Biotelemetry-based monitoring of fish-habitat interactions as an informative window into habitat management in a multi-species fish community in Toronto Harbour

by

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A thesis submitted to the Faculty of Graduate and Postdoctoral Affairs in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

in

Biology

Carleton University, Ottawa, Ontario

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Abstract

Understanding how animals interact with habitat is a fundamental ecological question with applied implications for conservation and management of biodiversity. In the Laurentian Great Lakes, coastal wetlands provide critical habitat for over 80% of fish species in the community; however, over 70% of all wetlands have been lost and many of the remaining wetlands have seen declines in habitat quality. I used acoustic telemetry to track the space use behaviour of Largemouth Bass (*Micropterus nigricans*), Northern Pike (Esox lucius), Common Carp (Cyprinus carpio), and Yellow Perch (Perca flavescens) in coastal habitat of Toronto Harbour, Lake Ontario. In Chapter 2, I found that Northern Pike, and Yellow Perch had higher daily site fidelity in restored areas, while Common Carp had lower daily site fidelity in restored areas. Each species exhibited highest daily site fidelity during the summer and lowest during the fall. Overall, daily site fidelity estimates were highest in warm, shallow, vegetated, and sheltered regions of the harbour. In Chapter 3, I found that the size and degree of overlap in activity spaces was influenced by season and body size. Generally, activity spaces were largest in the summer and smallest in the winter. The degree of overlap between individual activity spaces was greatest during both of these seasons, but overall, overlap was quite low. In general, the estimated activity spaces were moderately sized compared with those reported in the literature. In Chapter 4, I found that variation in activity was influenced by species, habitat, season, diel period, and body size. Generally, Largemouth Bass exhibited greater activity levels compared to Northern Pike; however, there was considerable variability within both species. The greatest differences in the activity levels between species were observed in colder, exposed habitats, whereas, in coastal vegetated

and wetland habitats, the differences were less pronounced. For both species, activity levels were highest during late summer and early fall and much reduced during the winter months. A behavioural understanding of the interactions between an organism and its environment is essential for better understanding of habitat use and improve our ability to predict responses to habitat degradation and habitat restoration.

Acknowledgements

I wish to sincerely acknowledge my co-supervisors, Steve Cooke and Susan Doka, for their support, patience, and guidance. In particular, impressing upon me the importance of collaboration in doing and sharing science. Thank you for all the opportunities to attend management meetings and scientific conferences and perform fieldwork. Thank you for sharing in my successes and supporting me in my 'nonsuccesses'. I also wish to extend my genuine appreciation to some of the mentors in the Fish Ecology and Conservation Physiology Lab at Carleton University that helped along the way, including Jon Midwood, Jill Brooks, Robert Lennox, Jake Brownscombe, Lee Gutowsky, Nick Lapointe, and Elodie Ledee.

A number of colleagues at Toronto and Region Conservation were integral to this research. Rick Portiss, Gord MacPherson, and Thomas Sciscione were steadfast in their enthusiasm, support, and receptiveness to the Toronto Harbour Fish Habitat Assessment study. They championed the benefits of knowledge derived from this acoustic telemetry study. Staff in the Environmental Monitoring and Data Management group including Brian Graham, Don Little, Breanna Hallihan, and Brynn Coey, and with Fisheries and Oceans, including Christine Boston, were instrumental in supporting field components of this research project. I wish to extend special acknowledgement to Adam Weir for his dedication, enthusiasm, and camaraderie for 4 years' worth of fieldwork.

I thank all the people involved with the Great Lakes Acoustic Telemetry Observation System (GLATOS) for facilitating engaged meetings, a supportive and collaborative culture for Great Lakes fish 'telemeterists', and for developing the GLATOS database and R package. Throughout my academic career, I attended at least

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seven GLATOS Annual Meetings and count myself extremely lucky to have been connected to so many dedicated fisheries professionals.

I also wish to thank several people who provided feedback on earlier versions of this thesis: Lenore Fahrig, Julie Morand-Ferron, and Mark Ridgway.

Dedication

To my Rous and Verhoek families – you have supported me in countless and immeasurable ways during this pursuit. I am forever grateful for the collective emotional, logistical, and financial support that each one of you provided.

To my wife, Emily, and our sons, Carson and Shaw, you have given me the strength and resolve to follow my passions. Emily, you have been by my side for my entire post-secondary academic career; through all the ups and the downs. Your unwavering support, unconditional love, and fierce commitment have meant the world to me. Carson and Shaw, daily you share with me moments of immense joy and pride.

Preface

This thesis represents a scientific contribution which is a component of a decade long study that has included many different graduate students and postdoctoral research associates. Much like previous scientific contributions from this project have informed the present thesis, subsequent studies and analyses are ongoing with a focus on exploring movement patterns among individuals via network analysis, characterizing different behaviour types, and generating calibrations of accelerometers that can eventually be applied to some of the data reported in this thesis. In that sense, this thesis is foundational to future work while also building on the efforts of the students before me. This is an exciting aspect of scientific collaboration on a large and complex project but recognize that it generates as many questions as it seeks to answer.

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Thesis Format and Co-Authorship

This dissertation contains three data chapters written in manuscript format, which are at various stages of the publication process in peer-reviewed journals. As a consequence, there is some repetition between chapters to remain consistent with my contributions to the scientific literature. While this dissertation contains my research, many co-authors contributed to the data chapters. Here I list my contributions to each chapter, as well as that of my co-authors.

Chapter 2. Telemetry-Determined Habitat Use Informs Multi-Species Habitat Management in an Urban Harbour.

Rous, A. M., J. D. Midwood, L. F. G. Gutowsky, N. W. R. Lapointe, R. Portiss, T. Sciscione, M. G. Wells, S. E. Doka, and S. J. Cooke. 2017. Telemetry-determined habitat use informs multi-species habitat management in an Urban Harbour. Environmental Management 59: 118-128.

I designed the study, conducted data collection, performed data analysis, and wrote the manuscript. Midwood and Gutowsky contributed to data analysis. Midwood and Lapointe contributed to data collection. Midwood, Lapointe, Portiss, Sciscione, Wells, Doka, and Cooke contributed to study design and manuscript preparation.

Chapter 3. Examination of the fine-scale seasonal space use and overlap of three species of fish in a coastal embayment of the Laurentian Great Lakes.

Rous, A. M., J. D. Midwood, N. W. R. Lapointe, R. Portiss, T. Sciscione, M. G. Wells, S. E. Doka, and S. J. Cooke.

I designed the study, conducted data collection, performed data analysis, and wrote the manuscript. Midwood and Lapointe contributed to data collection. Midwood, Lapointe, Portiss, Sciscione, Wells, Doka, and Cooke contributed to study design and manuscript preparation. The manuscript is in preparation for submission to a journal.

Chapter 4. Habitat-specific variation in annual locomotor activity behaviour of two teleost fish residing in a set of coastal embayments of the Laurentian Great Lakes.

Rous, A. M., J. D. Midwood, J. W. Brownscombe, R. Portiss, T. Sciscione, M. G. Wells, S. E. Doka, and S. J. Cooke.

I designed the study, conducted data collection, performed data analysis, and wrote the manuscript. Brownscombe contributed to data analysis. Midwood contributed to data collection. Midwood, Brownscombe, Portiss, Sciscione, Wells, Doka, and Cooke contributed to study design and manuscript preparation. The manuscript is in preparation for submission to a journal.

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1.0 General Introduction

<u>1.1 Habitat Use</u>

In the most general sense, habitat is the space where an organism lives. More specifically, habitat is a product of the available biotic and abiotic conditions and resources needed for an organism to move, forage, find shelter, and reproduce (Hall et al. 1997; Kearney 2006; Johnson 2007). It can be highly dynamic and involves behavioural responses in space and time (Fig. 1.1; Orians and Wittenberger 1991; Minns et al. 1996a; Mayor et al. 2009). Habitat use behaviour is a complex cause and consequence of predator-prey relationships, intra- and interspecific competition, resource selection, niche partitioning, and population demographics (Rosenzwieg 1981; Legendre et al. 1991; Morrison et al. 2012). Habitat forms the foundation for healthy and productive biotic systems (Morrison et al. 2006), and this is particularly relevant for fish (Boisclair 2001; Lapointe et al. 2014). Aquatic systems are a three-dimensional matrix of habitats where specific habitats can be further defined as having similar physical, chemical, and biological attributes (Wiens 1976; Lapointe et al. 2014). Generally, these habitats are spread across the landscape in a heterogeneous fashion (Wiens 1976). By necessity, organisms are distributed in heterogeneous or clumped distributions, selecting for patches that offer benefits and resources that contribute to growth, survival, and reproduction (Matthiopoulos 2003). Patchy habitats can promote species coexistence (Johnson et al. 1992). For example, structural complexity of a habitat often reduces predator capture efficiency leading to high prey densities in structurally complex habitats (Crowder and Cooper 1982). Homogeneous or sparse habitats can lead to local extinction of either organism. Resource partitioning is an important process driving differential space use of

all animals (Schoener 1974; Toft 1985; Martin 1996). Animals may partition resources along a number of resources dimensions or axes. Schoener (1974) suggested that habitat dimensions were most important, followed by food-type dimensions and temporal dimensions.

