most southern station on the map, at 500 m from the site of release.
Figure 3.5. Typical water velocity flow field when Edmonds Lock is not in operation, with the average water level (elevation) upstream and downstream of Edmonds Lock and Dam at 106.48 m and 103.61 m, respectively, during the study period. Arrows indicate the direction and velocity (m/s) of water flow, with arrows size- and color-graduated such that the larger and ‘redder’ the arrow is, the higher the velocity. Highest flows can be seen beneath the Edmonds Dam near the site of capture. Residency Index (see Fig. 4) has been overlaid to show fish residency at receiver stations in combination with water velocities.
Figure 3.6. Detection events for tagged round goby that entered Edmonds Lock \((N = 9)\) for the full monitoring period. Red circles represent acoustic receivers: four receivers were placed directly within the lock chamber in each corner, and two receivers were placed outside the lock on the upstream and downstream side. After inspecting individual fish detections, it became clear the five receivers at the same depth (elevation) (i.e., the four lock chamber receivers and the site-of-release receiver) had overlapping detection ranges, and because our range and detection efficiency testing inside the lock chamber failed, these receivers were grouped into a single station to determine mean locations for each detection event (represented by small blue circles). Based on this figure, it appears that round goby outside the lock at the site of release may be ‘heard’ by downstream-lock receivers. Vice versa, fish inside the lock on the downstream side may be detected by the site-of-release receiver. Accordingly, unless detections occurred on upstream lock (chamber) receivers, the fish was not considered to have truly entered the lock. The receiver outside, upstream the lock is at a higher elevation (+ 3 m), and its detection range did not appear to overlap with the other receivers. Only one round goby was detected on the upstream receiver outside Edmonds Lock, and for only 15 min before re-entering and remaining in the lock chamber.

3.5. Discussion
Although research has evaluated dispersal rates and movement patterns of round goby in both North America (Lynch and Mensinger 2012; Šlapanský et al. 2020) and Europe (Azour et al. 2015; Brandner et al. 2018; Christoffersen et al. 2019), no studies have yet used telemetry to track a new round goby invasion to inform control actions. The coverage of our telemetry array allowed for a finer-scale resolution of when fish moved either away from the release site (downstream), into the lock chamber, or above (upstream) the lock. Of the 43 round goby acoustically tagged and detected, nine (21%) were detected inside the lock. Most fish entered the lock during non-operational hours via open downstream gate valves (67%), and similarly the five fish that entered and exited the chamber also did so also through open valves, indicating that the downstream gates are indeed permeable to round goby. The elevated platform in the upstream portion of the lock (referred to as a “gate sill,” see http://www.rideauinfo.com/canal/img_lock_anatomy.html) and its upstream gates, however, appeared to act as an almost complete barrier to upstream movement under the conditions studied here. Except for one fish that was briefly detected for 15 min on the station immediately outside upstream of the lock, no round goby were detected upstream.

The one round goby that successfully passed upstream appeared to be able to do so as a result of normal (daytime) lock operations. By combining our telemetry data with water-level data, we were able to match lock operations with fish entry and exit times (Online Resource 4). When water levels in the lock chamber are low (i.e., same elevation as downstream water levels), the gate sill on the upstream end of the lock is exposed, physically preventing upstream passage attempts (Fig. 3A and 3C). When lock chamber water levels are high, however, round goby are presented with the opportunity to navigate the gate sill and move upstream. Although the upstream gates perpetually leak, providing some level of flow, these low velocities likely do not prevent a fish from moving upstream, and may even attract fish movement (Tierney et al. 2011). The water-level loggers detected stable, raised water levels inside the lock chamber for 68 min, indicating that the upstream gates were continuously open. It took considerable time (~one hour) for the round goby to navigate to the elevated upstream portion of the lock chamber and exit through open upstream gates after they were opened (Fig. 7). Round goby can use a “burst-and-hold” swimming mode, whereby they hold onto substrate, with more textured surfaces aiding in a fish’s ability to hold position (Tierney et al. 2011; Egger et al. 2020). It was during the extended open-gate, low-velocity timeframe that the fish was likely able to employ this swimming mode to scale the lock chamber walls, which are rough and textured (J.N. Bergman, personal observations), and traverse upstream successfully. Recent research has indeed shown that while it may require more energy, round goby are entirely able to navigate vertical anthropogenic structures (Bussmann and Burkhardt-Holm 2020). It may be possible for round goby to avoid navigating the vertical gate sill and instead traverse a sluice tunnel to move upstream, provided the lock is full, not operating, and the tunnel valves have been left open (though according to the Edmonds Lockstation Operators, this seldom occurs; personal
communication). We did not place acoustic receivers inside the tunnels because of high turbulences, so it is unclear which pathway the fish took to pass upstream. Additionally, while we can confirm that the upstream gates were open, we do not know if the intake valves were left open during that timeframe. Edmonds Lock, as well as most other locks in the Rideau Canal, is still hand-operated and requires a considerable amount of time and energy to operate; as such, lockmasters will leave gates open post-lockage if another boat is expected to arrive from that direction. In this case, leaving the upstream gates open (or potentially a tunnel valve open) resulted in an opportunity for upstream passage. The round goby that exited upstream, however, did not truly disperse, as it returned to the lock chamber. Re-entry into the lock from the upstream end could have occurred one of two ways: (1) the fish may have been pulled into a sluice tunnel and back into the chamber during lock filling or (2) it may have naturally swam back into the lock when the upstream gates were open for a lockage (Online Resource 4).

Most of the round goby in our study exhibited little or no movement, remaining near the release site for the entire study period (94 days), with only 26% (11/43) demonstrating larger-scale movements (i.e., roamers). The smaller individuals of unknown sex were all residents. Most roamers were detected in the Rideau River channel, with four individuals moving upstream against current (Fig. 5) to the site of capture. It is unclear if these four roamers exhibited true homing capabilities as we are unaware of any studies conducted to validate homing in translocated goby. However, seasonal migrations and general homing have indeed been documented in round goby (Sapota and Skóra 2005; Walsh et al. 2007; Marentette et al. 2011; Christofferson et al. 2019), and Tierney et al. (2011) noted round goby exhibit a general pattern of positive rheotaxis (i.e., fish turn to face oncoming current) and move upstream more than downstream. Because of this tendency to move upstream, it may be that these fish movements, against current to return home, were directed and not random. Additionally, Marentette et al. (2011) documented male round goby to move more than females; while we lacked the sample size to resolve sex-specific movements between residents versus roamers, four of the five individuals that were detected at stations farthest from the site of release were male.

Given their benthic lifestyle, lack of swim bladder, and small home ranges, site fidelity and/or a preference for inactivity appears common for round goby (Wolfe and Marsden 1998; Ray and Corkum 2001; Šlapanský et al. 2020). Similar to our findings, other research has indicated at least a portion of a round goby population will undertake larger-scale range expansions, pioneering new areas (Gutowsky and Fox 2011; Brownscombe and Fox 2012; Šlapanský et al. 2020). However, the rate at which individuals disperse can vary both spatially and temporally. During winter months, when temperatures are very low in Ontario, it is likely that round goby are relatively inactive (Lee and Johnson 2005). In spring (a season our study did not capture) and autumn (a season when most of our tags were no longer being detected), however, round goby range expansions likely occur (Brownscombe and Fox 2012);
thus, we may have missed larger-scale movements during these times. For example, using capture-mark-recapture methods, Lynch and Mensinger (2012) found 89% of individuals in the Duluth-Superior harbour of Lake Superior were stationary, with occasional movements of up to 50 m/day, though few large-scale movements occurred during warm-temperature months (e.g., June and July). The most rapid rate moved by round goby was documented by Christofferson et al. (2019) via acoustic telemetry in the Baltic Sea, where fish covered distances 1.5-2 km in less than one day as part of overwintering migrations. In our study, the farthest a fish dispersed was 500 m after 27 days, which generated a maximum dispersal rate of 18.5 m/day, a rate similar to Šlapanský et al. (2020) (22.33-m/day downstream). The relatively short battery life (i.e., maximum 131 days) of acoustic tags suitable for round goby in the Rideau Canal limited our ability to track individuals long term; as such, it would be useful to conduct subsequent telemetry studies in late fall and early spring, immediately before and after ice-on and ice-off, respectively, to evaluate potential seasonal differences in movements.

We did not find size-biased movements, though there has been debate about whether smaller or larger round goby are the pioneers that lead an invasion front into new areas. Where Šlapanský et al. (2020), Brownscombe and Fox (2012), and Bergstrom et al. (2008) found that the smallest round goby were pioneers (possibly as a result of being outcompeted by larger individuals), Gutowsky and Fox (2011), Brandner et al. (2013), and Brandner et al. (2018) documented round goby at the invasion front to be significantly larger. Reports of sex ratios at invasion fronts are also mixed (e.g., female-biased: Brandner et al. 2013, Brandner et al. 2018, Janáč et al. 2019; male-biased: Corkum et al. 2004; Azour et al. 2015), even within the same river system. For example, in the Trent-Severn Waterway—an analogous system to the Rideau Canal also located also in Ontario—Gutowsky and Fox (2011) found invasion fronts to be male biased, whereas Brownscombe and Fox (2012) found individuals in newly expanded areas to be female biased. There additionally have been instances where no sex-bias was recorded at the invasion front (i.e., 1:1 sex ratio; Šlapanský et al. 2017). It is unclear what may be causing the disparity in sex ratios across different studies, but it is possibly a result of differing sampling time/season, sample techniques, and/or could simply be the result of high variation within and among populations (Šlapanský et al. 2017). Observed sex ratios could also be a product of invasion pathway; for example, downstream dispersal of larval round goby (which have been collected over 2 km from known spawning habitat; Hensler and Jude 2007) would likely result in a downstream population with no sex bias and smaller individuals compared to the (source) upstream population. Establishing how a new population was introduced (e.g., larval drift versus bait bucket), and the size- and sex-specific movements of that population, could be vital in determining the age of the invasion and using that information to decide what management actions might be most effective in controlling that specific population.
It is our belief the round goby population we sampled in the Rideau Canal represents a newly-established source population and invasion front. First, the Rideau Canal is a highly managed system that is regulated and monitored closely by Parks Canada, which often entails draining locks and/or surrounding areas to conduct maintenance during the non-navigation season. Fish salvages are conducted when areas are drained for larger infrastructure projects, with species identification and abundance recorded; indeed, this is how round goby were first discovered in the Rideau Canal. The only other lockstation where round goby have been reported in the Rideau Canal is at the triple-flight Kingston Mills Lockstation (see http://www.rideau-info.com/canal/locks/46-49-kingstonmills.html), the southern terminus that connects the system to Lake Ontario (where an established, known population of round goby exists; Fig. 1). Round goby have only been reported in the most downstream lock chamber (lock 49, closest to Lake Ontario), with the exception of two individuals being reported in the basin between lock 46 and 47, but not upstream of the lockstation in Colonel By Lake (EDDMapS 2021). This again suggests that locks, for the most part, serve as natural barriers to round goby upstream passage. Second, we were unable to capture round goby using methods commonly employed in areas with high densities. For example, in Hamilton Harbour, Lake Ontario, where round goby can be found in high abundances, minnow traps are very effective (Mehdi et al. 2021). In contrast, minnow traps deployed in our study area were ineffective, regardless of the time of day or the length of time deployed, or the bait used. Our failure to catch round goby in minnow traps suggests a low-density population, another characteristic of a newly established invasion. Although we cannot precisely state the age of the invasion, based on round goby being exclusively found in a central portion of the waterway, at low densities, and with a female-biased sex ratio, we believe this round goby population in the Rideau Canal is <5 years old (introduced earliest in 2014; see Bergstrom et al. 2008; Thorlacius et al. 2015; Brandner et al. 2018).
Figure 3.7. Overlay of fish detections and lock operations. Fish FCA9, an 82 mm (TL) female with a large-size tag and no glue applied to the incision, is the only round goby that appears to have successfully passed through Edmonds Lock. The black, thick lines indicate fish detections, and the grey dashed line indicates the depth inside the lock chamber. The shaded red area represents the portion of the detection period when the fish was detected outside and upstream of the lock. Water levels inside the lock chamber remained consistent with upstream-water levels for 68 min indicating the upstream gate(s) were open. During this period, the round goby had the opportunity to navigate upstream and leave the lock. The fish was detected for 15 min outside of the lock, and then re-entered the chamber, concurrent with a downstream lockage. It is possible that the fish re-entered the lock when the upstream gates opened for a boat, or the fish may have been pulled back into the chamber via sluice tunnels when lockmasters were filling the lock. The fish was not detected upstream, outside of the lock again.

3.5.1. Limitations

Anthropogenic waterways and canals are well recognized globally as vectors of exotic species transfer (Daniels 2001; Panov et al. 2009; Marsden and Ladago 2017; Lin et al. 2020). Though navigation locks have been reported to lack the necessary attractant flows to facilitate upstream dispersal (Coker 1929; Moen et al. 1992; Wilcox et al. 2004), research has nevertheless shown that fish can use locks to move upstream (Tripp et al. 2014; Kim and Mandrak 2016; Lubejko et al. 2017; Finger et al. 2020). Round goby have used canals in North America to disperse (e.g., the Chicago Ship and Sanitary Canal, Kolar and Lodge 2000, Wilcox et al. 2004; New York State canal system, George et al. 2021; Welland Canal
et al. 2016); however, fine-scale movement patterns and dispersal methods of round goby in canals and via locks are not well studied or understood. In this context, our study provides one of the first telemetry-based accounts of round goby movement, though there are several limitations that should be acknowledged. First, 53% of tagged fish were detected for seven or fewer days (Online Resource 1, Fig. S5). This short detection time is likely linked with the porosity of the acoustic array in the downstream riverine areas where detection range is <25 m and receivers were widely spaced. It is also possible that the detection range and efficiency of receivers inside and near the lock varied during lockages, as these events produce considerable anthropogenic noise. Tag transmissions (from range and detection testing) were not detected frequently or consistently enough to analyze lockage-specific receiver range and efficiency. However, we did find that tag transmissions were sporadically detected during both operating and non-operating hours, suggesting that other aspects of the environment beyond turbulence and flows from lockages are responsible for poor detection efficiencies (e.g., surrounding hard surfaces that can refract acoustic signals). Because round goby are benthic and prefer rocky habitats, tagged fish may have been using benthic refuge in ways that prevented tag transmissions from being heard by receivers. Some of our fish may have been eaten by predators, which then swam outside the detection range of the array. However, given that this is a new invasion site, we predict reduced predation because of low round goby densities and because local predators may still be naive to round goby as a prey item (Brownscombe and Fox 2013). We did not precede this field study by conducting a laboratory experiment to assess tagging effects as we wanted to focus on rapidly deploying tags in fish in the field to quickly provide information to managers and also to assess fish movements as early in the invasion as possible. Behrens et al. (2017) found that round goby survive the tagging process with tags that constitute up to 4.3% of their body mass, though 6.7% of their tagged fish showed signs of tag expulsion when the tag burden was >3%. As such, we acknowledge the possibility that the 15 individuals who were detected only at the site-of-release receiver may have simply been expelled tags (Online Resource 1, Table S5). Nevertheless, round goby are known to have small home ranges, and the site of release constituted ideal round goby habitat with an abundance of food (zebra mussels *Dreissena polymorpha*; Raby et al. 2010) and rocky refuge. Likely an artifact of battery life, the larger tags were detected for considerably longer amounts of time compared to smaller tags (average of 15.63 more days; 0.04-g heavier). For others conducting work on small-bodied fish, the larger tags may be worth using exclusively. Finally, although no statistical effects of glue application to the surgical site were detected, 73% of roamers did not have glue applied to their incision, and so it may be that glue was limiting fish movement.