In addition to the demonstrable influences that physical habitat has on animal distributions, a number of other abiotic factors shape animal space use (Brown et al. 1995). Temperature is widely recognized as a major driver of animal distributions (Sunday et al. 2012). For aquatic ectotherms, especially those living in temperate climates, temperature is often regarded as one of the most influential factors; water temperature is often considered the "master" environmental factor influencing fish (Brett 1964; Regier et al. 1996). Temperature selection tends to place a fish within the temperature range that generally maximizes physiological functions (e.g. digestion) and performance (e.g. growth, locomotion; Coutant 1987). Temperature optima can vary with life-stage as well as with the particular activity being performed. Some aquatic systems such as nearshore coastal environments are regarded as being thermally heterogeneous and dynamic (McCormick and Fahnenstiel 1999; Miranda et al. 2000; Minns and Wichert 2005; Vaudo and Heithaus 2013). Dissolved oxygen can also be a limited resource in the cool, deep waters of lakes in the summer and can be depleted at an increased rate with nutrient input from urban and agricultural activities (Coutant 1987). During the summer stratification, when the hypolimnion is isolated from oxygenated surface waters, the result can be hypoxic or even anoxic conditions (Gertzen et al. 2016). Under the ice, dissolved oxygen can also get depleted. Regardless of season, oxygen depletion can constrict the availability of suitable habitats for aquatic organisms. For example, as the

oxygen is progressively depleted during winter from the substrate to the ice-water interface, Northern Pike move increasingly higher in the water column towards the water-ice interface (Casselman 1978; Casselman and Lewis 1996).

Spatial connectivity of habitats is essential for species persistence in fragmented landscapes (Hanski 1999). It is well accepted that animals make regular daily movements within a region (e.g., inshore/offshore movements, diel vertical movements), and these movements are generally captured as part of an animal's home range in animal space use studies. Further, seasonal or annual migrations are well documented across the animal kingdom. There is a paucity of studies documenting movements between discrete habitat regions (i.e., between rivers separated by a lake environment). Habitat connectivity has received considerable attention in aquatic linear systems (rivers and streams; e.g., Wiens 2002). However, lake systems are examples of fragmented landscapes with suitable habitats nested within a broader habitat matrix that is unsuitable to many resident biota (Stewart-Koster et al. 2015).

1.2 Aquatic Habitat Restoration and Management

Alteration of physical habitat and degradation of water quality associated with urbanization, industrial activities, agriculture and other development, coupled with introduction of invasive species and resource exploitation, have had devastating effects on freshwater ecosystems around the globe (Richter et al. 1997; Strayer and Dudgeon 2010). There has been a greater loss of biodiversity in freshwater systems than any other ecosystem (Dudgeon et al. 2006; Reid et al. 2018). In response to the negative impacts of habitat loss on the productivity of animal populations, habitat restoration (and similarly

termed activities such as rehabilitation, creation, and enhancement) is practiced by nearly every conservation organization (Bernhardt et al. 2005). It is generally accepted that newly restored aquatic areas can contribute positively to the biodiversity and productivity of local animal populations. Habitat availability is often regarded as the primary factor that limits population and community recovery in degraded ecosystems, and physical habitat is thus often targeted in restoration (Bond and Lake 2003), aside from water quality improvements (Pan et al. 2016). However, specific responses of different fishes to changes in the physical structure of habitat are variable (Rogers and Bergersen 1999; Smokorowski and Pratt 2007). Furthermore, most research on the responses of fish to habitat restoration has focused on single species (i.e., salmonids; Poplar-Jeffers et al. 2009) or a single usage of habitat (i.e., spawning habitat; Kondolf et al. 1996). These fish habitat projects have had variable degrees of success or lack thereof (Taylor et al. 2019; Foote et al. 2020) at different levels, ranging from life-stage (e.g., smolts), species level, or whole assemblage (Ruiz-Jaen and Aide 2005). The intent of a habitat restoration project often dictates the implementation scope, ranging from whole-system improvements, to targeted vegetation planting, or installation of gravel beds. While some comparative work has validated (or rejected) the efficacy of some of these techniques (e.g., salmonid structures; Stewart et al. 2009), these evaluations have often been focused on the narrow scope (i.e., spawning success) or intent of the restoration (i.e., produce more fish for anglers), but rarely do they evaluate the performance of the features for the entire fish community or aquatic ecosystem in general.

The majority of habitat restoration or creation projects fail to adequately monitor the effectiveness of the habitat restoration (Block et al. 2001). This is often the result of

poor program design but can also be partially explained by limited funding and the desire to devote most funding to the habitat project itself; which is often very expensive. Without proper validation of expected outcomes, however, managers may be employing techniques that do not reflect the best practices available or ones that are only locally suited. For example, in restoring habitat for fish communities, more submerged aquatic vegetation may mean more recruitment and more refuge habitat for some species or lifestages but it may also mean reduced foraging efficiency for some species or life stages (Cooper and Crowder 1982), or even worse, provide more resources and space for nonnative fishes (Caskenette et al. 2018). In cases where funding is available to monitor the long-term success of restoration, traditional methods for evaluating success rely on measurements of abundance, richness, or community composition (Paller et al. 2000; Moerke and Lamberti 2003; Ruiz-Jaen and Aide 2005). These methods are usually discrete 'snapshots' in time that may not be representative of biologically relevant endpoints that determine demographic success such as survival in nursery habitat or reproductive success in spawning grounds (Lindell 2008; Farrugia et al. 2014). Observing the year-round behaviour of fish in restored habitats is essential to inform managers about the spatiotemporal function of the habitat (Marra et al. 2015).

1.3 Considerations of Scale in Conservation and Restoration

Different species are likely to respond to their habitat at varying spatial scales, however, most studies focus on the response at one, often short-term, spatial scale (Holland et al. 2004; Hale et al. 2019). As a consequence, habitat conservation and restoration has typically focused on small spatial scales and short temporal scales (Lewis et al. 1996). However, animal movement occurs across multiple spatial and temporal

scales (Nathan et al. 2008). For example, movement encompasses local movements, like foraging bursts, and long-distance, seasonal migrations. Collectively, one can examine every elemental step (i.e. distance between positions) and stop or identify segments and phases related to different goals such as foraging within a patch and travelling between patches. The study of fish movement has recognized that habitat selection can be scale dependent (Mayor et al. 2009). However, to monitor habitat use, we must consider it to be spatially and temporally bounded (Morris 2003). Intuitively, space use patterns are often-scale dependent (Webb et al. 2009; Avgar et al. 2013), and as such a major challenge facing ecology is translating observations taken at small spatial and temporal scales into expected patterns across larger spatiotemporal scales (Levin 1992; Lima and Zollner 1996; Morales and Ellner 2002; Schick et al. 2008). To understand the influence of scale on animal movement, we must have knowledge on how animals perceive and respond to their environment (With 1999; Johnson et al. 2002; Nams 2005) because processes operating at multiple spatiotemporal scales determine the lifetime track of an animal across a landscape (Nathan et al. 2008). The design of effective habitat restoration initiatives requires increased attention to the scale-related problems presented by large, connected systems (Lewis et al. 1996). Indeed, resource managers have increasingly appreciated that site-level habitat restoration, without a strategy towards cumulative landscape processes has rarely achieved the desired results for populations (Lewis et. al 1996).

1.4 Tracking fish with Acoustic Telemetry

Continuous observation of space use by wild animals is challenging. The spatiotemporal scale often exceeds the capabilities of the observer and inclement weather

or seasons can disrupt observation. Capturing and marking individuals has been a longstanding approach for investigation of space use but requires recapture of the marked individual and it fails to provide continuous observation. Aquatic animals can live at great depths and may surface infrequently or not at all. In fisheries research, studies of space use have relied heavily on capture techniques traditionally designed to estimate population dynamics, such as gillnets, trap nets, minnow traps, trawl nets, and electrofishing to collect data (Ford 1989; Murphy and Willis 1996; Lorenzen et al. 2016). Furthermore, monitoring efforts have often focused on endpoints, such as changes in abundance and richness or community composition. These surveying techniques only record a 'snapshot' of animals at single points in time and space, and yield relatively few sightings for rare species living in inaccessible environments (Aarts et al. 2008). Also, the mere presence of animals at a site is not substantial evidence that the site contributes positively to individual or community fitness (Aldridge and Boyce 2007; Lindell 2008). Fish are commonly used as bio-indicators of aquatic habitat condition (see Whitfield and Elliott 2002, for full review). Since fish are sensitive to a wide array of environmental variables (Karr 1981; Minns et al. 1994; Randall and Minns 2002), broader scale assessment of their space use behaviour can provide valuable information on the status and health of an urban ecosystem.

Early efforts to estimate site fidelity and home range of fish relied on visual observations (e.g., scuba, snorkeling; Lewis and Flickinger 1967; Werner et al. 1977; Chapman and Mackay 1984). All of these studies have provided valuable information for core ecological questions surrounding space use and habitat science, but they remain limited by discrete observation periods (i.e., habitat use only during summer periods or

habitat use once per month). Winter period habitat use or full annual cycle usage is rarely captured (Marra et al. 2015), and this may be particularly prevalent in aquatic systems in northern climates where waterways freeze for long periods (Jackson et al. 2001).