3.5.2. Management implications and future directions
Managing invasive fish passage through locks on the Rideau Canal poses a unique challenge, as any strategies implemented cannot negatively impact navigation or boater safety, and ideally would not (further) restrict native aquatic wildlife movements (e.g., fish, turtles). Electrical barriers, for example, would be inappropriate to use in this system, which is highly used by recreational boaters and paddlers (kayaks, canoes, paddle boards), and which would prevent native species movements and migrations. Free-standing structural barriers, like gates or screens, would also be difficult to implement as they would have to pose no impact to navigation (i.e., not be placed in the channel) and not affect other native species (especially migratory at-risk species, like American eel *Anguilla rostrata* and snapping turtle *Chelydra serpentina*, which Parks Canada is federally mandated to protect). Carbon dioxide barriers could be used to reduce round goby passage and may be applicable to the Rideau Canal as they do not interfere with navigation or river flow (Cupp et al. 2021). However, testing to date indicates that most species and fish sizes show avoidance behaviours to carbon dioxide barriers (Treanor et al. 2017; Rahel and McLaughlin 2018), and so again this option would fully fragment the system, not allowing for selective passage strategies (i.e., permitting and restricting passage to native and invasive species, respectively). Acoustic (Isabella-Valenzi and Higgs 2016) and/or pheromone traps (Corkum et al. 2008; Bajer et al. 2019) could be deployed in higher density regions to passively capture round goby and control the local population, though these methods require a high level of sustained effort and would not result in eradication.

Eradication of aquatic organisms, even when restricted to small water bodies, has proven difficult (Rytwinski et al. 2019). When management efforts to eradicate or control aquatic species have indeed been successful, it was because action was taken quickly (Simberloff 2014) and/or sufficient funds and personnel were available to achieve management goals (Larson et al. 2011). Although eradication attempts of round goby have been unsuccessful and costly (e.g., Dimond et al. 2010), the population in the Rideau Canal is likely a new invasion and so there may be an opportunity for control by preventing further spread through a combination of several conservation measures. To reduce the likelihood of upstream dispersal, two actions – modifying infrastructure and lock operations – could be effective. Two-thirds of tagged round goby that entered the lock did so during non-operational hours through open downstream valves. Because valves on the downstream gates must be left open during non-operational hours, a grate or screen could be attached to the valves to prevent round goby from entering. These screens, however, would have to be maintained for biofouling and debris removal, and it could increase drag therefore slowing operation (i.e., draining) time. Alternatively, a relatively minor infrastructure modification could be implemented, whereby a water-release valve above the highest known downstream water level is installed on the downstream gate. Research suggests that in-stream barriers which force round goby to overcome gravity (i.e., climb an air-exposed, vertical wall) should be impassable (Pennuto and Rupprecht 2016); as long as the overflow valve does not slowly drain water
along the gate, round goby should be incapable of exploiting it as an entry pathway. As the Rideau Canal is a National Historic Site of Canada, historical elements must be preserved, so there may be some restrictions to gate modifications. However, given that gates are wooden it may be a low-cost solution that would not need to be maintained (Valerie Minelga, Parks Canada, personal communication). Second, keeping gate doors and tunnel valves closed unless necessary – A change in lock operations – would reduce the dispersal opportunities. Recommendations to close upper and lower gates when not in use to prevent fish from passing through locks has been suggested for other navigation systems as well (e.g., Soo Locks, Sault Ste. Marie, Michigan; LSBP 2014). To better integrate movement and velocity data, future work could investigate the energetic demands of movement paths and associated swimming velocities encountered, in lab and field scenarios, to inform lock-specific management. This was outside the scope of this article given the coarseness of our detection data (i.e., 20 s signal transmission rate and/or sporadic detections, see Fig. 7 and Online Resource 3). Modifying lock- and-dam infrastructure and operations to minimize invasive species passage has been investigated (Lubejko et al. 2017; Fritts et al. 2021; Zielinski and Sorensen 2021), though we are not aware of any such work with round goby.

The solution to managing round goby downstream dispersal is less clear. In 2020 and 2021, the two years following our telemetry tracking study, free diving and snorkel surveys were conducted in the region downstream of Edmonds Lockstation and a higher abundance of round goby were observed near the station 500 m from the original site of capture, indicating downstream dispersal is occurring as expected. We did not track movements of juveniles (<50 mm), and given that juvenile round goby have been documented to disperse downstream rapidly (Tavares et al. 2020), we may have missed key insights into range expansion. However, the number of round goby observed markedly decreased close to Kilmarnock Lake (Online Resource 1, Fig. S1), ~1.5 km downstream of Edmonds Lockstation. Kilmarnock Lake is a shallow, heavily vegetated lake with mostly mud and sand bottom; poor habitat characteristics for round goby (Young et al. 2010). As such, the lake may slow downstream dispersal. In early spring when macrophytes are not yet dense, round goby may traverse this area more easily, though if there is no suitable habitat then further dispersion would be minimized. Rocky substrate is essential for round goby to carry out their life cycle (Kornis et al. 2012), and so the wetland-like Kilmarnock Lake may at the very least impede colonization opportunities, though we note that high numbers of round goby have indeed been captured on muddy, vegetated shoals in the nearby St. Lawrence River, Québec, Canada (Morissette et al. 2018). Similar lock operation modifications, whereby gates are kept closed when not in use, could be implemented at the next downstream lock to minimize dispersal into the northern portion of the waterway.
Finally, and of arguably greatest importance, are public education and outreach efforts. Despite the illegality of transporting and releasing bait fish in Ontario, it is highly likely that round goby were introduced into the Rideau Canal via a bait bucket release event. Although a population of round goby exists in Lake Ontario, it is unlikely that they naturally dispersed upstream through 14 lockstations undetected, and anglers have indeed been implicated as highly mobile invasion vectors (Keller and Lodge 2007; Bronnenhuber et al. 2011; Kilian et al. 2012; Drake and Mandrak 2014). Management and conservation efforts that promote public awareness, stewardship for the natural environment, and compliance to regulations should be pursued to reduce any additional unwanted introductions into new areas.

3.6. Conclusion

This study used biotelemetry as a tool to investigate fish behaviour at a new round goby invasion in the Rideau Canal, providing data to help inform conservation actions at this location. We recommend future studies examine passage rates and movements of both native and invasive fish in the Rideau Canal, as efforts to minimize round goby dispersal may also reduce upstream movements of native fishes (i.e., resulting in a need to develop selective passage strategies; Rahel and McLaughlin 2018; Altenritter et al. 2019). Implementing and evaluating management strategies, like modifying lock operations and infrastructure, may provide options to control this invasion. Although previous work has been conducted to evaluate effects of acoustic tagging on round goby (Behrens et al. 2017), no work has been done using individuals as small as the fish in our study. Additionally, predation-type acoustic tags have shown promise (Halfyard et al. 2017), and so it would be useful in the future to use this technology to determine if and/or how many tagged goby are preyed upon. Any conservation strategies implemented must be monitored to verify effectiveness. As with most invasive species management efforts, outreach campaigns will be vital to spread conservation messaging and minimize future round goby introductions. With more than 60,000 km of canals with anthropogenic barriers worldwide (Revenga et al. 2000), many of them highly-managed waterways analogous to the Rideau Canal, our work may serve as a model for future use of telemetry to rapidly assess invasive species movement in other systems in North America and beyond.
Chapter 4: Multi-year evaluation of muskellunge (*Esox masquinongy*) spatial ecology during winter drawdowns in a regulated, urban waterway in Canada

4.1. 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.

4.2. 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 and 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 and 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 and 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 2022b). 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 and 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 and 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 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.
Figure 4.1. 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).

4.3. Materials and methods

4.3.1. 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 km² 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 (RVCA 2015). The Jock River watershed is considerably larger at 556 km² (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 (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).

4.3.2. 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 and Hadley (1979) and Casselman and 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 and 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 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 postsurgical 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.

4.3.3. 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.

4.3.4. 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, 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 and 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.

4.3.5. Data analysis

4.3.5.1. 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.

4.3.5.2. 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.

4.3.5.3. 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 over-wintering 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
We assessed the distribution of receiver RI values using the descdist 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 and Dutang 2014). We then fit a generalized linear mixed model (GLMM) using the glmmTMB function (package glmmTMB; Douma and 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 and 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: \(P = 0.007, \text{cor} = 0.755\)). 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 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).

4.3.5.4. 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).

4.4. 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.

4.4.1. 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 m². 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 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 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.
4.4.2. 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 first drawdown season and one day during the second drawdown season.

![Figure 4.2. Overlay of depth mapping and muskellunge residency index (RI) analysis.](image)

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.
Figure 4.3. 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.
Figure 4.4. **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.

4.5. **Discussion**

4.5.1. **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 and Stouder 1989) and/or predation (Harvey and 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., 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).

Figure 4.5. 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.

4.5.2. 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 and Gervais 2016; Di Rocco and 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 sub-sided 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).

4.5.3. 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 and 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 and Patalas 1984; Carmignani and 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.

4.5.4. 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.

4.6. 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.
Table 4.1. Tracking and biological data for acoustically tagged muskellunge (N = 23). 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).

<table>
<thead>
<tr>
<th>Detection category</th>
<th>Release date</th>
<th>Release date water temp (°C)</th>
<th>Fish ID</th>
<th>Total length (mm)</th>
<th>Tag burden</th>
<th>TDD</th>
<th>Overwintering area</th>
<th>Drawdown season 1: 2020-2021 (N = 13)</th>
<th>Drawdown season 2: 2021-2022 (N = 15)</th>
</tr>
</thead>
<tbody>
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<tr>
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<td>6DA8</td>
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<td>A253</td>
<td>1080</td>
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</tr>
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<td>D1</td>
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<td>2020-07-29</td>
<td>26.68</td>
<td>EC9A</td>
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<td>12.92</td>
<td>127F</td>
<td>901</td>
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<td>42</td>
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<td></td>
<td>2020-10-16</td>
<td>12.65</td>
<td>F9B5*</td>
<td>845</td>
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<td>Date</td>
<td>Value 1</td>
<td>Value 2</td>
<td>Value 3</td>
<td>Value 4</td>
<td>Value 5</td>
<td>Value 6</td>
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<td>453A</td>
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<td>104</td>
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<td>6216</td>
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<td>125</td>
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<td>C20E</td>
<td>711</td>
<td>0.31%</td>
<td>85</td>
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<td>2020-10-27</td>
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<td>623E*</td>
<td>270</td>
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<td>4</td>
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</tr>
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<td>D1/2-X</td>
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<td>707</td>
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<td>2020-10-15</td>
<td>12.92</td>
<td>D3EE*</td>
<td>685</td>
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<td>8</td>
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<td>2020-08-07</td>
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<td>54FD</td>
<td>611</td>
<td>0.47%</td>
<td>44</td>
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<td>D1/2</td>
<td>2020-08-07</td>
<td>25.05</td>
<td>4155</td>
<td>748</td>
<td>0.29%</td>
<td>126</td>
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<tr>
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<td>D3FF</td>
<td>639</td>
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<td>115</td>
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<td>42</td>
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<td>638D</td>
<td>760</td>
<td>0.25%</td>
<td>21</td>
<td>Segment 2</td>
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</table>
Table 4.2. Environmental characteristics and residency index (RI) of river segments and acoustic receivers in the Eccolands Reach for the 2020-2021 and 2021-2022 drawdown seasons. 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. Rec=Receiver. Receiver E10 malfunctioned during the first drawdown season and was excluded from analysis.

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

*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.*
Table 4.3. **Summary of statistical test outputs.** 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.

**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

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

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

<table>
<thead>
<tr>
<th>Predictor variable</th>
<th>Estimate</th>
<th>SE</th>
<th>z-value</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>-5.871</td>
<td>0.957</td>
<td>-6.133</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td><strong>Benthic structure: low</strong></td>
<td>3.073</td>
<td>0.564</td>
<td>5.446</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>
Benthic structure: high & 0.695 & 0.704 & 0.988 & 0.323  \\
√Velocity & 3.682 & 1.931 & 1.906 & 0.057*  \\

AICc: -68.06 | Number of observations: 21 | Marginal R²: 0.802

*Note that the intercept is benthic structure: medium.*

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

<table>
<thead>
<tr>
<th>Predictor variable</th>
<th>Estimate</th>
<th>SE</th>
<th>z-value</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>-3.750</td>
<td>0.440</td>
<td>-8.532</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>River segment 2</td>
<td>2.454</td>
<td>0.485</td>
<td>5.057</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>River segment 3</td>
<td>1.076</td>
<td>0.545</td>
<td>1.974</td>
<td>0.048</td>
</tr>
<tr>
<td>Drawdown season 2020-2021</td>
<td>-0.155</td>
<td>0.324</td>
<td>-0.480</td>
<td>0.631</td>
</tr>
</tbody>
</table>

Number of observations: 21 | Marginal R²: 0.733

*Note that the intercept is Segment 1.*

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

<table>
<thead>
<tr>
<th>Predictor variable</th>
<th>Estimate</th>
<th>SE</th>
<th>z-value</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>-9.066</td>
<td>5.460</td>
<td>-1.660</td>
<td>0.097*</td>
</tr>
<tr>
<td>Total length (mm)</td>
<td>0.004</td>
<td>0.007</td>
<td>0.533</td>
<td>0.594</td>
</tr>
<tr>
<td>Benthic structure: low</td>
<td>5.987</td>
<td>3.670</td>
<td>1.633</td>
<td>0.102</td>
</tr>
<tr>
<td>Benthic structure: high</td>
<td>4.860</td>
<td>4.120</td>
<td>1.157</td>
<td>0.247</td>
</tr>
<tr>
<td>√Velocity</td>
<td>1.071</td>
<td>10.063</td>
<td>0.106</td>
<td>0.915</td>
</tr>
</tbody>
</table>
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 × √velocity  
0.009  0.013  0.701  0.483

Number of observations: 295 | Conditional R²: 0.500 | Marginal R²: 0.427

Note that the intercept is TL × benthic structure: medium.