Modern methods to track animal movement patterns often involve the application of animal-borne electronic tags (biotelemetry; Cooke et al. 2004; Cooke et al. 2016). Electronic tags communicate with receivers either passively (e.g. passive integrated transponders) or actively (e.g. acoustic or radio transmitters, satellite tags), or else log data onboard (e.g. light-based geolocators; see Cooke et al. 2004; Hussey et al. 2015). Transmitting tags provide effective technology for tracking animal movement without the need to recover the tag. These tools are especially useful for investigating aquatic animals that cannot be directly observed in their environment (Hussey et al. 2015; Crossin et al. 2017). Importantly, environmental and physiological data can also be collected using electronic tags attached to fish that either transmit or log information (Payne et al. 2014; Wilson et al. 2015; Cooke et al. 2017). Standard biotelemetry sensors include accelerometers that measure fine-scale positions of the tag in three axes to reconstruct swimming activity (e.g., O'Toole et al. 2010; Landsman et al. 2015; Brownscombe et al. 2017) or temperature loggers that measure the ambient temperature experience (e.g., Peat et al. 2016). Together, these tools provide never before captured insight into the daily lives of animals that can be applied to make fundamental discoveries about individual or population space use patterns and test hypotheses relevant to conservation and restoration (Wilson et al. 2008; Matley et al. 2022). To date, biotelemetry has provided evidence of habitat preferences of various species of fish, but until recently, has rarely been used in post-restoration validation monitoring (Lapointe et al. 2013; Veilleux et al. 2018) or to

truly inform habitat management (Cooke et al. 2016).

1.5 Great Lakes Nearshore Fish Communities

In the Laurentian Great Lakes, coastal wetlands provide critical spawning, nursery, foraging and refugia habitat for over 80 % of fish species in the community (Jude and Papas 1992; Randall et al. 1996; Wei et al. 2004; Midwood and Chow-Fraser 2015). However, within the Great Lakes basin, over 70% of all wetlands have been lost (Whillans 1982; Snell 1987; Midwood and Chow-Fraser 2015). Many of the remaining wetlands have seen declines in habitat quality (Chow-Fraser 2006; Cvetkovic and Chow-Fraser 2011) and are further threatened by increasing human development (Niemi et al. 2007). Wetlands provide high primary productivity and structurally complex habitat (Jude and Pappas 1992).

Current fish population monitoring schemes to evaluate ecosystem health in the Great Lakes use local or regionally derived indices of biotic integrity, which consider the fish community trophic composition, including invasive species (Brousseau et al. 2011; Hoyle et al. 2018). Suitable habitat is a fundamental component for maintaining productive fish populations (Lapointe et al. 2014). Habitat loss or modification is a major driver of declining fisheries productivity (Randall et al. 2012); hence the focus on improving or restoring economically important fisheries has often been rooted in restoration or creation of novel fish habitat. Following an individual's behaviour in these new sites allows for comparisons of behaviour that has fitness consequences, and can identify critical resources, and provide information on the mechanisms through which habitats contribute to ecosystem functions (Lindell 2008).

Studies of fish movement and spatial ecology within the Great Lakes have provided resource managers with important knowledge on the temporal and spatial distributions of fishes within and between the lakes and their tributaries (Landsman et al. 2011; Brooks et al. 2017). These studies have addressed mechanistic relationships about the reproductive biology of fishes (e.g. movements to and from spawning sites, locations of spawning activities, and spawning behaviours), responses to environmental conditions and disturbances, including natural (e.g. seasonal flooding, drought events) and anthropogenic (e.g. power plant discharge, barriers to fish movement) factors, identification of critical habitats (e.g., nursery areas), and the movement patterns of invasive species (Lennox et al. 2023).

1.6 Study Area and Species Information

It is estimated that Toronto Harbour had a historic maximum marsh area of 610 ha from 1789 to 1962 (Whillans 1982). By 1979, nearly 100% of the area had been lost (Whillans 1982) due to the urban development within the Greater Toronto Area (GTA), which now exceeds a population of six million residents. The watersheds and extensive coastal waters (42km of shoreline) in and around the City of Toronto have a long history of agricultural and urban disturbance that led to this region being designated by the International Joint Commission as an Area Of Concern (AOC) in 1987 with 11 Beneficial Use Impairments (BUIs), eight of which are still listed as impaired, including 'degradation of fish and wildlife populations' and the 'loss of fish and wildlife habitat' (Toronto Region RAP 2007). Guided by a Remedial Action Plan, extensive restoration efforts have been undertaken throughout the AOC including: improvements to wastewater infrastructure (e.g., combined sewer separation), addition of aquatic habitat

structure to 'soften' or create complexity along hardened slips and shorelines, and the creation and restoration of coastal wetland habitat (Toronto Region RAP 2007). Within Toronto Harbour, restoration efforts to date have increased the amount and quality of aquatic habitat. Fish monitoring has focused on community metrics and change, but a more mechanistic understanding of how fish are using the increased and changed habitat is needed to support RAP targets.

Today, Toronto Harbour ($\sim 15 \text{ km}^2$) is a set of large coastal embayments connected to Lake Ontario, situated directly adjacent to the downtown core of Toronto, Ontario, Canada. For the purposes of this thesis, the harbour is operationally divided into the inner harbour and the outer harbour (Figure 1.2). The inner harbour is dominated by two uses: the city waterfront (urban and industrial landscape) and the Toronto Islands (a series of channels and islands). The city waterfront primarily consists of hardened (concrete) shoreline with urban and industrial land use directly adjacent (Leisti et al. 2020). The Toronto Islands are a series of interconnected channels that are connected to the inner harbour, but not the outer harbour. The Islands have primarily vegetated shorelines and land use is a mix of semi-urban and natural land use. The eastern gap (a channel) joins the inner and outer harbours and both harbours are directly connected to Lake Ontario proper: one connection for the inner harbour is via the western gap channel connected to Humber Bay and then to the open lake, and the other via the mouth of the outer harbour. The outer harbour contains an interconnected series of embayments known as Tommy Thompson Park (TTP).

Tommy Thompson Park is located on a man-made peninsula that was started in the early 1970's and construction is ongoing. The peninsula is made from infill

materials, is used for contained disposal sites (CDSs), and has been modified to naturalize portions of Toronto Harbour and restore lost coastal features. This aquatic and terrestrial park projects 5 km into Lake Ontario and covers a total surface area over 250 ha (TRCA 2000). To create a more thermally and structurally complex system, the aquatic portions of the park were functionally divided into three cells and four embayments (TRCA 2000; Figure 1.2); the cells historically and currently being used as CDSs. In addition to providing aquatic habitat, the cells in the park have continued to function as deposition sites for dredged material from the active harbour areas and the mouth of the Don River, which were then capped when active dumping into each cell is completed.

Habitat restoration in Toronto Harbour has consisted of a variety of techniques including: shoreline profile modification, aquatic vegetation planting, and placement of shallow shoals, shoreline aggregates, and log tangles. This complex, and heterogeneous aquatic habitat provides an important location to study the ecological drivers of habitat use and movement within and between habitats at a variety of spatiotemporal scales.

Toronto Harbour is characterized by substantial thermal variability, including cold water intrusions that can quickly drop water temperature in the harbour by as much as 15°C in 4 hours; even well protected, shallow embayments can experience temperature drops of up to 10°C (Hlevca et al. 2015). These cold water intrusion events are largely driven by periods of strong winds from west-southwest. These events usually occur between 4-10 times every summer (Hlevca et al. 2018; Doka et al. 2018). Peat et al. (2016) found evidence of behavioural thermoregulation by Largemouth Bass and Northern Pike in the Toronto Harbour. Both species were observed at temperatures

higher than what was being recorded at acoustic receiver stations in the near vicinity, up until 20°C, when Northern Pike began to actively seek cooler microhabitats (Peat et al. 2016).

Many conservation organizations and practitioners are moving away from singlespecies management in the context of habitat restoration and management in lieu of ecosystem management at the landscape level (Minns et al. 1996a; Simberloff 1998). To date, however, most telemetry-based, animal space use studies have tracked individuals of one species but there is increasing recognition of the importance of understanding multi-species movement patterns and interactions (Cooke 2008; Hussey et al. 2015). In some cases, researchers simultaneously tracked two species when the focus of the study demanded (i.e., predator-prey relationship). The mix of open coast and sheltered embayment habitats in Toronto Harbour supports a fish community that includes native and non-native species from all three representative thermal guilds (Dietrich et al. 2008; Midwood et al. 2022). In the embayment habitats, the dominant groups, by biomass, are Catostomids (primarily White Sucker, Catostomus commersonii) and Cyprinids (including Common Carp, Cyprinus carpio). Groups like Esocids (i.e., Northern Pike, Esox lucius), Percids (i.e., Yellow Perch, Perca flavescens), and Centrarchids (i.e., Largemouth Bass) only make up between 3 and 7 percent each (Dietrich et al. 2008). In embayment habitats, the average biomass per unit effort of generalists has increased since 1999, while the average biomass per unit effort of specialists has decreased. The proportion of degradation-tolerant species by catch per unit effort to the rest of the fish community has shown a general decline in embayments from 1989 to 2005 (Dietrich et al. 2008). Finally, Hoyle et al. (2018) found that indices of biotic integrity scores were

lower than predicted based on other similar Lake Ontario nearshore areas. Notably, the proportion of the fish community comprised of piscivores approached target levels. Taken together, there are mixed signals that Toronto Harbour fish community is improving. Here, I use a multi-species approach to better understand the spatial ecology of the fish community as a whole. Species were selected from the fish community to represent different trophic levels, thermal preferences (Chu et al. 2014), or resource management interests (i.e., game species and non-native species). Largemouth Bass is the dominant, resident, warmwater predator and Northern Pike is the dominant, coolwater piscivore in this system. Both species are important game species targeted by anglers. Yellow Perch is a mid-trophic level feeder and potential prey item for piscivores. Common Carp is a benthic feeder, as well as, a non-native species that can have negative impacts on spawning and nursery, vegetated habitat of native fishes (Parkos et al. 2003).

There is considerable literature on the space use and movement patterns of Largemouth Bass (e.g., Hanson et al. 2007), Northern Pike (e.g., Kobler et al. 2008), Common Carp (e.g., Penne and Pierce 2008), and Yellow Perch (e.g., Radabaugh et al. 2010) in a variety of lake and riverine environments. There are comparatively fewer accounts of space use patterns for any of these fishes across multiple spatial scales or in highly urbanized habitats (i.e., a harbour, but see Carter et al. 2012 and Murphy et al. 2012). However, I believe this is the first account using biotelemetry to describe the spatial ecology of these fishes in the context of restored habitats in a highly urbanized aquatic system (Fig. 1.3).

1.7 Thesis Objectives

Freshwater ecosystems are experiencing unprecedented threat, and the subsequent

loss of biodiversity is alarming. In response, habitat restoration and management activities are ubiquitous in freshwater ecosystems. This thesis investigates the space use behaviour of multiple fish species in a highly urbanized coastal embayment of the Laurentian Great Lakes that is subject to ongoing habitat restoration activities. In Chapter 2, I investigate the broad-scale spatiotemporal drivers of habitat use in restored habitat areas using a model of daily site fidelity. I hypothesize that fish will preferentially occupy restored habitats because restored habitats provide higher quality habitat than the nonrestored habitats. Specifically, fishes that prefer structurally complex habitat will spend proportionately more time occupying restored habitats where structural complexity is higher while fishes that are less dependent on aquatic macrophytes and tolerant of poorer water quality will spend proportionately less time occupying restored habitats. In Chapter 3, I investigate the size and degree of overlap in seasonal activity spaces among three coexisting species of freshwater fish in Embayment C of Tommy Thompson Park I hypothesize that both the size and degree of overlap of activity spaces will be influenced by season. Specifically, I predicted that activity space estimates will be largest during summer and smallest during winter because space use size is largely driven by foraging demands and food availability that are at their lowest during the winter season. I predicted that the degree of overlap would be largest during winter because minimizing energy expenditure becomes more important than protection from predators or access to food resources. I also hypothesize that both the activity space estimates and the degree of overlap will be related to fish body size. Specifically, I predicted that activity space estimates and the degree of overlap would increase with body size because larger fish need to use more space in order to meet the greater metabolic requirements (i.e., more

food) that come with being larger. In Chapter 4, I investigate the annual cycle activity patterns of two fish species from different thermal guilds across multiple habitat types in a set of costal embayments. I hypothesized that variation in the activity patterns for both species will be dependent on habitat type because the heterogeneous distribution of abiotic and biotic resources. Specifically, I predict that individuals will exhibit higher locomotor activity patterns in habitats that are deeper and have lower levels of submerged aquatic vegetation. I further hypothesize that activity patterns will differ between species due primarily to variation in foraging behaviour and home range size. Specifically, I predict that Largemouth Bass will exhibit higher locomotor activity patterns than Northern Pike. Taken together, this research reveals how a multi-species approach to animal space use behaviour can provide greater mechanistic understanding to inform managers of the efficacy of habitat restoration actions.



Figure 1.1: Diagram depicting the spatial and temporal scales of fish population use of habitat (adapted from Minns et al. 1996a). Chapter 2 (Blue Circle) of this thesis examines site fidelity, which span the spatiotemporal scales of Region and Home Range. Chapter 3 (Orange Circle) of this thesis examines home range and core use areas, which span the spatiotemporal scales of Home Range, Habitat, and Patch. Chapter 4 (Green Circle) of this thesis examines activity level, which span the spatiotemporal scales of Habitat and Patch.



Figure 1.2: Acoustic telemetry array in Toronto Harbour. Dots indicate the position of each acoustic receiver. Rings denote receivers that are currently part of the array. Labels indicate regions of the Harbour.


Figure 1.3: Images of the Toronto Harbour Fish Habitat Assessment. Clockwise, from top left – boat electrofishing in the Toronto Islands, capture of a Northern Pike for acoustic transmitter implantation, suturing a Largemouth Bass after acoustic transmitter implantation, and acoustic receiver data download. Images courtesy of staff from the Toronto and Region Conservation Authority.

Chapter 2. Telemetry-Determined Habitat Use Informs Multi-Species Habitat Management in an Urban Harbour

2.1 Abstract

Widespread human development has led to impairment of freshwater coastal wetlands and embayments, which provide critical and unique habitat for many freshwater fish species. This is particularly evident in the Laurentian Great Lakes, where such habitats have been severely altered over the last century as a result of industrial activities, urbanization, dredging and infilling. In Toronto Harbour, extensive restoration efforts have been directed towards improving the amount and quality of aquatic habitat, especially for fishes. To evaluate the effectiveness of this restoration work, use of the restored area by both target species and the fish community as a whole must be assessed. Individuals from four species (Common Carp, Largemouth Bass, Northern Pike and Yellow Perch) were tagged and tracked continuously for one year using an acoustic telemetry array in the Toronto Harbour area of Lake Ontario. Daily site fidelity was estimated using a mixed-effects, logistic regression model. Daily site fidelity was influenced by habitat restoration and its interactions with species and body size, as well as season and its interactions with species and body size. Daily site fidelity was higher in restored sites compared to non-restored sites for Yellow Perch and Northern Pike, but lower for Largemouth Bass and Common Carp. For all species, daily site fidelity estimates were highest during the summer and lowest during autumn. The approach used here has merit for evaluating restoration success and informing future habitat management activities. Creating diverse habitats that serve multiple functions and species are more desirable than single-function-oriented or single-species-oriented designs.

2.2 Introduction

Alteration of physical habitat and degradation of water quality associated with urbanization, industrial activities, agriculture and other development, coupled with introduction of invasive species and resource exploitation, have had devastating effects on freshwater ecosystems around the globe (Richter et al. 1997; Strayer and Dudgeon 2010). There has been a greater loss of biodiversity in freshwater systems than any other ecosystem (Dudgeon et al. 2006). A range of aquatic flora and fauna has been negatively affected, resulting in species extirpations, loss of productivity and alterations in ecosystem function (Carpenter et al. 2011). In freshwater ecosystems, fishes not only play integral roles as apex predators or forage species, they also generate important ecosystem services that directly benefit humans, such as the cultural and economic aspects of commercial, subsistence and recreational fisheries (Holmlund and Hammer 1999; Lynch et al. 2016).

In the Laurentian Great Lakes, coastal wetlands provide critical spawning, nursery, foraging and refugia habitat for over 80% of fish species in the community (Jude and Papas 1992; Randall et al. 1996; Wei et al. 2004; Midwood and Chow-Fraser 2015). However, within the Great Lakes basin, over 70% of all wetlands have been lost (Whillans 1982; Snell 1987; Midwood and Chow-Fraser 2015). Many of the remaining wetlands have seen declines in habitat quality (Chow-Fraser 2006; Cvetkovic and Chow-Fraser 2011) and are further threatened by increasing human development (Niemi et al. 2007). Suitable habitat is a fundamental component for maintaining productive fish populations (Lapointe et al. 2014). Habitat loss or modification is a major driver of declining fisheries productivity (Randall et al. 2012); hence the focus on improving or

restoring economically important fisheries has often been rooted in restoration or creation of novel fish habitat.

In response to the negative impacts of habitat loss on the productivity of animal populations, habitat restoration (and similarly termed activities such as rehabilitation, creation and enhancement) is practiced by nearly every conservation organization (Bernhardt et al. 2005). It is generally accepted that newly restored aquatic areas can contribute positively to the biodiversity and productivity of local fish populations. However, specific responses of different fishes to changes in the physical structure of habitat are variable (Rogers and Bergensen 1999; Smokorowski and Pratt 2007). Furthermore, most research on the responses of fish to habitat restoration has focused on a single species (i.e., salmonids; Poplar-Jeffers et al. 2009) or a single usage of habitat (i.e., spawning habitat; Kondolf et al. 1996). These fish habitat projects have had variable impacts at different levels, ranging from life-stage (e.g., smolts), species level or whole assemblage (Ruiz-Jaen and Aide 2005). The intent of the project often dictates the implementation scope, ranging from whole-system improvements, to targeted vegetation planting or installation of gravel beds. While some comparative work has validated (or rejected) some of these techniques (e.g., salmonid structures; Stewart et al. 2009), these evaluations have often been focused on the narrow scope or intent of the restoration and rarely do they evaluate the performance of the features for the broader fish community/aquatic ecosystem in general (but see Moerke and Lamberti 2003 for an example of monitoring responses of a fish community responses to stream restoration).