**General linear model (lm)**

**River segment-drawdown model**: drawdown ~ river segment

<table>
<thead>
<tr>
<th>Predictor variable</th>
<th>Estimate</th>
<th>SE</th>
<th>z-value</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>2.134</td>
<td>0.017</td>
<td>124.638</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>River segment 2</td>
<td>-0.053</td>
<td>0.023</td>
<td>-2.331</td>
<td>0.048</td>
</tr>
<tr>
<td>River segment 3</td>
<td>-0.344</td>
<td>0.023</td>
<td>-15.207</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

Multiple R²: 0.973 | Adjusted R²: 0.967 | F²,8= 145.6 | P-value < 0.001

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

Non-constant variance score test: χ² = 3.172, df = 1, P-value = 0.075

Note that the intercept is River segment 1.
Chapter 5: Ecological connectivity of invasive and native fishes in a historic navigation waterway

5.1. Abstract

Anthropogenic waterways, interconnected by navigation barriers (locks, dams), are uniquely difficult to manage given interest in enabling native species connectivity while minimizing invasions. Canada’s historic Rideau Canal Waterway, a 202 km navigable route located in eastern Ontario connected by 23 lockstations, embodies this challenge. The lock(s) and water-control dam that compose each lockstation may each offer a connectivity pathway, though to what extent is currently unclear. We used acoustic telemetry (native largemouth bass [Micropterus salmoides] and northern pike [Esox lucius], invasive common carp [Cyprinus carpio]; \(N = 224\)) and mark-recapture (\(N = 9564\); 15 species) to evaluate fish connectivity relative to lock operations and environmental data over three years (2019-2021). Forty-one passages by 28 native fishes were recorded, with 49% of passages through locks. No common carp passages were detected; movements indicate they favoured higher-flow areas beneath dams, regions with no pathway upstream. Most passages were downstream and, of concern to obligate upstream migrators, we found that multi-flight and larger locks appear impassable to upstream movements. Our results suggest lockstations are barriers that minimize, but not entirely restrict, connectivity.

5.2. Introduction

Global biodiversity has declined so severely that our world is now experiencing the sixth mass extinction (Ceballos et al. 2017). Nowhere, however, are biodiversity losses more extreme than in freshwater ecosystems: monitored populations of freshwater vertebrates have declined by an average of 84% since 1970, with freshwater fish populations experiencing some of the greatest losses (WWF 2020). The panoply of threats driving freshwater biodiversity declines (reviewed in Reid et al. 2019) often act synergistically (Craig et al. 2017) and can be exacerbated by climate change (Döll and Bunn 2014); thus, conservation and restoration efforts can only be effective if they are based on a clear understanding of system-specific processes and the distinct threats to them (Lin et al. 2020). For example, in modified freshwater systems like waterways and canals, key threats to biodiversity include system fragmentation and connectivity loss (Grill et al. 2019) and the diffusion and consequential impacts of invasive species (Kim and Mandrak 2016). Today, most North American river systems have experienced major connectivity loss due to direct (e.g., structural barriers like dams and levees) and indirect (e.g., altering hydrological regimes) human actions (Nilsson and Berggren 2000; Grill et al. 2019). Fragmentation alone can impose detrimental effects to aquatic wildlife, and can intensify other pressures such as pollution, invasive species, and harvest. Inland waterways with anthropogenic barriers, such as navigation locks and hydropower or water-control dams, have been considered an “ecological paradox”
(Bergman et al. 2021) because their construction creates a route between previously isolated watersheds and ecoregions, therefore offering new (and potentially better) habitat for species to carry out their life history, yet they can also facilitate the introduction and spread of non-native species and pathogens (Rahel 2013; Gallardo and Aldridge 2018; Leuven et al. 2019).

Anthropogenic waterways and canal systems are integrated systems of both humans and the environment, making them inherently social-ecological systems that should be managed as such (Bergman et al. 2021). They are constructed with human-use in mind (i.e., the ‘social’ aspect), usually for navigation (including historical uses such as military transportation) and/or recreation, however waterways provide habitat for a wide range of species and other ecosystem services (Lin et al. 2020) and are therefore fundamentally ecological. For example, managing biological invasions in a waterway requires knowledge of a species’ biological capability of dispersal and establishment, but also how lock and/or dam operations and infrastructure may influence movements. While locks and dams may provide a connectivity pathway to aquatic species, the degree of connectivity across waterways is relatively understudied, making it difficult (if not impossible) to develop and apply management actions. Here, we evaluated the longitudinal connectivity of one such social-ecological system, Canada’s historic Rideau Canal Waterway, as experienced by both native and invasive fishes. Construction of the 202 km Rideau Canal Waterway (hereafter, “RCW”) was completed in 1832 and connected the Rideau and Cataraqui watersheds, forming a continuous route between the Ottawa River at Canada’s capital city of Ottawa to Lake Ontario at the city of Kingston. Although originally the waterway was constructed by the British Royal Engineers for commercial shipping and national defense (Bumsted 2003), today it is operated primarily for recreation by the federal agency Parks Canada. Because the RCW remains a major engineering feat of the 19th century, and still operates based on European slackwater technology (see https://www.pc.gc.ca/en/docs/r/on/rideau/whl-lhm/chap3/chap3C), it is designated as a National Historic Site of Canada and UNESCO World Heritage Site. The RCW passes primarily through lands traditionally used by the Algonquin, Iroquois, Mississauga, and Mohawk Nations. Indigenous Peoples of North America have had strong connections with waterways for thousands of years; waterways were integral for fishing, hunting, gathering, and transportation and trade, as well as cultural and spiritual gatherings. The construction of the RCW significantly impacted the Haudenosaunee and Anishinaabeg Peoples connection with these lands and waters (Parks Canada 2022a). We recognize and deeply appreciate their historic connection to this place and their stewardship of these lands and waters.

Selectively managing barriers in waterways to promote connectivity for native species while simultaneously minimizing invasive species dispersal – a conservation strategy known as ‘selective fragmentation’ (Rahel and McLaughlin 2018) – offers an effective management solution for waterways (e.g., see Wilcox et al. 2004; Kim and Mandrak 2016; Fritts et al. 2021). The RCW’s 23 operating
lockstations, composed of 45 navigation locks (i.e., several lockstations include multi-flight locks), appear to offer some level of connectivity to native (e.g., Gillis et al. 2010; Turcotte et al. 2022) and invasive (Bergman et al. 2022) species, however a longitudinal movement study to evaluate both native and invasive fish connectivity has not been conducted. Here, we refer to a lock as a chamber with gates at both ends that allows water to be let in or let out to raise or lower vessels from one water elevation to another (i.e., to move upstream or downstream), while a lockstation (LD) describes the entire site composed of land and associated structures (i.e., the lockmaster house), the lock(s), the water-control dam and weir, and any other navigation or water-management structure. Additionally, while more researchers are evaluating navigation locks as a connectivity pathway to fishes, most studies focus on a single lockstation and/or in large, shipping waterways, and few monitor both invasive and native species movements (though see Tripp et al. 2014 & Kim and Mandrak 2016). Movement ecology research produces knowledge of individual species movements that can enable decision-makers to implement evidence-based management strategies (Allen and Singh 2016; Cooke et al. 2022). To develop any selective fragmentation strategy in the RCW, we must first assess to what extent native and invasive fishes move throughout the system and the potential factors influencing connectivity.

The RCW is home to two invasive fishes: (1) common carp (Cyprinus carpio; hereafter “carp”), native to Eurasia and (2) round goby (Neogobius melanostomus), native to the Black and Caspian Seas. A combination of early sexual maturation, rapid growth, and ecological plasticity contributed to the rapid expansion of introduced carp populations (Weber and Brown 2009). Numerous studies have reported the effects of one of the “world's most ecologically harmful invasive species” (Lowe et al. 2000; Weber and Brown 2009, Kulhanek et al. 2011) though, promisingly, research indicates carp movement ecology data can support successful control efforts (e.g., Bajer et al. 2011; Donkers et al. 2012; Taylor et al. 2012). Previous work evaluated dispersal potential of the round goby invasion in the RCW (see Bergman et al. 2022), however the extent to which carp navigate the waterway is unknown. Accordingly, we used two fish tracking methods, acoustic telemetry (2019-2021) and mark-recapture (2018-2023), to assess connectivity relative to lock operations and environmental conditions. We selected northern pike (Esox lucius) and largemouth bass (Micropterus salmoides) as our two native study species to acoustically track because of their contrasting movement ecology (i.e., northern pike are migratory whereas largemouth bass are more resident; Midwood and Chow-Fraser 2015) and shared recreational importance (Bence and Smith 1999; Rous et al. 2017). Carp were chosen as our model invasive species because: 1) they can negatively affect (Weber and Brown 2011), and have similar habitat associations to (Gertzen et al. 2017; Brownscombe et al. 2023), largemouth bass and northern pike and 2) may serve as a partial Asian carp analogue and thus a proxy for preventive dispersal policies (via similar swimming performance; Bzonek 2017; Finger et al. 2020). The Laurentian Great Lakes are currently at risk of an Asian carp invasion likely via the Chicago Area Waterways System; thus, information on how carps use
navigation locks to disperse will be critical to managers. Our objectives were to determine: 1) the species-specific passability of lockstations, including identifying the use of navigation locks versus dams, 2) the influence of environmental variables and lock operations on the direction and timing of passages, and 3) how fish interact with waterway infrastructure and the influence of native versus invasive species. We also opportunistically evaluated potential differences in fish behaviour before and during the COVID-19 pandemic related to global restrictions and lockdowns (i.e., the anthropause, “a period of considerable slowing of modern human activities”; Rutz et al. 2020).

Figure 5.1. Full acoustic telemetry array, spanning 45.7 km, to monitor native and invasive fish connectivity in Canada’s historic Rideau Canal Waterway. Receivers were deployed during the navigation season, from mid-May to mid-October, during 2019-2021. Each circle denotes an individual acoustic receiver, color-coded to be reach specific. Arrows point to each lockstation (LD) and the Rideau Ferry bridge which delineates Big Rideau Lake (Reach 1) and Lower Rideau Lake (Reach 2). Water flows in the northeasterly direction. The Narrows and Kilmarnock LDs serve as the southern and northern termini, respectively. Reach designations are as follows with color designation in parenthesis:
Reach 1 - Narrows LD to Rideau Ferry (salmon); Reach 2 - Rideau Ferry to Poonamalie LD (pale blue); Reach 3 - Poonamalie LD to Smiths Falls Detached LD (green); Reach 4 - Smiths Falls Detached LD to Smiths Falls Combined LD (yellow); Reach 5 - Smiths Falls Combined LD to Old Slys LD (orange); Reach 6 - Old Slys LD to Edmonds LD (teal); Reach 7 - Edmonds LD to Kilmarnock LD (purple); Reach 8 - Kilmarnock LD downstream (pink). We documented fish passage events at all LDs except Narrows. Information about each LD and reach can be found in Tables 1 and 2. For a figure of the full 202 km Rideau Canal Waterway, and enlarged images of our acoustic array, see Appendix S1: Figs. S1-4.

Figure 5.2. Enlarged acoustic telemetry array at, and images of, Edmonds Lockstation (LD). (A): Example of receiver array at a LD to monitor fish passage events and interactions with infrastructure. LDs in the waterway are composed of a navigation lock(s) and water-control dam. The circles denote receivers, with blue circles indicating receivers deployed upstream (Reach 6) and purple circles indicating receivers deployed downstream (Reach 7) of Edmonds LD. Receivers were deployed above and below locks at all LDs monitored. The Edmonds Dam was monitored by receivers in 2019 and 2020, though not all dams had coverage during our study due to equipment constraints. (B): The Edmonds Lock chamber as water levels are being lowered. The gates in the image are the downstream gates. Note the hand cranks on the gate, which lockmasters use to manually operate the lock. (C): The
Edmonds Lockstation has a 167-m-long and 4.1-m-high stone arch dam consisting of a 96 m overflow stone weir and a 7.5-m-long waste-weir of stacked logs. The dam creates a slackwater section to the upstream double-flight LD, Old Slys. There are no fish pass systems in place at LDs in the Rideau Canal Waterway, making navigation locks the most plausible upstream connectivity pathway.

5.3. Materials and methods

5.3.1. Study area and acoustic-receiver array

We tracked fish movements using acoustic telemetry during the 2019, 2020, and 2021 navigation seasons (annually from mid-May to mid-October) in the RCW. Our telemetry array spanned 45.7 km, from Narrows Lockstation (44°42'10.8"N 76°17'44.2"W) to Kilmarnock Lockstation (44°53'04.5"N 75°55'49.4"W), including coverage of navigation locks (hereafter, “locks”) at the seven lockstations within this stretch (Table 1). We selected this portion of the RCW to study because it acts as a representation of structures and environments present in the full waterway: it includes both single- and multi-flight locks, electrically-operated versus manually-operated locks, and the various environment types that can be found throughout system (Table 2). Although most LDs in the RCW have a single lock (i.e., only one lock chamber), several have multiple locks-in-flight connected to each other by gates. Additionally, most locks are operated manually, by human power and gravity, except at three LDs with electrically-operated locks (at Black Rapids, Smiths Falls Combined, Newboro; see Appendix S1: Fig. S1). All locks in the RCW have the same length (41 m) and width (10 m), however the lock lift (i.e., water column depth including the sill elevation of the upper and lower lock gates) varies based on the elevation difference between the two adjacent reaches. The differential in water-level elevation between reaches in our acoustic array indicates upstream passages should occur exclusively through locks as dams are too high for fish to jump. There may be cases during spring freshet when elevation differentials are minimized, and fish may be provided a chance to move upstream via the weir or through the radial gate at Poonamalie LD, though we expect higher flow rates to make upstream passages via dam structures challenging if not impossible for fishes. Thus, our focus was on lock connectivity given most dam heights impede upstream movement. The region between Narrows LD and Poonamalie LD is 31.3 km long and includes Big Rideau Lake and Lower Rideau Lake, two water bodies delineated by the Rideau Ferry bridge. Given the size and habitat differences between Big Rideau Lake and the shallower, more riverine Lower Rideau Lake (max depth 25 m), we designated each lake as a unique reach (Fig. 1).