The majority of habitat restoration or creation projects fail to adequately monitor the effectiveness of habitat restoration (Block et al. 2001). This is often the result of poor

program design, but can also be partially explained by limited funding and the desire to devote most funding to the habitat project itself, which is often very expensive. Without proper validation of expected outcomes, however, managers may be employing techniques that do not reflect the best practices available or ones that are not locally suited. In cases where funding is available to monitor the long-term success of restoration, traditional methods for evaluating success rely on measurements of abundance, richness or community composition (Paller et al. 2000; Moerke and Lamberti 2003; Ruiz-Jaen and Aide 2005). These methods are usually discrete 'snapshots' in time that may not be representative of biologically relevant endpoints that determine demographic success such as survival in nursery habitat or reproductive success in spawning grounds (Lindell 2008; Farrugia et al. 2014). Observing the year-round behaviour of fish in restored habitats is essential to inform managers about the spatiotemporal function of the habitat. To date, biotelemetry has provided supportive evidence regarding habitat preferences of various species of fish, but until recently, has rarely been used in post-restoration validation monitoring (Lapointe et al. 2013) or to truly inform habitat management (Cooke et al. 2016).

Many conservation organizations and practitioners have moved away from singlespecies management in the context of habitat restoration in lieu of ecosystem management at the landscape level (Simberloff 1998). To date, however, most telemetrybased animal movement studies have tracked individuals of one species, but there is increasing recognition of the importance of understanding multi- species movement patterns and interactions (Cooke 2008; Hussey et al. 2015). In Toronto Harbour, a large system of embayments situated on the northern shore of Lake Ontario, specific habitat

restoration activities aimed at improving the overall aquatic habitat conditions by creating sheltered embayments with wetland areas have occurred over the last two decades and further projects have been proposed. To better measure the fish community response to these restoration efforts, we used a multi-species tagging approach. We selected four species from the fish community to represent different trophic levels, thermal preferences or resource management interests (i.e., game species and non-native species). Largemouth Bass (*Micropterus nigricans*) is the dominant resident warm- water predator and Northern Pike (*Esox lucius*) is the dominant coolwater piscivore in this system. Both species are important game species targeted by anglers. Yellow Perch (Perca *flavenscens*) is a mid-trophic level feeder and potential prey item for piscivores and Common Carp (Cyprinus carpio) is a benthic feeder, as well as, a non- native species that can have negative impacts on spawning and nursery-vegetated habitat of native fishes (Parkos et al. 2003). There is considerable literature on the space use patterns of Largemouth Bass (e.g., Hanson et al. 2007), Northern Pike (e.g., Kobler et al. 2008), Common Carp (e.g., Penne and Pierce 2008) and Yellow Perch (e.g., Radabaugh et al. 2010) in a variety of lake and riverine environments. There are comparatively fewer accounts of space use patterns for these fishes in highly urbanized habitats (i.e., a harbour, but see Carter et al. 2012 and Murphy et al. 2012). However, we believe this is the first account describing the spatial ecology of these fishes in response to habitat restoration in a highly urbanized aquatic system. Using a model of daily site fidelity, we evaluated the spatiotemporal use of restored habitat areas for these four species in Toronto Harbour. Restored habitats are designed to improve the structure and function of existing habitat. We hypothesize that fish will preferentially occupy restored habitats

because restored habitats provide higher quality habitat. Specifically, fishes that prefer structurally complex habitat will spend proportionately more time occupying restored habitats where structural complexity is higher while fishes that are benthic and tolerant of poorer water quality will spend proportionately less time occupying restored habitats.

2.3 Methods

2.3.1 Study Site

Toronto Harbour area (~15 km²) is a set of large coastal embayments connected to Lake Ontario, situated directly adjacent to the downtown core of Toronto, ON, Canada. Historically, the eastern region of Toronto Harbour was an expansive marsh complex at the mouth of the Don River known as Ashbridge's Bay. After this wetland area was drained and reclaimed to serve as industrial port lands, only a fragment of this original bay remains (separated from the current Toronto Harbour by the reclaimed land). For our purposes, the harbour is operationally divided into the inner harbour and the outer harbour (Figure 2.1). The inner harbour is dominated by two uses: the city waterfront (urban and industrial landscape) and the Toronto Islands (a series of channels and islands). The outer harbour contains an interconnected series of embayments known as Tommy Thompson Park (TTP). The eastern gap (a channel) joins the inner and outer harbours, and both harbours are directly connected to Lake Ontario proper: one connection for the inner harbour is via the western gap channel connected to Humber Bay and then the open lake, and the other via the mouth of the outer harbour. TTP is located on a man-made peninsula that was started in the early 1970's and construction is ongoing. The peninsula is made from infill materials and has been modified to naturalize

portions of Toronto Harbour, and restore lost coastal features. This aquatic and terrestrial park projects 5 km into Lake Ontario and covers a total surface area over 250 ha (TRCA 2000). To create a more thermally and structurally complex system, the aquatic portions of the park are functionally divided into three cells and four embayments (TRCA 2000; Figure 2.1). In addition to providing aquatic habitat, the cells in the park have continued to function as deposition sites for dredged material from the active harbour areas and the mouth of the Don River, which are then capped when active dumping into each cell is complete. Heavy construction in Cell 1 was completed in 2006. The Cell 2 confined waste disposal facility stopped receiving dredge material during the mid-2000s. Cell 3 was receiving dredge material during the study period. The telemetry receiver in Cell 3 was placed outside of the area where sediment material was being deposited.

Habitat restoration activities in Embayments A, B and C, Cell 1, and Spadina slip have consisted of a variety of broadly grouped techniques including, but not limited to: shoreline modification (slope profile and linear complexity) and creation (spawning channels, and island crests and peninsulas), shoreline vegetation planting and creation of areas to facilitate establishment (riparian, emergent and submergent), structural habitat addition (e.g., anchored log tangles, boulder clusters, submerged log cribs and stump fields, reefs and shoals), and control of non-target organisms (e.g., Common Carp exclusion gates; Wilcox and Whillans 1999). In Cell 1 and Spadina Slip, the areas of restoration work include both the littoral zone and the benthic region of the limnetic zone. In Embayments A, B, C and D, the restoration work has largely been confined to the littoral zone.

2.3.2 Telemetry Array

To track the space use of tagged fish in Toronto Harbour, we deployed a passive acoustic telemetry array (see Donaldson et al. 2014 for overview of acoustic telemetry methods and terminology). For this study, 39 Vemco VR2W receivers (Vemco Ltd., Halifax) were strategically positioned throughout the harbour to cover a variety of habitat sites, as well as key movement corridors (Figure 2.1). In shallow areas (<5 m), acoustic receivers were attached to a rope approximately 1 m above a steel or concrete anchor with a Castro float at the top to keep the receiver positioned vertically. Anchors were tethered to the nearest attachment point on shore by submerged steel cable. In deeper water (up to 10 m), the anchor was connected by floating rope to an additional weight approximately 20m away from the primary anchor weight. Receivers were retrieved every 6 months to offload data, remove any accumulated bio- fouling and check receiver condition. Receivers were then redeployed in the same locations. Range testing (see Kessel et al. 2014) was conducted at a subset of receivers in different habitat types and in different seasons to inform receiver placement, and varied from 400 to 1500 m (see Veilleux 2014).

2.3.3 Fish Tagging

All fish in this study were captured via boat electrofishing (SR-18EH, 6.0–7.0 A, 60 Hz, 340V DC, Smith-Root, Inc., Vancouver, WA) between May and September 2012. After capture, each fish was held in the boat live well and transported to an on-shore surgery location. Post-surgery, all tagged fish were released at their original capture location. Largemouth Bass, Common Carp and Yellow Perch were anesthetized using a

portable electroanesthesia system (PES) (Smith-Root, Inc., Vancouver, WA), which has been demonstrated to be an effective tool for anesthetising fish for handling (Vandergoot et al. 2011; Trushenski and Bowker 2012; Rous et al. 2015). Preliminary trials with Northern Pike anesthetized using the PES showed poor long-term survivorship (Personal Observation, S.J. Cooke). Consequently, Northern Pike were anesthetized using a 60ppm eugenol bath (Anderson et al. 1997), which improved long-term survivorship (S.J. Cooke, unpublished data). For surgery, fish were moved from the live well with a wetted net onto a padded surgical table with the fish in a supine position. During surgery, lake water was continuously passed through the gills of the fish except for Northern Pike, where the water contained a 30 ppm eugenol solution. Each individual was measured for total length. Prior to implanting an acoustic transmitter into an individual, the transmitter and all surgical tools were disinfected in an iodine solution and rinsed. An incision (<10 mm) was made with a sharp scalpel on the ventral surface of the fish. Curved forceps were used to lift the skin and body wall to avoid any injury while making the incision. The transmitter was inserted into the coelomic cavity of the fish. The incision was closed using two simple interrupted sutures (Ethicon PDS II, 3/0, FSL needle). Largemouth Bass (N = 18), Common Carp (N = 18) and Northern Pike (N = 17) were tagged with Vemco V13TP transmitters (13mm×48mm, 13g in air, 69kHz, mean delay=200s, Vemco Ltd., Halifax), while Yellow Perch (N = 9) were tagged with smaller Vemco V9 transmitters (9) $mm \times in air$, 69 kHz, mean delay = 340 s, Vemco 21 mm, 2.9 g Ltd., Halifax).