All receivers used in this study were Lotek Wireless Inc. WHS 4250 acoustic receivers (416.7 kHz) programmed to log on a continuous cycle. The regions surrounding LDs were separated into four unique approaches: downstream lock approach, downstream dam approach, upstream lock approach, and downstream lock approach. We define the downstream and upstream lock approaches as the area,
within 100 m, downstream and upstream the lower and upper lock gates, respectively. All locks were monitored by two adjacent (<5 m) receivers on the upstream and downstream sides (i.e., lock-approach receivers). When possible, receivers were also deployed in excavated lock channels (e.g., see Appendix S1: Fig. S2-4). In 2019, receivers were deployed inside Edmonds Lock (N = 4, one in each corner of the lock chamber) for a separate study, but detections from these “lock-chamber receivers” were included. We also opportunistically deployed receivers near dams (i.e., “dam-approach receivers”) based on equipment availability. The following upstream and downstream dam approaches were monitored in 2019 and 2020: Poonamalie, Smiths Falls Combined, and Edmonds. The upstream dam approaches at Smiths Falls Combined and Kilmarnock were monitored in 2019 and 2020, however the downstream dam approaches provided logistical difficulties and were not monitored (e.g., waters too shallow and vegetated, respectively). A receiver was deployed in the downstream dam approach at Old Slys in 2020, however there was no coverage of the upstream dam approach at Old Slys either year due to equipment constraints. Note that in 2020, the Poonamalie downstream dam approach receiver malfunctioned and did not detect any transmissions, and coverage of the Edmonds downstream dam approach was reduced from three receivers to one. Additionally, receivers were deployed away from infrastructure (>200 m), relatively evenly throughout reaches, in lacustrine and riverine areas to evaluate general space use (referred to as “non-LD receivers”; see Fig. 1 and 2, and Appendix S1: Fig. S2-4). A similar number of receivers were deployed in 2019 (N = 71) and 2020 (N = 64). Due to equipment constraints, only lock-approach receivers (N = 26) were deployed in 2021. Information about detection range and efficiency testing can be found in Appendix S1: Table S1, and Figs. S5 and S6. Briefly, range testing results indicate 1) receivers in shallow, and especially vegetated, areas have low detection ranges (<100 m) and 2) lock-chamber and lock-approach receiver detection ranges may overlap, so in the case of passage events, we required a fish to be detected on a non-LD receiver in the new reach to be considered a true passage.

5.3.2. Acoustic and anchor tagging

Captured fish were handled in compliance with guidelines of the Canadian Council for Animal Care (CCAC) and approved by the Carleton University Animal Care Committee (AUP #119284). Fish sampling occurred from May-October 2019 and July-August 2020 during daylight hours between 0700 and 2000. All largemouth bass and northern pike acoustic tagging concluded in 2019; 26 additional carp were acoustically tagged and released in 2020 in Reaches 3 and 6. If a fish appeared in distress (e.g., equilibrium imbalance, change in ventilation rate, lack of movement when gently prodded; Tsitrin et al. 2020) it was immediately released and not used in this study. Fish were captured using boat electrofishing and standard hook-and-line angling. For electrofishing, we used a Smith-Root electrofishing boat (2.5 Generator Powered Pulser; Smith-Root Inc., Vancouver, WA, USA) to sample
littoral areas. To reduce the risk of injuring fish within proximity of the electrical field, we used pulsed
direct-current at a rate of 60 pulses/sec (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. The majority of carp and largemouth bass were captured via electrofishing (98%
and 70%, respectively), whereas most northern pike were captured via angling (68%).

Upon capture, fish 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 (details on surgical
methods below). We implanted 56 largemouth bass, 65 northern pike, and 54 carp with a small or large
disinfectected (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=1522 days; large tag: L-AMT-14-12, 8.0 g in
air, 45×14×14 mm, expected battery life=3114 days). We also included data from 49 northern pike that
were acoustically tagged with the same large-model tag but that transmitted signals at a 5 s interval
(expected battery life=1009 days). These individuals were captured upstream (Reach 6) and
downstream (Reach 7) of Edmonds Lock and experimentally released inside the lock chamber for a
different project. Note that one individual was released (accidentally) upstream ~25 m from Edmonds
Lock. We refer to these individuals hereafter as “experimental northern pike”. Thus, 224 acoustically-
tagged fishes were included in this study. Of the 175 individuals with 20 s tags (i.e., non-experimental
northern pike), 60% were translocated from their site of capture (<1000 m) and surgically tagged and
released in protected lock channels during poor weather conditions that created an unstable
environment on our vessel (i.e., high winds and/or waves); note, however, all fish were released in their
capture reach. Tag burden was calculated by dividing the acoustic tag weight in air by the fish weight
(both in grams) and multiplying by 100. Mass measurements were not taken in the field; instead, they
were generated using models from Schneider et al. (2000). Tag burden was low, likely incurring no
negative effect on fish behaviour or survival (mean ± SD for largemouth bass, northern pike, and carp:
1.0-0.3%, 1.0-0.5%, 0.3-0.6%; Appendix S1: Table S2) (Bridger and Booth 2003; Jepsen et al. 2005).

Surgical implantation of acoustic tags followed methods by Bergman et al. (2023) with minor
modifications. We used Smith-Root electric fish-handling gloves to immobilize fish for surgery,
positioned on the head and caudal peduncle. Gloves were set to the lowest current setting (4 mA) to
immobilize the fish but allow continuous respiration. A small (<1 cm) incision was made centrally on the
midline, posterior to the pectoral fins using a sterilized No. 21 scalpel. The initialized tag was inserted
into the body cavity and the incision closed with 1-2 simple, interrupted sutures (PDS II polydioxanone
suture, violet monofilament, 2-0). We measured total length (TL; mm) and marked each acoustically-
tagged fish with an external anchor tag (FLOY TAG and Mfg., Inc., Seattle, Washington, USA), inserted
into the epaxial muscle ventral to the dorsal fin for mark-recapture analysis (Appendix S1: Fig. S7). Post-
surgery, all individuals were monitored for behaviour changes or distress (Tsitrin et al. 2020). No fish
showed any apparent adverse effects from surgery and were released when equilibrium was gained
and strong swimming actions were observed, which occurred almost immediately post-surgery (Davis
2010; Landsman et al. 2015). All non-acoustic target species captured during angling and electrofishing
efforts, larger than 69 mm TL, were anchor tagged and released in their capture reach. The species, TL,
anchor tag ID, date tagged, and release location were documented for each individual. We coordinated
tagging efforts at local black bass (*Micropterus* spp.) fishing tournaments to bolster our sample sizes,
spread awareness of our mark-recapture study in the RCW, and engage anglers in reporting captures
of tagged fishes.

5.3.3. Lock operation and environmental data

We evaluated fish passage data in relation to environmental variables and lock operations. Parks
Canada provided lock operation reports that included total daily lockages at each LD, and flow rate
(m³/s) data (protected data) from the Poonamalie Dam as a proxy for discharges in the system. Water
temperature (°C) was measured by an Onset HOBO U20-001-01 Water Level Logger (Bourne,
Massachusetts, USA) installed on the riverbed in the West Branch Rideau River at the Watson’s Mill
Dam (~45 km upstream Kilmarnock LD). The HOBO logger recorded water temperature once per day.
Hereafter, water temperature is referred to as “temperature.” Discharge, temperature, and lockage
frequency data were averaged bi-weekly (days 1-15 and 16-30/31 each month) for analysis. Data was
not provided past October 13 each year as this is the non-operational period (end of navigation season)
of the RWC where no lockages occur.

5.3.4. Data analyses

5.3.4.1. Raw telemetry data filtering

All data processing and statistical analyses were conducted using R version 3.6.2 (R Core Team 2019).
Areas near locks and dams are inherently “noisy” environments and can result in a high number of false
positive detections (Tuononen et al. 2022); thus, several filters were employed to identify and remove
likely false positives. Detection filtering closely followed methods by Algera et al. (2020), Tuononen et
al. (2022), and Bergman et al. (2023). We applied a combined minimum lag-interval filter that filters data
by tag transmission rate (here, 20 s or 5 s) and requires at least two detections to be recorded within
600 s, and a minimum power requirement filter (>9 dBm). The final filter, a “detection event” filter
(Holbrook et al. 2019), grouped final (filtered) individual detections into discrete events defined by
movements between receivers and sequential detections at the same receiver separated by a
predefined timeframe (3600 s). We required each detection event to have >2 detections and carefully inspected the final dataset, finding all events appeared plausible. Our final dataset was composed of 26,700 detection events (589,603 individual detections) from 53 largemouth bass, 87 northern pike, and 53 carp (193 fishes detected; three largemouth bass, 27 northern pike [most of which were simply released >1000 km from a receiver used in this study], and one carp were not detected post-filtering). If an individual was detected on multiple receivers and/or across multiple years, we assumed the fish was alive. As such, abacus plots did not indicate mortality events (see Appendix S3).

5.3.4.2. Passage data

Passage events were identified using detections from the longitudinal telemetry array. We define a “passage event” as the required movement across a LD to be detected in a new reach. Passages could be: 1) documented whereby passages occurred during the navigation (tracking) season and were therefore detected via receivers or 2) undocumented if a fish conducted a passage outside the navigation season. For example, if a fish was detected in a new reach the subsequent year, we considered each LD that required crossing to be a passage event. If a fish was detected on any receiver upstream a LD, and subsequently detected on any receiver downstream that LD, we considered it a downstream passage and vice versa for upstream passages. We used the lock- and dam-approach receivers to determine the connectivity pathway for passage events. If detections were too sparse to determine the connectivity pathway, “unknown” was denoted.

To evaluate potential drivers of passages, we developed a suite of generalized linear mixed models (GLMM) using the glmmTMB function (package glmmTMB; Douma and Weedon 2019; Brooks et al. 2022). The first model we created assessed biological and environmental factors that may have influenced individual fishes to conduct a passage. Each individual fish was assigned a “0” or “1”, classifying if they did not or did conduct a passage, respectively, during the study (binary, categorical variable). We fit the model to evaluate potential effects of tag burden (continuous), TL (continuous), temperature (continuous), upstream LD distance (continuous), downstream LD distance (continuous), and discharge (continuous) on individuals that conducted a passage. Upstream and downstream LD distances were calculated using the distHaversine function in the geosphere package to measure the shortest distance between two points (here, release location to the upstream and downstream LDs; Hijmans 2019). Release reach and species were included as random effects to account for variation in species-specific sample sizes for each reach. We ran residual diagnostics using the DHARMa package (Hartig 2022) to test model assumptions. Additionally, we used the check_overdispersion function to evaluate overdispersion and the check_collinearity function to assess collinearity (requiring low correlation, VIF <5) (both from the performance package; Lüdecke et al. 2021). Akaike’s Information
Criterion, corrected for small sample sizes (AICc), was used (Burnham and Anderson 2014; Anderson et al. 2021) via the dredge function from the *MuMIn* package (Bartoń 2023) to confirm best model fit. The model with the lowest AICc value was designated as our final (reduced) model.

We fit two additional GLMMs to investigate the effects of discharge, temperature, lockage frequency, and TL in relation to passage direction (upstream or downstream; categorical) and species (categorical). The average daily discharge rate and temperature, and total number of lockages that day at the LD crossed, were assigned to each individual passage. Only detected passages were included in these models ($N = 26$), as environmental and lock operation data cannot be assigned to an undetected passage event that occurred outside the navigation season. TL was only included in the passage direction model given inherent size differences between the two species. A random intercept for individual fish (fish ID) was included in each model because several fish conducted multiple passages (i.e., multiple observations from a single individual). Model assumptions were tested as described above.

### 5.3.4.3. **LD interactions**

We evaluated how largemouth bass, northern pike, and carp interacted with LD infrastructure in the RCW across the 2019 and 2020 navigation seasons to evaluate potential 1) species-specific relationships with infrastructure and 2) effects of the anthropause on behaviour. As noted above, our longitudinal array was reduced in 2021 to only monitor locks and therefore detection data was not included from that year. We excluded experimental northern pike to control for potential atypical behaviour post-translocation. The total number of individual largemouth bass, northern pike, and carp included in analysis for 2019 and 2020 were 53 and 15, 38 and 8, and 27 and 42, respectively. All (detected) fish included in interaction analysis were mature, except six largemouth bass, five northern pike, and eight carp.

A Residency Index (RI) was calculated to quantify approach-area residency as a measure of species-specific interaction with infrastructure using the *GLATOS* package (Kessel et al. 2016). RI is calculated by dividing the distinct number of days detected at a receiver by the total number of days detected at any receiver for each individual. As such, RI values are proportional, ranging from 0 to 1, with a value of 1 indicating continuous residency at a given station. RI was selected as it minimizes potential bias of large numbers of detections at a given receiver generated by only a few (more sedentary) individuals. Individual receivers across the full array were assigned to an approach area (upstream dam approach, downstream dam approach, upstream lock approach, downstream lock approach). To determine if fish instead selected for habitats away from infrastructure, we also included all receivers >200 m from LDs and classified them as “away” (i.e., “non-LD receivers”). We grouped the two receivers downstream of...
Edmonds Lock (<50 m apart) and the three receivers downstream of Edmonds Dam in 2019 (<100 m apart) together. We also included the four Edmonds Lock chamber receivers in 2019 in the “downstream lock approach”. The two receivers upstream the Smiths Falls Combined LD, above the lock and dam approaches, had overlapping detection ranges; because we were unable to differentiate which LD approach area fish were truly in, we simply classified detections on these receivers as “away”. RI values were generated separately for the 2019 and 2020 navigation seasons, at each approach area (including “away”), and averaged to provide a mean RI ± SD for each species. RI was not statistically analyzed due to low sample sizes; instead, we use RI to illustrate fish interactions with infrastructure in the RCW.