2.3.4 Analysis of Daily Site Fidelity

The detection history of each tagged fish from 22 September 2012 to 23 September 2013 was collated into a database (1 768 299 total detections). For each

individual, we calculated the proportion of detections per receiver station per day. Prior to analysis, influential observations, multi-collinearity and relationships between the response and explanatory variables were assessed using Cleveland dotplots, scatterplots and conditional box and whisker plots. Daily site fidelity (the proportion of detections per individual per receiver station per day) was assumed to be binomially distributed because it represented the number of successes (detections at an individual receiver) and the number of failures (total detections at all other receivers). Explanatory variables included equinox-based seasons (winter, spring, summer, autumn), species, restoration status of the habitat (yes/no), site exposure (continuous covariate) and body size (divided into five classifications per species based on quartiles; Table 2.1). A habitat site was considered restored if there had been previous documented restoration activities completed by the local habitat managers in proximity to the location of the acoustic receiver. In assigning this status, we did so broadly such that we did not discern between the spatial extent of the restored area or the individual types of technique (e.g., shoreline modification or structural habitat addition). All the restored areas are composites of all or many of the techniques described. Site exposure is the relative level of exposure in the Toronto Harbour determined by estimating the mean fetch at each receiver via a wind fetch model. Continuous covariates were centered and standardized [i.e., (value mean)/standard deviation] to aid with model convergence. Based on the study design, both individual fish ID and receiver station were included as crossed random effects. Given the statistical design, we fitted generalized linear mixed models with restricted maximum likelihood (Zuur et al. 2009). We expected the error to be normally distributed. Model selection was performed by generating a set of candidate models (n = 13) that

were compared using second-order AIC (Akaike 1998; Mazerolle 2015). The set of candidate models includes those that can be justified based on knowledge of the factors that influence site fidelity, rather than an exhaustive set considering all possible candidate models. Multi-model assessment was conducted to identify the best approximating model from the set of candidate models (Burnham and Anderson 2002). Fitted values from the top model were plotted to illustrate the relative influence of the fixed effects (Wickham 2016). All candidate models were validated by plotting the normalized residuals and testing for overdispersion (i.e., the occurrence of more variance in the data than predicted by a statistical model; Bolker et al. 2009) using methods described by Zuur et al. (2009). Possible spatial autocorrelation in the residuals was assessed by plotting the size of the residuals at each receiver coordinate. Data exploration and analyses were carried out in the R statistical environment (R Core Development Team 2014).

2.5 Results

The total number of detections varied by species. Northern Pike comprised 741 539 or 42% of the 1 768 299 total detections. Common Carp and Largemouth Bass each comprised 451 712 or 26%, and 446 201 or 25% of the detections, respectively. Yellow Perch comprised 128,847, or 7% of the total detections.

The top model of daily site fidelity included terms for restoration status, species, season, body size, restoration × species, restoration × body size, species × season, species × body size, d and season × body size (Table 2.2). Site exposure did not appear in the top model to explain daily site fidelity for fish in Toronto Harbour.

Pooling seasons, daily site fidelity was higher in restored sites than in nonrestored sites for Yellow Perch (+10.4%) and Northern Pike (+2.2%), but lower for Largemouth Bass (-3.8%) and Common Carp (-10.7%; Table 2.3). Across all seasons and restoration status, daily site fidelity decreased with body size for Northern Pike, but increased with body size for perch, except during summer (Figure 2.2). For Largemouth Bass, large individuals had higher site fidelity in restored areas compared to non-restored areas, but smaller individuals had lower site fidelity in restored areas compared to nonrestored areas.

Yellow Perch showed the highest daily site fidelity of all species, as a typical individual occupied a single receiver station 100% of the time on a given summer day, with far more variation in each other season. Generally, all species showed their highest site fidelity estimates during the summer and lowest estimates during autumn. Pooling across body size and restoration status, daily site fidelity estimates in the summer were 0.48 (0.28–0.68, 95% CI) for Largemouth Bass, 0.41 (0.23–0.63, 95% CI) for Common Carp, 0.99 (0.30–1.0, 95 % CI) for Yellow Perch, and 0.61 (0.39–0.81, 95 % CI) for Northern Pike. In contrast, daily site fidelity estimates in the autumn were 0.32 (0.16–0.52, 95 % CI) for Largemouth Bass, 0.29 (0.15–0.50, 95 % CI) for Common Carp, 0.57 (0.34–0.76, 95 % CI) for Yellow Perch, and 0.34 (0.17–0.58, 95 % CI) for Northern Pike.

Median site fidelity estimates were highest for receiver stations in the Toronto Islands and TTP (Embayment C, Cell 2 and Cell 3; Figure 2.3). Daily site fidelity was estimated to be lowest in areas along the waterfront of the Inner Harbour and the interface between the Outer Harbour and Lake Ontario.

Species	Minimum	25%	Median	75%	Maximum
Largemouth Bass	307	408	470	476	535
Common Carp	470	515	658	693	741
Yellow Perch	216	224	225	241	271
Northern Pike	556	733	811	972	1003

Table 2.1 Body size quartiles per species tagged

Total length measurements were in mm.

Table 2.2 Model selection statistics for models on the proportion of recorded detections/day (daily site fidelity). AICc is the biascorrected Akaike Information Criterion; Δ AICc is the difference in bias-corrected AIC between a given model and the top ranked model; wAICc is the relative weight of the bias-corrected AIC; Log(*L*) is the log-likelihood of the models; *K* is the number of parameters. All models contain fish ID and station name as a random intercept.

Fixed effects	AICc	ΔAICc	wAICc	Log(L)	K
Restoration + Species + Season + Body.size + Restoration:Species + Restoration:Body.size + Species:Season + Species:Body.size + Season:Body.size	1654067	0	1	-827004	30
Restoration + Species + Season + Exposure + Restoration:Species + Species:Season	1655837	1769	0	-827896	23
Restoration + Species + Season + Restoration:Species + Species:Season	1655837	1769	0	-827897	22
Restoration + Species + Season + Body.size + Species:Season + Species:Body.size + Season:Body.size	1658657	4589	0	-829302	26
Species + Season + Species:Season	1659539	5471	0	-829752	18
Restoration + Species + Season + Species:Season	1659541	5473	0	-829752	19
Restoration + Species + Season + Body.size + Species:Season + Species:Body.size	1659543	5475	0	-829749	23
Restoration + Species + Season + Body.size + Exposure	1663669	9601	0	-831822	12
Restoration + Species + Restoration: Species	1685146	31078	0	-842563	10
Species	1687862	33794	0	-843925	6
Restoration + Exposure	1687965	33797	0	-843928	5
Restoration	1687865	33798	0	-843929	4
Restoration + Species + Body.size + Species:Body.size	1687866	33799	0	-843922	11

sites Non-restored sites
% 36.9%
40.0%
//o 49.7%
% 56.9%

Table 2.3 Pooled daily site fidelity estimates for each species on receivers in restored and non-restored areas.



Figure 2.1: Receiver locations of the Toronto Harbour Acoustic Telemetry Array. Circles represent receivers (n=39). Red circles represent receivers in restored areas; black circles represent receivers in non-restored areas. Labels denote regions discussed in the text.



Figure 2.2: Daily site fidelity estimates for each species (*M. nigricans, C. carpio, P. flavescens, and E. lucius*) by body size. Solid lines and dark shading represent daily site fidelity estimates +/- 95% CI for sites in non-restored areas; dashed lines and light shading represent daily site fidelity estimates +/- 95% CI for sites in restored areas.



Figure 2.3: Median daily site fidelity for each receiver (n=39) in Toronto Harbour. Red circles represent receivers in restored areas; black circles represent receivers in non-restored areas. The size of the circle is relative to the proportion of the daily site fidelity, where larger circles represent greater site fidelity.

2.5 Discussion

The habitat restoration work in Toronto Harbour has aimed to enhance both the quantity and the quality of the coastal wetland, sheltered embayment, and rocky / woody habitat available for the fish community. Our study reveals that two native species that were tracked in the harbour (Northern Pike and Yellow Perch) had higher site fidelity estimates in restored habitat areas, compared to non-restored areas. In contrast, nonnative Common Carp had lower site fidelity estimates for restored compared to nonrestored habitats. Overall, Largemouth Bass had lower site fidelity estimates for restored compared to non-restored habitats, but there was an interaction with body size where large individuals had slightly higher site fidelity in restored habitat areas, compared to non-restored areas. Restored habitats, which include a variety of physical structures, provide a more complex heterogeneous environment for both for sit-and-wait predators like adult Northern Pike, which tend to use deep weed edges or other cover to wait for prey to appear (Casselman and Lewis 1996), while also providing the necessary cover components for Largemouth Bass and Yellow Perch to avoid such predation events. In a lake with high habitat heterogeneity, Yellow Perch movement rates were lower than in a simple lake (Radabaugh et al. 2010). In our system, Yellow Perch tended to stay in restored areas possibly because of the increased habitat complexity and heterogeneity in these areas. Similarly, Northern Pike need dense vegetation for spawning, foraging and to reduce vulnerability to predation for smaller individuals (Casselman and Lewis 1996). In Toronto Harbour, our analysis of the spatial distribution of fish habitat use identified several 'hotspots' of high site fidelity. Fish tended to spend a large portion of their time in Cells 2 and 3 of TTP, and the channels of the Toronto Islands, especially the southwest

extent of this area. The fish that used these areas were less likely to split their time between two or more adjacent habitats where receivers were located compared to other areas in the harbour. These areas represent some of the more sheltered portions of the harbour, include both areas with and without restored habitat, and support the development of submerged aquatic vegetation beds.

Daily site fidelity was seasonally dependent. For all four species, site fidelity estimates were highest during the summer, while estimates were lowest during autumn for all species. With the onset of warmer temperatures in the summer, fish tended to move from inshore habitat towards slightly deeper offshore habitat but where submerged vegetation still exists (Headrick and Carline 1993; Penne and Pierce 2008). Higher water temperatures in the summer can force coolwater fish to seek out the coolest habitats with optimal depth. Vehananen et al. (2006) and Kobler et al. (2008) reported that movement rates of Northern Pike were highest during the summer. However, several authors have reported contradictory findings in regard to the seasonal movement rates of Northern Pike (Diana et al. 1977; Jepsen et al. 2001). At our Toronto study site, frequent intrusions of cold water from Lake Ontario inundate the harbour and reach several of the sheltered embayments (Hlevca et al. 2015). As such, throughout the summer Northern Pike may be able to remain in close proximity to productive warm- water habitats where their preferred prey is located, instead of making movements between coolwater and warmwater habitats for feeding forays (Headrick and Carline 1993). Despite their preference for cool water habitat, Yellow Perch have lower movement rates during the summer (Radabaugh et al. 2010), which likely explains their complete site fidelity during this season. Largemouth Bass are typically more sedentary than Northern Pike and

therefore more highly resident during the summer (Mesing and Wicker 1986; Sammons and Maceina 2005; Hanson et al. 2007). Once the submerged aquatic vegetation cover is high enough to provide complex habitat for cover and refuge, Largemouth Bass have sufficient habitat for foraging and there is little incentive to move widely among habitats (Hanson et al. 2007; Ahrenstorff et al. 2009). Cooling water temperature and fall turnover in autumn may force fish to move more to search out prey and retreat from their resident summer habitats into optimal overwintering habitats. Studies have found that higher movement rates occur during autumn for Largemouth Bass (Karchesky and Bennett 2004; Sammons and Maceina 2005; Hanson et al. 2007), Yellow Perch (Radabaugh et al. 2010) and Common Carp (Penne and Pierce 2008), which supports our observation of reduced site fidelity during this season. Finally, during winter fish tend to have lower activity levels and would be less likely to move large distances between habitats but will make movements in response to prey availability and oxygen concentrations, especially Northern Pike (Casselman and Lewis 1996; Baktoft et al. 2012).

Daily site fidelity in our study was dependent on fish size. Foraging and predation risk heavily influence the habitat choice and movement behaviour of many species. For Northern Pike specifically, site fidelity decreased with body size. Casselman and Lewis (1996) found that the relationship between abundance of adult Northern Pike and macrophyte coverage was inversely related to body size. Large individuals tend to reside in less dense aquatic vegetation, so that they can strike more easily and locate larger prey items, while smaller individuals are more likely to select areas with more dense cover to reduce vulnerability to predation (Chapman and Mackay 1984; Casselman and Lewis 1996). Larger individuals need more food and are more likely to move between habitats

to search for prey than smaller individuals because the former are at a lower risk for predation (Kobler et al. 2008). In contrast to the negative relationship we found for pike, site fidelity increased with body size for Yellow Perch. Similarly, Bauer et al. (2009) found that small Yellow Perch were more active than larger individuals in two South Dakota lakes. Additionally, in the lake with more complex habitats, smaller individuals were located farther from shore. In simple habitats with limited areas for refuge, the ideal despotic distribution would predict that individuals, particularly smaller individuals, are forced to move extensively to avoid predation (Gilliam and Fraser 1987; Newman and Caraco 1987).

2.6 Conclusion

The functionality of a restored habitat is an important consideration when deciding on the design and assessing the success of restoration (Cortina et al. 2006; Herrick et al. 2006). Surveying the fish community of a habitat traditionally involves using non-selective fishing methods, such as electrofishing and trap netting. These methods are useful for comparing trends in annual and seasonal catch, species richness and abundance at standardized locations (Pope et al. 2010). However, they are seasonally, and weather restricted, labour intensive and only capture a snapshot of the community in space and time (Fausch et al. 1990; Harris 1995; Pope and Willis 1996). Determining whether the fish community uses different habitats for foraging, spawning, nursery and/or refuge sites and whether non-native species are using the area is crucial information for habitat managers (Minns 2001; Lapointe et al. 2014; Cooke et al. 2016). Traditionally, biotelemetry has benefitted restoration projects by providing information regarding the habitat preferences of various fishes (Lapointe et al. 2013), but until recently, has rarely

been used in pre-restoration and post- restoration validation monitoring. To date, acoustic telemetry studies of fish movement and behaviour in restored estuarine habitat has revealed important habitat function for juvenile Gray Smooth-hound Sharks (*Mustelus californicus*) (Espinoza et al. 2011) and Shovelnose Guitarfish (*Rhinobatos productus*) (Farrugia et al. 2011).

We demonstrate the utility of passive acoustic telemetry for continuously tracking multi-season spatial habitat use concurrently for multiple fish species. This allowed us to confirm that the restoration efforts in Toronto Harbour appear to be successful as these areas are being highly used by two of the target native species, but less highly used by a non-native fish. The combination of biotelemetry and traditional biodiversity surveying methods could prove an ideal approach to assessing the success of restoration projects given that collectively they provide information on both ecological patterns and processes (Herrick et al. 2006).

For restoration ecologists and habitat managers alike, understanding the responses of communities to habitat restoration activities is crucial in determining the success of restoration projects (Lake 2001). Here, we demonstrate the spatial ecology of several members of the fish community in restored and non-restored habitat areas of a large set of coastal embayments. We acknowledge that an ideal design to assess restoration success would be a before-after- control-impact design (Underwood 1994). We did not have pre-restoration information on the distribution of fish in this system, but it is fair to say that the regions that were restored were previously void of complex habitat after it was stripped out or infilled as part of the harbour's development. Also notable in this study were the interactions of species, body size and season on site fidelity. All factors

collectively influenced the patterns of habitat use and movement behaviour. Given this, managers can plan for and design multi-species and multi-life stage habitat restoration projects. For example, it may be possible to identify habitats that are undesirable for invasive fishes, but of high value to native fishes thus providing opportunities for restoration activities to target the species groups of interest. Indeed, habitat managers and restoration planners working on Toronto Harbour are already incorporating such concepts arising from telemetry data into their development of future plans in an effort to ensure that habitats frequented (inferred as habitat preference) by the non-native Common Carp are not unintentionally created.

Our results demonstrate that aquatic habitat restoration aimed at improving the overall habitat conditions were collectively beneficial for target fishes and effective at limiting use by a non-native fish. In an ideal world, all habitat restoration would be done with some level of understanding of the specific habitat needs and preferences in mind of key members of the fish community, especially if these are site specific. However, in practice such efforts would be resource intensive. As such, any efforts to incorporate telemetry techniques to evaluate restoration activities, such as completed here, could help to not only address site-specific issues, but also improve the broader evidence base regarding ecological restoration.

Chapter 3. Examination of the fine-scale seasonal space use and overlap of three species of fish in a coastal embayment of the Laurentian Great Lakes.

3.1 Abstract

Habitat heterogeneity promotes species coexistence as it provides spatial refuges that can free overlapping species from agonistic interactions. Examining the size and degree of overlap in activity spaces can provide insight into the quality or function of habitat from the perspective of the animal. To evaluate the habitat quality of a ~45 Ha coastal embayment, I investigated the size and degree of overlap in seasonal activity spaces among three coexisting species of freshwater fish using fine-scale, high-resolution telemetry data. The majority of tracked individuals used the embayment in all seasons, but there were seasonal differences in the size of the activity spaces (i.e., largest in summer and smallest in winter) and the degree of overlap between individual activity spaces (i.e., higher in summer and winter). Body size influenced the size of activity space, but not the degree of overlap. Generally, activity spaces were moderately sized relative to the size of the embayment (e.g., average 95% activity space = 8.1 ha, 18.4 ha, and 19.2 ha, for Northern Pike, Largemouth Bass, and Common Carp, respectively) and overlap among individual activity spaces was low. Based on those space use characteristics, I inferred that the habitat in this coastal embayment is intermediate in quality. Greater understanding of the space use behaviour of animals can inform the effectiveness of management actions in aquatic habitats intended to conserve and restore functional habitat.

3.2 Introduction

How animals use space in their environment is a fundamental component of behavioural ecology. Space use behaviour is a complex consequence of predator-prey relationships, intra- and inter-specific competition, habitat use and selection, niche partitioning, and population demographics (Tilman and Karieva 1997). Understanding differential space use behaviour of a variety of taxa has long been a focus for behavioural ecologists (Werner et al. 1977; Smith and Ballinger 2009; Pearce et al. 2013). Resource partitioning is an important process driving the differential space use of all animals (Schoener 1974; Toft 1985; Martin 1996). Animals may partition resources along a number of resource dimensions or axes. Schoener (1974) suggested that habitat dimensions were most important, followed by food-type dimensions, and temporal dimensions (e.g., seasonality). While resource partitioning may also be the consequence of inherent physiological differences (Reinert 1984).