5.4. Results

Over the duration of our study, 86% (193/224) of acoustically-tagged fishes were detected. For the first (2019), second (2020), and third (2021) navigation seasons, 85% (168/198), 35% (79/224), and 11% (24/224; note only lock-approach receivers were deployed in 2021) were detected, respectively. It is likely the decline in tags detected is due to 1) early tag battery failure, as only large-size tags were detected in 2021, or 2) porosity of our acoustic array whereby fish swam outside the detection range of our receivers. Because we detected most fish at least once, we do not expect to have missed inter-reach passages in 2019 or 2020 (i.e., as above, defined by being detected on any receiver in a reach and then detected on any receiver in a new reach). We likely missed non-lock passages in 2021, unless fish were detected on lock receivers at some point before and after the passage.

Across the three years, temperature ranged from 12.26–26.87 °C (mean = 21.99 °C) and discharge ranged from 3.89–37.82 m³/s (mean = 7.71 m³/s). Temperature was significantly cooler in 2019 compared to 2020 and 2021 (P<0.001). Discharge rates were significantly faster in 2019 (P<0.001; mean = 9.70 m³/s) and slower in 2021 (P=0.023; mean = 5.48 m³/s), with flows in 2020 (mean = 7.93 m³/s) similar to 2019 though lacking the higher spring freshet velocities (see Fig. 3). A total of 39789 lockages occurred across the seven LDs during the study. Lockage frequencies varied annually, with 13902 lockages in 2019, 11654 lockages in 2020, and 14233 lockages in 2021. There were significantly fewer lockages in 2020 (P<0.001) due to COVID-19 pandemic restrictions (i.e., delayed navigation season start, limited non-local tourism permitted). July and August were months with the warmest temperatures and greatest number of lockages (mean ± SD: 20 ± 8 and 20 ± 7 lockages/day, respectively), with May, June, September, and October being cooler and having considerably lower lockage frequencies (6 ± 4, 9 ± 7, 10 ± 6, 6 ± 4 lockages/day, respectively). A summary of statistical test outputs for models evaluating abiotic factors by year is reported in Appendix S2: Table S1. For average lockages/day for each LD each year, see Fig. 3 and Table 1.

5.4.1. Passages
5.4.1.1. Acoustic telemetry

Twenty-three fish, comprising eight largemouth bass and 15 northern pike, conducted 35 passages in 2019 and 2020; our telemetry array did not detect passages in 2021. Northern pike accounted for 69% of passages (24/35) with largemouth bass conducting the remaining 11 passages (31%). Six individuals were experimental northern pike, five of which had been captured upstream (Reach 6). Three largemouth bass and five northern pike conducted multiple passages. The range and average distance (metres) largemouth bass and northern pike traveled to conduct a passage was 52-2207 and 952, and 58-8365 and 1313, respectively. The range and average time (days) between release and passage for largemouth bass and northern pike was 0-440 and 66, and 0-446 and 91, respectively. We did not detect carp passages during our study. For detailed information about each passage, see Table 3.

Most passages were confirmed to have occurred in the downstream direction (77%; 27/35), with 12 occurring via locks and five via dams. Telemetry data was too coarse, or the passage was undetected (i.e., occurred outside the navigation season), to reveal the pathway for ten downstream passages. Eight passages (23%) occurred in the upstream direction. Five upstream passages occurred via locks and the pathway was unclear for the remaining three (two were undocumented and telemetry data was too coarse for the third). Collectively, 49% (17/35) of passages occurred via locks. We recorded passages at all LDs in our telemetry array, except Narrows LD. However, upstream passages only occurred at the Poonamalie, Smiths Falls Detached, and Edmonds LDs. The locks at these three LDs are single-flight and manually-operated with a lesser lock lift (2.2-2.8 m) compared to other locks in the system (e.g., Smiths Falls Combined LD has a lock lift of 7.6 m; Table 1). We found no significant influence of tag burden, TL, temperature, upstream or downstream LD distances, or discharge on individuals that did, or did not, conduct a passage (see Biological and environmental influences on fishes that conducted a passage; Appendix S2: Table S2).

Nine passages occurred outside the tracking season (i.e., undocumented). For the remaining 26 documented passages, we evaluated the influence of abiotic variables (i.e., discharge rates, temperature, lockage frequencies) on the direction of, and species conducting, passages (see Abiotic and biological influence on passage direction and species; Appendix S2: Table S2). The first model revealed that discharge significantly affected the direction of passage ($P=0.042$) whereby upstream passages only occurred at lower flows ranging from 5.16-9.44 m$^3$/s (mean = 6.91 m$^3$/s) whereas downstream passages could occur at higher flows ranging from 5.34-31.48 m$^3$/s (mean = 14.39 m$^3$/s). Temperature, lockage frequency, and fish size (TL) did not significantly influence passage direction. The second model revealed no significant differences between largemouth bass and northern pike (Appendix S2: Table S2).
5.4.1.2. Mark-recapture

Fifteen species were externally anchor tagged \((N = 9564)\) including bluegill \((Lepomis macrochirus; N = 1132)\), pumpkinseed \((Lepomis gibbosus; N = 182)\), black crappie \((Pomoxis nigromaculatus; N = 35)\), rock bass \((Ambloplites rupestris; N = 184)\), yellow perch \((Perca flavescens; N = 99)\), brown bullhead \((Ameiurus nebulosus; N = 47)\), white sucker \((Catostomus commersonii; N = 50)\), walleye \((Sander vitreus; N = 55)\), smallmouth bass \((Micropterus dolomieu; N = 3000)\), muskellunge \((Esox masquinongy; N = 55)\), lake trout \((Salvelinus namaycush; N = 1)\), largemouth bass \((N = 3808)\), northern pike \((N = 832)\), and (common) carp \((N = 82)\) (Appendix S1: Table S3). The vast majority \((8732; 91\%)\) of externally-tagged fishes were released in large lakes that span the portion of the RCW from Poonamalie LD to Davis LD (collectively referred to as the “Rideau Lakes”). This bias is the result of partnerships with angling tournaments that permitted us to externally tag individuals prior to live release. Recaptures were reported for 564 individuals \((6\% \text{ recapture rate})\). Fifty-four individuals were recaptured multiple times, totaling 636 recapture events. Five externally-tagged individuals conducted passages at the Newboro, Davis, and Narrows LDs, comprising three largemouth bass and two smallmouth bass, with one largemouth bass crossing two LDs (Table 3). We documented <1\% of externally-tagged fishes conducting a passage.

5.4.2. LD Interactions

Mean RI for the two navigation seasons was relatively low at LDs for each species, ranging from zero to \(0.25 \pm 0.46\) (Appendix S1: Table S4; Fig. 5). The “away” area \((\text{i.e., } >200 \text{ m from LD infrastructure})\) had considerably higher RI values, ranging from \(0.48 \pm 0.51\) to \(0.85 \pm 0.24\) (Appendix S1: Table S4; Fig. 5). Carp had a higher affinity for both downstream dam and lock approaches, whereas northern pike showed higher residency for downstream lock and upstream dam approaches. Largemouth bass residency was generally low at all LD-approach areas, indicating a general disinterest in infrastructure. We documented an increase in residency for all three species in the upstream dam approach in 2020 (see Appendix S1: Fig. S8) and northern pike at downstream lock approach. There was no notable difference in residency between years for largemouth bass and carp away from infrastructure between years. In all other cases, residency decreased in 2020.
Figure 5.3. Abiotic information (left panels) and fish passage data for acoustically-tagged northern pike and largemouth bass (right panels). Black rhombuses with a solid line, grey rhombuses with a fine-dotted line, and white rhombuses with a thick-dotted line represent the 2019, 2020, and 2021 navigation seasons, respectively. The navigation season each year in the Rideau Canal Waterway runs from mid-May to mid-October. Discharge rate (m$^3$/s), daily lockage frequency, and (water) temperature (°C) data, averaged bi-weekly, are provided in the left panels. Discharge rates were highest in spring 2019. Lockage frequency and water temperature followed similar trends each year, peaking in July and August, though there were less lockages in 2020 as a result of COVID-19 lockdowns and restrictions. Cumulative passages for largemouth bass and northern pike are provided by month in the right panels. Northern pike conducted the most passages, with a peak number of passages ($N = 9$) in June 2019. No acoustically-tagged common carp passages were recorded and, therefore, this species was not included in the figure. No passage events were recorded in 2021. Note that mark-recapture fishes that passed LDs are not included here (see Table 3).
Figure 5.4. Boxplots illustrating the relationship between passage direction and abiotic variables, (water) temperature (°C), lockages, and discharge (m³/s), for northern pike and largemouth bass. Our results suggest that during the navigation season, fishes move upstream more often during periods of warmer temperatures and higher lockage frequencies. Individuals were only able to pass upstream when discharge rates subsided to <10 m³/s ($P=0.042$). Both northern pike and largemouth bass showed similar responses to abiotic variables. Boxes represent the boundaries of the upper and lower quartiles, lines inside boxes represent medians, and whiskers represent the minimum and maximum values.
5.5. Discussion

5.5.1. Waterway connectivity

To our knowledge, this study is the first to evaluate longitudinal native and invasive fish connectivity in a UNESCO-designated waterway using acoustic telemetry. Similar research that directly monitored movements of invasive and native fishes, using tracking techniques like telemetry, was conducted in large, commercially-important waterways like the Mississippi River (e.g., Tripp et al. 2014; Finger et al. 2020; Fritts et al. 2021; Turney et al. 2022) and Laurentian Great Lakes’ canals (e.g., the Welland Canal - Kim and Mandrak 2016; St. Marys River - Currie et al. 2017). Our results indicate that LDs in the RCW minimize, but do not entirely restrict, fish connectivity. It is important to acknowledge that LDs in the RCW were constructed to overcome navigation barriers, like waterfalls or rapids, that likely represent historical barriers to movement (Watson 2006; also see Turcotte et al. 2022). As such, LDs may actually be permitting more fish connectivity than historical barriers. Additionally, because construction of the RCW connected previously disconnected watersheds, there is likely overall higher levels of connectivity across the region compared to pre-construction. Nevertheless, passages in our study were relatively uncommon; only 10% of acoustically-tagged fishes conducted a passage, with <1% of mark-recapture individuals passing a LD. Specifically, we documented 11 largemouth bass conducting 15 passages (three mark-recapture individuals), 15 northern pike conducting 24 passages, and two smallmouth bass each conducting a single passage (both mark-recapture individuals).

The finer-scale coverage of our telemetry array near locks provided evidence of fish use, in both the upstream and downstream directions. Navigation locks commonly lack the necessary attractant flow to facilitate upstream fish passage (Coker 1929; Moen et al. 1992; Wilcox et al. 2004), with most studies documenting limited native and invasive fish use (e.g., Tripp et al. 2004; Fritts et al. 2021). Similarly, we recorded only four (8%) and eleven (13%) (acoustically-tagged and detected) largemouth bass and northern pike, respectively, moving through locks. Passages by these individuals via locks, however, comprised roughly half of all passage events, highlighting the importance of locks as a conduit for inter-reach movements. We found only two other studies that monitored northern pike passage through locks: Kim and Mandrak (2016) reported one individual conducting a passage in the Welland Canal, whereas Currie et al. (2017) did not document any northern pike passages in the St. Marys River. Silva et al. (2017) noted that unpublished work in the Barmby Barrage and Lock in the United Kingdoms’ River Derwent recorded northern pike passing upstream, though details are not provided. A similar species, muskellunge (Esox masquinongy), has also been documented using navigation locks to access new areas (Muir and Sweet 1964; Gillis et al. 2010). We again discovered only two studies evaluating largemouth bass movements through locks: Kim and Mandrak (2016) did not document largemouth
bass passages in the Welland Canal, and Snyder et al. (2022) estimated 13% of individuals move upstream the Brandon Road Lock and Dam (BRLD) in Illinois’ Des Plaines River (via fin ray microchemistry). Overall, there is a lack of knowledge on the use of locks by northern pike and largemouth bass and, further, the above-listed studies evaluated connectivity in waterways with large shipping locks (e.g., the BRLD lock is 183x34 m; Welland Canal locks are 234x24 m) which are quite different to the smaller locks found in the RCW (i.e., 40x10 m).

We did not record any carp passages during our study, surprisingly, given that previous research documented them passing both upstream and downstream at LDs in the Mississippi River (Coker 1929; USACE 2016; Finger et al. 2019; Whitty et al. 2022) and Welland Canal (Kim and Mandrak 2016). There are several possible explanations as to why carp in the RCW appear confined to their respective reach. First, interaction analyses (see next section) indicated that carp in the RCW are more drawn to downstream dam approaches, areas with higher attractant flows, but that provide limited (if any) options to ascend upstream. Though carp were also detected in downstream lock approaches, and even inside the chamber (via lock-chamber receivers in Edmonds Lock; see Appendix S3 for fish #6307, #71B0, #A317, #BBED, #C221), locks appear difficult for them to navigate. Research has suggested that while fish may enter locks, there is a short amount of time upstream gates are open to guide a successful exit, and usually there is little flow to help guide fish upstream (Cooke et al. 2002; Travade and Larinier 2002). Additionally, fish inside locks may be entrained during emptying cycles and forced back downstream (Wilcox et al. 2004). Second, lock operations, and the motorized vessels that use locks, produce considerable anthropogenic noise; carp have a well-developed sense of hearing and, as such, may be deterred by sound especially in the RCW’s small locks (i.e., negative phonotaxis; Zielinski and Sorensen 2017; Dennis et al. 2019). We acknowledge, however, that research indicates carp habituate to sound (Murchy et al. 2016; Dennis and Sorensen 2020; Riesgraf et al. 2022), so individuals may eventually be capable of passing upstream via locks if enough time is spent in the area. Third, because the system is more connected in the direction of flow (i.e., 77% of passages were downstream), the lack of time carp spent near upstream approaches means less opportunity for downstream passage. Carp have indeed proliferated throughout the waterway and been present for decades, so while we may not have recorded any passages, inter-reach movements (naturally or via anthropogenic vectors) must be occurring at high enough frequencies to have supported dispersal and establishment.

Our results suggest that several abiotic – and likely, intertwined – factors are influencing connectivity. Disentangling the effects of temperature and discharge on fish movements in lotic systems is a challenge researchers commonly face as the relative importance of each can be system- and species-specific (Bunt et al. 2001; Swanson et al. 2021; Epple et al. 2022). Due to the low number of passages recorded during our study across the three years, it was difficult to interpret a relationship between
season and passage frequency, though we did note an effect of abiotic variables on passage direction. Upstream passages, by both northern pike and largemouth bass, occurred during periods of warmer temperatures, higher lockage frequencies, and lower discharge rates. Fritts et al. (2021) similarly documented fishes moving upstream through a lock by entering and exiting the chamber with upstream vessel tows, suggesting more lockages offer increased upstream passage opportunity. In summer months of July and August, temperature and lockage frequencies increase considerably, coinciding with lower flows as spring freshet subsides. Although we found no significant relationships between temperature or lockages on passage direction, discharge did have a significant effect whereby fish only moved upstream once flows subsided to <10 m$^3$/s. During periods of increased discharges, fish may be drawn away from locks towards higher-flow areas downstream of (impassable) dams. Fish being attracted to areas with highest discharges, and led away from true connectivity pathways (e.g., fish passage structures; or here, locks), is not uncommon (Clarke et al. 2008). As discharges slow in June and July, lockage frequencies increase, producing more flows in the downstream lock approach and potentially attracting fish.

While the relative lack of upstream passages suggests restriction of invasive species movement, it is conversely a concerning issue for native migratory species. The RCW is home to white sucker, an obligate migrator whose movements act as an important upstream vector of nutrients (Pratt et al. 2009; Childress et al. 2014) and, additionally, several at-risk migratory species like American eel (Anguilla rostrata) and snapping turtle (Chelydra serpentina) have been documented (see https://parks.canada.ca/lhn-nhs/on/rideau/nature/ee-p-sar). Connectivity of the at-risk painted turtle (Chrysemys picta; listed as Special Concern) in the RCW was evaluated by Turcotte et al. (2022) and, even though painted turtles can move by land, several of our findings parallel theirs. Using landscape genetics, they found that locks did not entirely impede gene flow across the aquatic landscape, though numerous locks in close proximity (e.g., flight locks) isolated two genetically-distinct northern and southern populations. Kim and Mandrak (2016) also found that flight locks limit fish dispersal in the Welland Canal. Similarly, we did not document any upstream passages at Old Slys, which includes a double-flight lock, or at the Smiths Falls Combined Lock, which has the largest lift in the system at 7.6 m. While we did record fish passing downstream across these LDs, both sites appear to fully impede upstream connectivity. Turcotte et al. (2022) also discovered that gene flow was stronger in the direction of water flow. They suggest flow may have facilitated downstream migrations of painted turtles, a finding supported by other work on invertebrates (Alp et al. 2012) and non-migratory fishes (e.g., threespine stickleback [Gasterosteus aculeatus], Caldera and Bolnick 2008; bullhead [Cottus gobio], Junker et al. 2012). Our findings further support the theory that systems may be more connected in the direction of flow as we mostly documented downstream passages and, moreover, we recorded downstream passages at all LDs in our telemetry array except Narrows.
Results from mark-recapture data revealed upstream and downstream fish passages at three additional LDs: Narrows, Newboro, and Davis (all single locks; lock lifts: 0.8, 2.7, 2.7 m, respectively). Further, two smallmouth bass, a non-acoustically tagged species, were documented crossing Narrows LD. The low number of mark-recapture individuals we documented crossing barriers (<1%) could be a function of the large waterbodies that most externally-tagged fishes were released in; fish in large lakes may have more suitable habitat available to carry out their life history and therefore not attempt inter-reach movements. Although managed at a whole-system level, the RCW is not environmentally homogeneous. The interconnected waterbodies that form the waterway differ considerably, and include large lakes (e.g., the Rideau Lakes) and riverine stretches, but also concrete canal-like environments that lack natural structure and generally have a lower capacity to support fishes (Cooke et al. 2020). Woolnough et al. (2009) indicated that a species’ home range—the distance regularly travelled by an organism which delineates the outer boundary of movement during everyday activities (Nathan et al. 2003)—can be attributed to the size of the waterbody in which that individual lives, whereby home range increases with increasing waterbody size. Most of our acoustic telemetry array was deployed in riverine areas and channelized habitats, which may lack the required or preferred habitat of species we acoustically tracked, resulting in more attempts by those individuals to pass barriers.

In addition, we did not conduct standardized recapture sampling and instead relied on anglers to report catches, which also likely contributed to lower recapture rates (note that mark-recapture methods generally suffer low recapture probabilities; Lees et al. 2021). Angler recapture (and report) rate in our study (6%) was the same as Keplinger (2021) (6% for channel catfish \textit{Ictalurus punctatus} in the South Branch Potomac River, West Virginia, USA) but higher than Pierce et al. (2021) (2% for largemouth bass in the upper Shark River estuary, Florida, USA). Few other studies have used mark-recapture to monitor passages across navigation locks, however our percentage (<1%) of mark-recapture fish that crossed barriers was lower than Klinge (1994) (4.7% for sea trout \textit{Salmo trutta} at the Hagestein Barrage, River Lek, Netherlands), Marson et al. (2006) (3.5% for a multi-species analysis of fishes in the Trent-Severn Waterway, Ontario, Canada), and Garrone-Neto et al. (2014) (5% and 3% for two potamotrygonid stingrays in the Upper Paraná River basin, Brazil). Although mark-recapture sampling can provide information on when and where an individual is recaptured, it fails to provide details on mechanisms or timing of passage across barriers.

5.5.2. Fish interactions with infrastructure and potential anthropause effects

Residency analysis indicated largemouth bass, northern pike, and carp spend most of their time away from infrastructure. Carp and largemouth bass showed high residency for areas away from infrastructure both years, while northern pike residency decreased in 2020. This may be because northern pike swam...
outside the detection range of our array, or shifted their space use to downstream lock and upstream dam approaches (which increased in 2020). Residency at infrastructure, for all species, was low, indicating fish did not have a strong preference for a specific approach area. There were a few notable residency patterns we describe below.

Among the three study species, largemouth bass associated the least with infrastructure. This was not unexpected given they are most abundant in areas with vegetation or other cover (e.g., woody debris) and low flows (Stuber et al. 1982; Love et al. 2011). However, the minimal time largemouth bass did spend near LDs was still sufficient to facilitate passages. Though upstream passages by largemouth bass were infrequent in our study (N = 4; including both mark-recapture and acoustically-tagged fish), other work has also documented upstream barrier attempts by largemouth bass (e.g., at fishways in the Grand River, Ontario; Bunt et al. 2001).

Northern pike spent the least amount of time beneath (impassable) dams, interacting more with approach areas that facilitate dispersal – beneath and above locks, and above dams – which may be why we documented the most passage events from this species. Note, however, that the lack of northern pike interactions with downstream dam approaches may be an artifact of our receiver deployment schedule. Northern pike commence their annual upstream spawning migration, and demonstrate highest movement activity, when spring water temperatures are between 6-10°C (usually at the end of March until mid-April in the RCW); activity decreases upon reaching spawning sites, and fish move back downstream thereafter (Ovidio and Philippart 2003; Pauwels et al. 2014). By May and June, when our receivers were deployed, water temperatures were already over 10°C, so we would have failed to detect spawning movements when northern pike might have been detected beneath dams. In addition, northern pike are typically considered limnophilic species associated with slower-flowing, lacustrine areas, usually only venturing into faster-flowing waters for suitable feeding and spawning grounds (Ovidio and Philippart 2003; Sandlund et al. 2016). The higher residency in slower-flowing approach areas by northern pike in our study support this notion. It is well documented that carp also select for shallow, vegetated habitats to carry out their life history (Penne and Pierce 2008; Banet et al. 2022) and, indeed, showed high residency in areas away from LDs. However, carp displayed elevated affinities for downstream approach areas, suggesting they are positively rheotactic and attracted to areas with higher flows (Cooke and McKinley 1999; Smith et al. 2005). As noted above, the higher carp residency beneath dams may explain the lack of passages.

We evaluated residency by year, for 2019 and 2020, to determine potential differences in behaviour before and during the COVID-19 pandemic. We opportunistically conducted this evaluation because, to our knowledge, this is the first evidence-based account of fish behaviour changes in a waterway in
response to the anthropause. However, caution should be exercised in assessing or using these results as our study was not designed to address this. First, we documented a decline in residency at downstream dam approaches and increase in upstream dam approaches for all three species. We believe shifts in residency at these approaches are related to discharge rates, and not the anthropause, as these areas are generally off-limits to motorized vessels and therefore act as a sort of ‘control’ between years. The lower discharges we documented in 2020 would have resulted in lower flows beneath dams, attracting less fish. Conversely, in 2019 when we recorded significantly higher flows in the system, fish may have avoided upstream dam areas to prevent entrainment. Note, however, that we tagged and released additional carp in 2020 in new reaches with upstream dam receivers. Given the increased sample size and spread across multiple reaches, residency of common carp in 2020 may more accurately represent their behaviour.

COVID-19 restrictions and travel bans (both internationally and within Canada) resulted in significantly less lockages in 2020; decreased lockage frequencies would result in reduced attractant flows downstream of locks and, theoretically, less opportunity for passage. We do not believe lock frequency is linked with passage via locks in the RCW as the 2021 navigation season experienced the highest frequency of lockages, but we did not document any passages. Thus, while we documented only five passages in 2020, compared to 21 in 2019, the relationship between lockage frequency and passage rate is unclear especially because upstream passages appear to occur during periods of higher lockage frequencies (as noted above). Largemouth bass showed similar residency at downstream lock approaches both years, whereas residency decreased for carp and increased for northern pike. Given interaction data indicates carp are drawn to higher-flow areas, the reduced lockages and associated flows in 2020 may be the reason they displayed a lower affinity to areas below locks. Lockage frequencies, however, also mean motorized boat traffic and associated anthropogenic noise. Navigation locks appear to pose an ecological trade-off as upstream passage conduits: increased lockages provide more attractant flow that could facilitate upstream dispersal, however they also expose aquatic animals to underwater noise that may result in avoidance behaviour (Rountree et al. 2020). Testing the effects of noise produced by lockages and recreational vessels on different invasive and native species will be an important aspect to consider for managers should navigation locks be operated to promote native fish passage (see Murchy et al. 2016).

Across both years, carp showed little interest in upstream lock approaches; however, residency decreased for both northern pike and largemouth bass. We believe this may be an artifact of our acoustic-tagging release sites, as many fish were released near upstream lock approaches in 2019. As such, 2020 may more accurately represent fish residency in upstream lock approaches. We documented 12 downstream passages through locks (nine in 2019 and three in 2020), so if fish do enter upstream
lock channels, they can indeed pass downstream. Our passage model (Appendix S2: Table 2) did not indicate a relationship between release proximity to upstream lock gates and passage, though we acknowledge that some individuals may have been passively transported downstream by current or other hydraulic factors.

Figure 5.5. Relationship between mean Residency Index (RI) at infrastructure approaches for acoustically-tagged fishes (invasive common carp, and native northern pike and largemouth bass) in the Rideau Canal Waterway during the 2019 and 2020 navigation seasons (2021 not included due to equipment constraints). Residency was evaluated at five approach areas: the downstream dam approach (DD), the downstream lock approach (DL), the upstream dam approach (US), the upstream lock approach (UL), and areas >200 m from infrastructure classified as “away” (A). All three species showed highest affinities for areas away from infrastructure, with overall low RI values near infrastructure (<0.25). See LD interactions, and Fish interactions with infrastructure and potential anthropause effects, for RI analysis methods and a discussion on findings, respectively.
5.6. Limitations

Although our study provides novel fish connectivity findings, there are certain limitations. First, we encountered significant restrictions due to COVID-19, whereby receivers could not be deployed until late June in 2020, resulting in the loss of spring data that year. Additionally, our telemetry array was reduced by ~60% in 2021. As such, we were unable to document non-lock passages or conduct residency analysis for that year. Second, while the incorporation of water temperature, lockage frequency, and discharge rate helped us understand abiotic influences on fish connectivity, it was not site-specific. We lacked daily discharge and temperature data at each LD that could have offered detailed insights into fish passage and interactions with infrastructure. Additionally, our lockage reports did not include the direction or timing (e.g., how long gates were open, time of day) of lockages, or vessel size. This information will be critical to include in future work to evaluate the mechanism of fish passage through locks in the RCW and determine if selective fragmentation strategies or conservation lockage efforts (i.e., the operation of lock systems specifically to enhance (native) fish passage; USACE 2022) could be developed and implemented. Third, given the low number of documented passages, we lacked the statistical power to determine seasonal patterns or include interactions in models. We recommend future work include higher sample sizes (of both fishes and receivers) or conduct a more focused study on fewer LDs to evaluate size- and season-specific connectivity at individual barriers. Finally, extending the monitoring period to year-round would provide important information on non-navigation season connectivity and species interactions with infrastructure, of particular interest being species whose reproductive period occurs outside the navigation season (e.g., northern pike). The incorporation of additional species with varying life histories, morphologies, and swimming capabilities will also be key in comprehensively understanding waterway connectivity.

5.7. Management considerations and conclusions

Parks Canada manages the RCW primarily to protect the commemorative integrity and universal value of the site, provide safe navigation of the waterway, all aspects of water management, and some aspects of environmental stewardship; biodiversity conservation is not a requirement, nor was it considered when the waterway was first created. Parks Canada is mandated to prioritize federally-listed species at risk and uphold the federal Fisheries Act which requires the protection of fish and fish habitat, and prevention or management of aquatic invasive species. Because modified waterways offer refuge to aquatic species from human-mediated disturbances and/or climate change (Lin et al. 2020), they may become particularly important systems in the face of extinction threats. To protect and promote the migrations of at-risk species, while simultaneously minimizing invasions, a selective fragmentation approach will be most plausible for managers to implement (Rahel and McLaughlin 2018). Selective
management of fish passage at LDs in the RCW, however, will be challenging at best, as approaches
cannot restrict navigation or threaten boater safety. For example, electric barriers would pose a
significant threat to recreational users, and structural barriers would have to be developed such that
they still permit navigation. Piczak et al. (2023) suggest the most effective selective fragmentation
method for common carp involves exploitation of sensory capabilities (e.g., visual, auditory, olfactory),
as sensory barriers would not physically restrict navigation or water flow. Sensory barriers could
therefore be applied at flight locks, which already appear to impede upstream movements, to augment
preventative entry or dispersal strategies to nonnative species. They note, however, that native species
may also be impacted, and call for further research to determine strategies to block non-native carp
species (including Asian carps), with no deleterious effects to native species. Moreover, selective
passage strategies in the RCW must also consider invasive round goby, which appear capable of using
locks to disperse. Bergman et al. (2022) found that modifying operations to ensure lock gates are closed
when not in use would reduce the chance for successful passages. This same operational behaviour
would also reduce the chance for an Asian carp entry into the Kingston Mill Lock, the southern terminus
of the RCW that connects to the Laurentian Great Lake Ontario.

Though more than 623,000 km of navigable river systems exist worldwide (Beyer 2018), there is limited
evidence on their longitudinal connectivity, especially in historic waterways. Engineered waterways,
interconnected by anthropogenic barriers, pose a unique challenge to managers as they have facilitated
many invasions and can act as “invasion highways” (Leuven et al. 2009), however they can also provide
connectivity to native species, offering access to potentially better habitats. It will be critical for managers
to carefully weigh the trade-offs between intentionally fragmenting the system to minimize the spread of
current (e.g., round goby) or new (e.g., Asian carp) invasions and enhancing connectivity between
reaches to support the migrations and movements of species at risk (e.g., American eel) and other
native wildlife. Communities along the Rideau Corridor rely heavily on tourism, particularly ecotourism
like boating, fishing, and other outdoor activities, to support their local economies (Parks Canada
2022a); protecting biodiversity and habitats in the RCW is not only imperative to conserve ecosystem
integrity, but also from an economic and cultural perspective. Given waterways are pervasive worldwide,
this research informs evidence-based management of interconnected waterways to strengthen
freshwater conservation in North America and beyond.

Chapter 5 - Tables
Table 5.1. Structural, lockage frequency, and fish passage information for each lockstation (LD). The number of locks per LD are provided, with Old Slys being the only multi-flight LD in our study. The lock lift, which is the water column depth inside the lock chamber including the sill elevation of the upper and lower lock gates, is provided in metres (m). Most locks in the Rideau Canal Waterway are manually operated to preserve the commemorative integrity and authenticity of the system, however the Smiths Falls Combined Lock is electrically operated. Average lockages per day, and the number and direction of fish passages, at each LD are presented. Note that the table is ordered by LDs from south to north (the direction of water flow).

<table>
<thead>
<tr>
<th>LD</th>
<th>Number of locks</th>
<th>Lock lift (m)</th>
<th>Lock operation type</th>
<th>Average lockages per day ± SD</th>
<th>Documented fish passages</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2019</td>
<td>2020</td>
</tr>
<tr>
<td>Narrows</td>
<td>1</td>
<td>0.8</td>
<td>Manual</td>
<td>22 ± 12</td>
<td>23 ± 11</td>
</tr>
<tr>
<td>Poonamalie</td>
<td>1</td>
<td>2.2</td>
<td>Manual</td>
<td>14 ± 8</td>
<td>15 ± 8</td>
</tr>
<tr>
<td>Smiths Falls Detached</td>
<td>1</td>
<td>2.6</td>
<td>Manual</td>
<td>12 ± 7</td>
<td>13 ± 7</td>
</tr>
<tr>
<td>Smiths Falls Combined</td>
<td>1</td>
<td>7.6</td>
<td>Electric</td>
<td>12 ± 7</td>
<td>11 ± 7</td>
</tr>
<tr>
<td>Old Slys</td>
<td>2</td>
<td>4.9</td>
<td>Manual</td>
<td>9 ± 6</td>
<td>8 ± 5</td>
</tr>
<tr>
<td>Edmonds</td>
<td>1</td>
<td>2.8</td>
<td>Manual</td>
<td>11 ± 6</td>
<td>9 ± 6</td>
</tr>
<tr>
<td>Kilmarnock</td>
<td>1</td>
<td>0.7</td>
<td>Manual</td>
<td>12 ± 7</td>
<td>10 ± 7</td>
</tr>
</tbody>
</table>
Table 5.2. Acoustic telemetry array information. We monitored fish movements ($N = 224$) across seven lockstations (LD) during 2019-2021, from the southern upstream terminus, Narrows, to the northern downstream terminus, Kilmarnock. The length of each reach, from upstream to downstream, is provided, as well as the environment types found within each reach. Note that the Rideau Ferry bridge is not a LD; we only consider it a demarcation between the two lakes. Forty-eight northern pike were experimentally released inside Edmonds Lock (Reach 6/7) for a different study. Experimental northern pike detections were only included once the fish exited the lock and were detected away from LD receivers. The range and mean total length (TL; mm) for the three acoustically-tagged species are included. Reaches were designated from south to north, in the direction of water flow.

<table>
<thead>
<tr>
<th>Reach</th>
<th>Upstream LD</th>
<th>Downstream LD</th>
<th>Reach length (km)</th>
<th>Environment type</th>
<th>Acoustically-tagged fishes (TL range, mean)</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Narrows</td>
<td>Rideau Ferry bridge</td>
<td>20.9</td>
<td>Lacustrine</td>
<td>Northern pike: (277-835, 510.92)</td>
<td>25</td>
</tr>
<tr>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Largemouth bass: (252-518, 359.45)</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Common carp: (185-874, 665.83)</td>
<td>0</td>
</tr>
<tr>
<td>2</td>
<td>Rideau Ferry bridge</td>
<td>Poonamalie</td>
<td>10.4</td>
<td>Lacustrine, riverine</td>
<td>4</td>
<td>10</td>
</tr>
<tr>
<td>3</td>
<td>Poonamalie</td>
<td>Smiths Falls Detached</td>
<td>3.7</td>
<td>Riverine</td>
<td>12</td>
<td>12</td>
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<td>4</td>
<td>Smiths Falls Detached</td>
<td>Smiths Falls Combined</td>
<td>0.6</td>
<td>Constructed channel</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Location 1</td>
<td>Location 2</td>
<td>Condition 1</td>
<td>Kilmarnock</td>
<td>Riverine, lacustrine</td>
<td>Riverine</td>
</tr>
<tr>
<td>---</td>
<td>------------</td>
<td>------------</td>
<td>--------------</td>
<td>-------------</td>
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</tr>
<tr>
<td>5</td>
<td>Smiths Falls Combined</td>
<td>Old Slys</td>
<td>1.4</td>
<td>Riverine</td>
<td>5</td>
<td>14</td>
</tr>
<tr>
<td>6</td>
<td>Old Slys</td>
<td>Edmonds</td>
<td>2.7</td>
<td>Riverine</td>
<td>9</td>
<td>7</td>
</tr>
<tr>
<td>6/7</td>
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<td>Lock chamber</td>
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<td>0</td>
<td>0</td>
<td>48</td>
</tr>
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<td>Kilmarnock</td>
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<td>Riverine, lacustrine</td>
<td>11</td>
<td>13</td>
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<td>8</td>
<td>Kilmarnock</td>
<td>N/A</td>
<td>Riverine</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Total</td>
<td>45.7</td>
<td></td>
<td>114</td>
<td>56</td>
<td>54</td>
<td>224</td>
</tr>
</tbody>
</table>
Table 5.3. Biological and passage information for acoustically tagged \((N = 23)\) and mark-recapture \((N = 5)\) fishes that conducted a passage.

For acoustically-tagged fishes, movements were monitored with receivers only during the navigation season. If a fish crossed reaches outside of the navigation (tracking) season and was detected in a new reach the subsequent year, we consider each lock-and-dam (LD) that requires crossing to be an individual passage (these events denoted by "undocumented"). The tag types describe the size (large/L or small/S) and transmission interval in seconds (5 or 20). Water temperature data was retrieved from a monitoring station at the Watson’s Mill Dam ~45 km upstream Kilmarnock LD. For mark-recapture fish, the tagging and recapture data are provided, and the total distance travelled between mark and recapture. Passage record lists multiple passage events. Species include largemouth bass (LMB), smallmouth bass (SMB), and northern pike (NP); we did not detect common carp passages. The passage direction (D=downstream; U=upstream), LD crossed, and pathway (via lock, dam, or unknown) are included. The table is ordered by species and then tag type, with mark-recapture fish listed last.

<p>| Fish ID | Species | TL (mm) | Tag type | Passage record | Tagging date | Passage/ recapture date | Passage date | Water temperature (^\circ C) | Time to passage (\text{days}) | Distance moved (m) | Passage direction | LD structure | Pathway |
|---------|---------|---------|----------|----------------|--------------|-------------------------|--------------|-----------------------------|-------------------|-----------------------|----------------|-----------|
| 0443    | LMB     | 386     | L-20     | 1              | 2019-05-31   | 2019-05-31           | 178          | 0                          | 52                | N/A                   | D             | Poonamalie | Lock       |
|         |         |         |          | 2              | 2019-05-31   | 2020-08-13           | 26           | 440                         | 2207              | N/A                   | D             | Detached  | Lock       |
| 1540    | LMB     | 393     | L-20     | 1              | 2019-05-17   | 2019-05-17           | 13           | 0                           | 70                | 18                    | D             | Edmonds   | Lock       |
| 2455    | LMB     | 396     | L-20     | 1              | 2019-05-18   | 2019-05-18           | 14           | 0                           | 70                | 22                    | D             | Edmonds   | Lock       |
| 2631    | LMB     | 456     | L-20     | 1              | 2019-05-14   | undocumented         | N/A          | N/A                         | 2170              | N/A                   | D             | Detached  | Unknown    |
|         |         |         |          | 2              | 2019-05-14   | undocumented         | N/A          | N/A                         | 559               | N/A                   | D             | Combined  | Unknown    |
| 3D51    | LMB     | 305     | L-20     | 1              | 2019-05-23   | 2019-06-06           | 18           | 14                          | 1325              | N/A                   | D             | Old Slys  | Unknown    |
| 2D00    | LMB     | 300     | S-20     | 1              | 2019-07-22   | 2019-09-04           | 22           | 44                          | 830               | N/A                   | D             | Detached  | Dam        |
|         |         |         |          | 2              | 2019-07-22   | 2019-09-07           | 21           | 47                          | 428               | N/A                   | U             | Detached  | Unknown    |
| 84B8    | LMB     | 304     | S-20     | 1              | 2019-07-22   | 2019-08-15           | 24           | 24                          | 1442              | N/A                   | U             | Poonamalie| Lock       |
| C64D    | LMB     | 292     | S-20     | 1              | 2019-05-23   | 2019-06-16           | 19           | 24                          | 1325              | N/A                   | D             | Old Slys  | Unknown    |
| 62E5    | NP      | 507     | L-20     | 1              | 2019-06-25   | undocumented         | N/A          | 285                         | N/A               | 285                   | D             | Poonamalie| Unknown    |</p>
<table>
<thead>
<tr>
<th></th>
<th>Date</th>
<th></th>
<th></th>
<th></th>
<th></th>
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<td>2019-06-17</td>
<td>20</td>
<td>3</td>
<td>2209</td>
<td>D</td>
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<td>Lock</td>
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<td>U</td>
<td>Edmonds</td>
<td>Lock</td>
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<td>9</td>
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<td>2019-06-09</td>
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<td>2</td>
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<td>D</td>
<td>Edmonds</td>
<td>Dam</td>
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<td>2020-07-01</td>
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<td>Lock</td>
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<td>2020-08-07</td>
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<td>U</td>
<td>Edmonds</td>
<td>Lock</td>
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<td>26</td>
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<td>D</td>
<td>Edmonds</td>
<td>Dam</td>
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<td>2019-06-15</td>
<td>20</td>
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**Mark-recapture fishes**

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<td>2021-07-10</td>
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Chapter 6: General discussion, conclusions, and future directions

This thesis evaluated several aspects of fish spatial ecology and connectivity in Canada’s historic Rideau Canal Waterway. Chapter 2 reframed our perspective of waterways as blended social-ecological systems. This chapter was important to “set the stage” for our subsequent projects, all of which carefully considered the research question from both an ecological and human-dimension approach. Chapters 3-5 involved the use of fish tracking techniques in conjunction with other disciplines (e.g., hydraulic engineering and/or management consultations) to answer questions related to connectivity and spatial ecology. We investigated how new invasions might spread via navigation locks in the RCW (Chapter 3) and how current water-management regimes impact overwintering of a large-bodied native fish whose population appears in decline (Chapter 4). Finally, we conducted a large-scale assessment of native and invasive fish connectivity, focusing on the use of navigation locks as a potential connectivity pathway (Chapter 5). Notably, a key aspect of this thesis is that all work conducted was highly collaborative and interdisciplinary: by working closely and respectfully and with waterway managers, hydraulic engineers, and social scientists, we were able to produce meaningful, comprehensive articles that are useful to a variety of disciplines whose end goals focus on wildlife conservation.

Our work on the round goby invasion front (Chapter 3) was particularly novel as it is the first telemetry-based study that evaluated round goby dispersal to inform management actions. Key findings include our discovery that round goby can use navigation locks to move upstream, though locks do appear to act as mostly a barrier to upstream dispersal. We also quantified the downstream rate of dispersal (18.5 m/day). Preventing downstream dispersion will be particularly difficult to manage in the RCW given any intervention applied would have to still permit safe navigation to recreationists (i.e., electrical barriers are not an option given safety concerns). Parks Canada could consider implementing sensory barriers, like carbon dioxide bubble screens, that still permit safe navigation but prevent fish movement. Additionally, locks could be dewatered at frequencies of Parks Canada choosing to evaluate presence and abundance of round goby, and subsequently develop management plans based on fish salvage findings. We provide two recommendations to managers to control the invasion including 1) structural modifications: attach a grate or screen to lock gate sluice valves to prevent round goby from entering lock chambers (as round goby were able to enter even when gates were closed) or install a water-release valve above the highest known downstream water level on the downstream gate and close gate sluice valves, and 2) change lock operations: ensure lock gates, tunnels, and valves are closed unless necessary to reduce dispersal opportunities. Because the round goby invasion was discovered while the population level was still relatively low, there is a unique opportunity to implement control actions quickly before the invasion expands.
Understanding how hydraulic flows and water levels affect fish spatial ecology has been vital in interpreting how, when, and why fish select for certain habitats. Ecohydraulics have been long considered important to include in conservation and management, and valuable in mitigation efforts to support wild fish populations (Chapter 4). By overlaying winter water-level decreases (i.e., drawdown) and flow rates with acoustic telemetry data, we were able to determine critical winter habitats of muskellunge in a portion of the RCW that experiences considerable annual drawdowns. This information will be particularly important for managers to consider if the population continues to decline; ensuring fish have access to suitable overwintering habitat is imperative for population viability. Importantly, we found that the drawdown reduced water levels to such a degree that the river became fragmented in several areas, restricting fish to their respective reach for the majority of the winter. We additionally – and unintentionally – discovered that muskellunge appear to be reproductively active weeks before Parks Canada refills the system in spring, suggesting spawning habitat may be limited during the drawdown period and a need for managers to consider adaptive management policies whereby the river is refilled based on water temperature and not time of year. Winter phenology of freshwater fishes is of particular importance from the perspective of climate change, specifically the start and end dates of winter, and overall duration (Shuter and Post 1990). Future projections suggest that over the next 100 years, winters will decrease in length and organism phenology will shift in concert (Christensen et al. 2007). 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; Winslow et al. 2017). For example, Farmer et al. (2015) found that the reproductive success of yellow perch (Perca flavescens) in Lake Erie declined significantly following shorter, warmer winters and Wedekind and Kueng (2010) linked warmer springs with weeks-earlier European grayling (Thymallus thymallus) spawning in Lake Thun, Switzerland. Reproductive phenology of freshwater fishes is not only cued by temperature changes; increased spring flows are another factor that initiate reproductive migrations and spawning (Bunn and Arthington 2002), so earlier ice-melts and increased flows in freshwater systems could also trigger earlier fish spawns. In this case, prioritizing the protection of both overwintering (which, of note, is not explicitly mentioned in Canada’s SARA) and spawning habitats is vital.

Although an increasing number of researchers and managers are recognizing the use of navigation locks as a fish connectivity pathway, few articles exist that tracked both native and invasive fish movements through them, and to our knowledge no work has been conducted in a smaller-scale (i.e., not a large shipping route like the Mississippi River) UNESCO-designated waterway (six historic canals have been assigned as UNESCO World Heritage sites: Amsterdam Canal Ring in the Netherlands, Canal du Centre in Belgium, Canal du Midi in France, Grand Canal in China, Pontcysyllte Aqueduct and Canal in the UK, and the RCW in Canada). It is important to note, however, that because each waterway
is biologically- and structurally-unique (i.e., lockstation design varies by waterway), managers should carefully consider relevant literature and tailor strategies to their waterway. We did discover three studies (Verhelst et al. 2018; Vergeynst et al. 2019; Vergeynst et al. 2021) conducted in the historic Albert Canal in Belgium, but each study evaluated native species exclusively (i.e., focusing solely on increasing connectivity for native species, not selective strategies even though invasive species are present like round goby, Jacobs and Hoedemakers 2013). Our goal here was to consider each barrier as being specifically porous to different species to create an integrative model across a landscape (i.e., the RCW) and advance our understanding of selective fragmentation. Furthermore, no research has assessed fish connectivity within or across reaches of the RCW, an important aspect to consider in promoting at-risk species conservation and total ecosystem health.

Our evaluation of invasive and native fishes across lockstations in the RCW, with a specific focus on navigation lock connectivity, provided key insights into the ecological connectedness of the waterway (Chapter 5). We documented several native fishes crossing barriers, including smallmouth bass, northern pike, and largemouth bass. Both smallmouth bass and northern pike are known to make spring migrations (Meixler et al. 2009), so passage events across barriers by these species was not a surprise, however we also documented largemouth bass, usually considered a more sedentary species (Midwood and Chow-Fraser 2015), passages, with several in the upstream direction, confirming intentional use of the lock. Navigation locks acted as a connectivity pathway in ~1/2 of all passage events recorded, indicating their importance in native species movements. Although we recorded common carp approaching – and even entering – lock chambers, no tagged individuals moved up- or downstream, suggesting the system may not be conducive to large-bodied, cyprinid dispersal. Although this finding suggests that navigation locks will not likely facilitate an invasive carp invasion from Lake Ontario (should they invade the Laurentian Great Lakes) into the RCW, this work should not deter managers from implementing barriers at entrances. Common carp have indeed proliferated throughout the RCW, indicating that they can disperse; we simply did not record any events. We also found that hydraulic factors may be influencing the direction of connectivity as the majority of passages were in the direction of flow, so invasive species may disperse more quickly in the downstream direction. Conversely, because native species can also move downstream more easily, if local extinctions occur then recolonization events downstream would occur more rapidly and, theoretically, gene flow would be higher in the downstream direction.

6.1. Future directions

There are several projects that should be conducted next to further our understanding of fish spatial ecology and connectivity in the RCW, and ensure managers are provided with the evidence needed to
protect wild fish populations in the system. In each chapter, specific recommendations for prospective research are offered. We propose several additional ideas below.

First, although this thesis provided information on fish connectivity in the RCW, we do not know the mechanism of movement through navigation locks. Constructing fish passage strategies to support migratory species requires an interdisciplinary, collaborative approach among managers, biologists and ecologists, and engineers. Both biological information (fish migrations, ecology, life history, etc.) and hydraulic engineering knowledge (to quantify the hydraulic conditions experienced by fish upstream, inside, and downstream a lock) are necessary to determine if locks could be operated in such a way that is conducive to passage for native migrating fish species (i.e., also known as “conservation locking”, Williams et al. 2012; USACE 2022). For example, Vergeynst et al. (2019) acoustically tagged two critically-endangered species, European eel (*Anguilla anguilla*) and Atlantic salmon (*Salmo salar*), to monitor their downstream migration phase in Belgium’s Albert Canal. By evaluating hydraulic conditions and lock operations and infrastructure, overlaid with fine-scale telemetry data (i.e., 2D movement data via a VPS array), they were able to determine where, how, and when fish moved downstream successfully and offer that information to managers to better promote downstream connectivity. Young et al. (2012) also used acoustic telemetry to monitor native Alabama shad (*Alosa alabamae*) upstream passage through the Jim Woodruff Lock and Dam in Florida’s Apalachicola River (USA) and verify if the lock could effectively facilitate passages. They found that higher attraction flows near the lock entrance were important to passing migrating Alabama shad, but that turbulence disoriented or repelled fish, negatively affecting their ability to locate and use the lock as a passage route. Researchers have also designed studies to consider the use of locks by invasive species. Finger et al. (2019) acoustically tagged native (walleye, channel catfish, and bigmouth buffalo [*Ictiobus cyprinellus]*) and invasive (common carp) fishes in the Mississippi River to determine if and how they passed through a Lock-and-Dam structure using a computational fish passage model that combined hydraulics with fish swimming performance. They found that the route taken for upstream passage – in this case, spillway gates or the lock chamber – was strongly dependent on water levels and velocities, and species-specific behaviour preferences, respectively. During high-velocity periods, fish were deterred or incapable of passing the spillway gates, but passage through the lock was not velocity dependent and instead was species-dependent (i.e., channel catfish always used the lock, walleye preferred the lock, common carp used both the lock and spillway gates). Importantly, they relate their findings to invasive silver and bighead carps, suggesting that carp species may be less likely than other species to use locks and could be blocked at these locations using taxon-specific deterrents. We recommend future studies, both in the RCW and other waterways, evaluate the mechanism of movement through locks for both native and invasive species, focusing on selective passage strategies. In the RCW specifically, such a study could
provide insights into why we did not document common carp passages and resolve under what circumstances passage does occur.

Second, the RCW is home to some of the oldest freshwater protected areas (FPAs) in Ontario, originally established in the 1940s, aimed primarily at protecting the largemouth bass fishery that was suffering from excessive recreational harvest (Ontario Department of Game and Fisheries 1945). A protected area is a “clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values” (IUCN 2008). Protected areas have been relatively overlooked as a conservation tool in stemming freshwater biodiversity declines, even though FPAs have potential to build resilience in the face of climate change (Frederico et al. 2016) and preserve not only biodiversity but also promote human well-being (Harrison et al. 2016). Additionally, the Convention on Biological Diversity Aichi Target 11 now acknowledges the importance of designated protected areas to protect biodiversity and ecosystem services, specifically in inland waters (https://www.cbd.int/sp/targets/). Despite protected areas being considered a “global cornerstone” in restoration efforts and biodiversity conservation, evidence of their effectiveness in rivers, lakes, and wetlands is mixed, with a recent review indicating that only 51% of case studies showed positive outcomes of protected areas (33% and 16% reported neutral and negative outcomes for freshwater conservation, respectively; Acreman al. 2020). Further, only 40% of case studies showed FPAs positively affected fish diversity, with little consideration to the critical habitats required across a migratory fish’s life (e.g., spawning and nursery areas, migratory corridors, feeding habitats; Bower et al. 2014). While Zolderdo et al. (2023) found that a fish sanctuary in Big Rideau Lake appears to offer spatial protections to largemouth bass during the open fishing season, no work has been conducted on other species. It would be especially useful to determine if FPAs in the RCW afford the same level of protection to migratory species, which are disproportionately threatened (Robinson et al. 2009).

6.2. Concluding remarks

It has been a pleasure and privilege to conduct this research with so many experts across disciplines. The underlying theme of this work is proactivity – to act now, using the evidence we have, to bend the curve of freshwater biodiversity loss and prevent future declines. Jane Goodall expressed, “the greatest danger to our future is apathy”, and so, it is our responsibility to take these words to heart and work with managers to develop conservation actions that promote a sustainable future for wildlife in Canada’s historic Rideau Canal Waterway.
Appendices

Appendix A: Scholarships supporting doctoral studies

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<td>2023</td>
<td>International Conference on Fish Telemetry - Travel Award</td>
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<td>International Association for Great Lakes Research - Travel Award</td>
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<td>The American Fisheries Society Fish Habitat Section Best Student Oral Presentation (Honorable Mention Status)</td>
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<td>2022</td>
<td>The Ontario Chapter of the American Fisheries Society EJ Crossman Award, Best Student Oral Presentation</td>
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<td>2022</td>
<td>Canadian Conference for Fisheries Research Clemens-Rigler Award</td>
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<td>2022</td>
<td>Wyndham Scholarship for Graduate Studies in Biology</td>
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<td>2021</td>
<td>Canadian Aquatic Resources Section of the American Fisheries Society Peter A. Larkin Award for Excellence in Fisheries (Runner-up)</td>
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<td>2021</td>
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<td>2015</td>
<td>NSERC Undergraduate Student Research Award</td>
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<td>2011</td>
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2010-2015  Florida Bright Futures Scholarship
2010-2013  University of South Florida Merit Scholarship

NSERC = Natural Sciences and Engineering Research Council of Canada

Appendix B: Publications during doctoral studies

†PhD chapter; *equal contributor

B.1. Peer-review journal articles

First-author publications

†Bergman JN, Negiel K, Landsman S, Glassman D, LaRochelle L, ... Cooke SJ (2022) Multi-year evaluation of muskellunge (Esox masquinongy) spatial ecology during winter drawdowns in a regulated, urban waterway in Canada. Hydrobiologia 1-23. DOI [LINK]


Bergman JN,* Buxton RT,* Lin HY,* Lenda M, Attinello K, ... Bennett JR (2022) Evaluating the benefits and risks of social media for wildlife conservation. FACETS 7:360-397. DOI [LINK] (featured as “top articles of 2022” by FACETS and Canadian Science Publishing)


Bergman JN,* Binley AD,* Murphy RE,* Proctor CA,* Nguyen TT,* ... Bennett JR (2020) How to rescue Ontario’s Endangered Species Act: A biologist’s perspective. FACETS 5:423-431. DOI [LINK]

**Co-author publications**


**B.2. Book chapters**


B.3. Articles in review


†Bergman JN, Bennett JR, Minelga V, Vis C, Fisk A, Cooke SJ (In revision; 19 Sep 2023) Ecological connectivity of invasive and native fishes in a historic navigation waterway. *Canadian Journal of Fisheries and Aquatic Sciences* - Manuscript ID cjfas-2023-0207

B.4. Articles in preparation


Appendix C: Non-peer review articles published during doctoral studies


Reid J*, Bergman JN* (2022) Creating a freshwater biodiversity “toolbox” to provide critical information to protect freshwater ecosystems. *Global Water Forum* LINK


Bergman JN (2021) What are the ecological impacts of winter water level drawdowns on muskellunge in Canada’s historic Rideau Canal? Exploring winter connectivity and habitat use to inform conservation strategies. *MCI*. LINK
Bergman JN, Cooke SJ (2020) Investigating fish connectivity in the Rideau Canal Waterway to inform conservation decisions. *RAEON LINK*


Bergman JN (2019) Stress Response of Sifakas to Seasonal Changes and Habitat Degradation: Things are Not What They Appear. *Society for Experimental Biology Autumn Issue LINK*


**Appendix D: Media coverage**

Scienceline of NYU Journalism. What happens when wild animals become social media sensations? Personal interview for online *article* (18 Sep 2023).


The Toronto Star Newspapers Ltd.: Invasive fish harbours Smiths Falls’ Edmonds Lockstation. Personal interview for newspaper *article* (20 Jan 2022).

Canadian Aquatic Resources Section of the American Fisheries Society Peter A. Larkin Award for Excellence in Fisheries: *2021 Larkin Award Results* (08 Dec 2021).


CityTV: Goby fish invading Rideau Canal (15 July 2019). *Personal interview for TV clip*.


CBC News: Invasive round goby fish found in Rideau Canal (12 July 2019). Online article, radio broadcast of interview, and personal interview for *TV clip*.

Carleton Newsroom: Where The Wild Fish Go: Carleton students play pivotal role in Rideau waterway research (9 July 2019). *Online article and personal interview*.
CTV: personal interview and filming crew (26 June 2019).


Appendix E: Additional files

Chapter 2
To access Supplementary Material, click the below DOI link and scroll to “Supplementary Material” for links to the electronic documents: https://doi.org/10.1139/er-2021-0026

Chapter 3
To access Online Resources 1-4, click the below DOI link and scroll to “Supplementary Information” for links to the electronic documents: https://doi.org/10.1007/s10530-021-02705-2

Chapter 4
To access Supplementary Materials A-E, click the below DOI link and scroll to “Supplementary Information” for links to the electronic documents: https://doi.org/10.1007/s10750-022-05085-3

Chapter 5
To access Appendices S1-2, click the below link to access the electronic documents: https://osf.io/2csfz/?view_only=220993d2f66244c0aa3fd3b3896f8305
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Parks Canada Dam Safety Engineering Inspection (EI), 2011. Site Data, 04 Black Rapids Dam. PDF available upon request from Parks Canada.


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