Notably, resource partitioning among fish has received substantial attention in the literature (Sale 1977; Werner et al. 1977; Mittelbach 1984; Ross 1986; Grossman et al. 1998; Jackson et al. 2001; Munsch et al. 2016). Temperate marine reef assemblages are more structured by trophic separation than habitat separation (Ross 1986). However, in temperate lakes and rivers, habitat segregation appears to be an equally important resource-partitioning axis (Ross 1986; Grossman et al. 1998; Jackson et al. 2001). In the littoral areas of freshwater lakes, spatial segregation of species was evident along three gradients; depth (distance from shore), vertical position in the water column, and structural complexity (Werner et al. 1977). In fact, Werner et al. (1977) concluded that

only one definitive example of segregation between two fish species occurred as a function of food partitioning. Furthermore, several species showed intra-specific differences in the spatial distribution of size-classes. In general, smaller size-classes of fish tend to be confined to areas of dense cover, likely as a consequence of predation risk (Werner et al. 1977).

Co-occurrence of conflicting species (e.g., intraguild predators) is quite common, even though these "enemies" are not predicted to coexist (Polis et al. 1989). One mechanism that can promote coexistence in spite of such conflict is habitat diversification. Habitat heterogeneity promotes species coexistence as it provides temporal and spatial refuges that can temporarily free overlapping trophic status species from agonistic interactions (Mittelbach 1988; Christensen and Persson 1993; Hampton 2004). For example, animals can choose to forage or rest in less preferred habitats in order to reduce the risk of contact with competitors (Lima and Dill 1990). Habitat diversification is strongly supported as the mechanism permitting species coexistence in lakes (Robinson and Wilson 1994).

While space use is a concept well covered in the literature, beginning with the home range concept from Burt (1943), relatively few studies have compared the degree of overlap in space use (Mazerole and Hobson 2004; Pearce et al. 2013; Knickle and Rose 2014). I consider space use overlap as the amount of physical space an individual or species shares with competitors, predators, or conspecifics while carrying out its regular activities to ensure growth, survival, and reproduction (McLoughlin et al. 2000). McLoughlin et al. (2000) developed a conceptual model for the spatial organization of individuals according to habitat quality. The following predictions emerge from that

conceptual model: i) in areas of high habitat quality, populations should be characterized by small home ranges and high home range overlap, ii) in areas of moderate habitat quality, home ranges get larger and overlap decreases, and iii) in areas of low habitat quality, home ranges continue to increase and overlap will increase.

Animals can minimize agonistic interactions by minimizing overlap in space. However, to understand the degree to which animals partition space, we require finescale knowledge of where they occur. By its simplest definition, spatial overlap can be quantified as the proportion of overlap between one animal's activity space (e.g., home range or territory) and that of another animal (Fieberg and Kochanny 2005). This simple approach is prone to bias when animals use the areas of overlap infrequently (Cooper et al. 2014). To improve the quantitative estimates of spatial overlap, several overlap indices have been developed that account for the frequency of use within the overlapped space (Cooper et al. 2014). Fieberg and Kochanny (2005) comparatively reviewed common overlap indices and demonstrated the appropriateness of the Utilization Distribution Overlap Index (UDOI) for measuring the degree to which two animals share the same space.

In the Laurentian Great Lakes, coastal wetlands provide critical spawning, nursery, foraging and refugia habitat for over 80% of fish species in the community (Jude and Papas 1992; Randall et al. 1996; Wei et al. 2004; Midwood and Chow-Fraser 2015). However, within the Great Lakes basin, over 70% of all wetlands have been lost (Whillans 1982; Snell 1987; Midwood and Chow-Fraser 2015). Many of the remaining wetlands have declined in habitat quality (Chow-Fraser 2006; Cvetkovic and Chow-Fraser 2011) and are further threatened by increasing human development (Niemi et al.

2007). Suitable habitat is a fundamental component for maintaining productive fish populations (Lapointe et al. 2014). Shallow waters are typically densely packed with individuals (Munsch et al. 2016). As a consequence, increased species interactions are expected. The space use behaviour of fish in nearshore areas is driven by trade-offs between predation risk and other life history requirements (e.g., foraging, digestion, spawning, etc.; He and Kitchell 1990; Lima and Dill 1990). Jackson et al. (2001) suggest that beyond abiotic controls, predation (direct and indirect) has very strong effects on structuring the spatial distributions of individuals within fish communities, while competition may also play an important role in the organization of fish communities.

I investigate the size and degree of overlap in seasonal space use among three coexisting species of freshwater fish using fine-scale, high-resolution telemetry data. I compare and contrast the space use behaviour and the spatial overlap from two-dimensional kernel utilization distributions (KUD) using acoustic telemetry location data for Largemouth Bass (*Micropterus nigricans*), Northern Pike (*Esox lucius*), and Common Carp (*Cyprinus carpio*). Largemouth Bass is a warmwater piscivore. Northern Pike is a coolwater piscivore. Common Carp is a warmwater benthic feeder. All three species show affinity for submerged aquatic vegetation (Lane et al. 1996a). Largemouth Bass have been classified as part of the 'coastal' taxocene of Great Lakes fishes – those species that are heavily dependent on wetlands, while Northern Pike and Common Carp have been classified as part of the 'transitional' taxocene – those species that use both the open water and nearshore environments (Jude and Pappas 1992; Wei et al. 2004). I test the influence of body size and season on the size and degree of overlap in activity space (95% KUD) and core use (50% KUD) areas for each species. I hypothesize that both the

size and degree of overlap of activity spaces will be influenced by season. Specifically, I predict that activity space estimates will be largest during summer and smallest during winter because space use size is largely driven by foraging demands and food availability that are at their lowest during the winter season. I predict that the degree of overlap would be largest during winter because minimizing energy expenditure becomes more important than protection from predators or access to food resources. I also hypothesize that both the activity space estimates and the degree of overlap will be related to fish body size. Specifically, I predict that activity space estimates and the degree of overlap would increase with body size because larger fish need to use more space in order to meet the greater metabolic requirements (i.e., more food) that come with being larger.

3.3 Methods

3.3.1 Study Site

The central Toronto waterfront and Toronto Harbour (~15 km²) is partly a set of large coastal embayments connected to Lake Ontario, situated directly along the downtown core or central waterfront of Toronto, ON, Canada. Historically, the eastern region of Toronto Harbour was an expansive marsh complex at the mouth of the Don River known as Ashbridge's Bay. After this wetland area was drained and reclaimed to serve as industrial port lands, only a fragment of this original bay remains (separated from the current Toronto Harbour by the reclaimed land). Tommy Thompson Park (TTP) is man-made peninsula located in the most south-easterly portion of Toronto Harbour that was started in the early 1970's and construction is ongoing (Figure 3.1). The peninsula is made from infill materials and has been modified to naturalize portions of

Toronto Harbour, and restore lost coastal features. This aquatic and terrestrial park projects 5 km into Lake Ontario and covers a total surface area of over 250 ha (TRCA 2000). To create a more thermally and structurally complex system, the aquatic portions of the park are functionally divided into three cells and four embayments (TRCA 2000). Embayment C is a ~45 ha sheltered embayment in Tommy Thompson Park characterized by shallow depth (primarily <4m) and moderate to high summer water temperatures (15-22° C; Hlevca et al. 2015; Peat et al. 2016). Submerged aquatic vegetation (SAV) is heterogeneously distributed and ranges from sparse SAV to dense stands of SAV. The bottom substrate and shorelines are dominated by sand mixtures (Midwood et al. 2019, Leisti et al 2020). Embayment C is hydrologically connected to the Outer Harbour, near the confluence of the harbour with Lake Ontario. It is also hydrologically connected to Cells 3, 2, and 1, respectively (Figure 3.1).

3.3.2 Acoustic Telemetry Array and Fish Tagging

To track the two-dimensional space use of fish in Embayment C, I deployed a fine-scale acoustic telemetry array (Vemco Positioning System; VPS) consisting of twenty-four acoustic receivers (Vemco VR2W 69 kHz, Vemco, Ltd., Nova Scotia, Canada). Receivers were located in a pseudo-grid arrangement to maximize spatial coverage and ensure adequate overlap of the receiver detection zones, while accounting for issues related to water depth, line of sight, navigation routes, and mooring buoys for recreational sailboats (Figure 3.1).

Acoustic receivers were held inside a PVC casing (without interfering with the detection cone from the top of the receiver) that was fixed into a concrete base and

reinforced with steel rebar. Receiver bases were tethered from an eyebolt in the concrete base to the nearest secure point on shore (e.g., tree) by submerged steel cable. Receivers were retrieved every six months to offload data, to remove any accumulated biofouling, and check receiver condition. Receivers were then redeployed in the same locations. Range testing (see Kessel et al. 2014) was conducted at a subset of receivers in different habitat types and in different seasons to inform receiver placement, and varied from 400 to 1500 m (see Veilleux 2014).

Fish were captured and tagged opportunistically between 2012 to 2015 as part of a large telemetry study occurring in the Toronto Harbour. All fish in this study were captured via boat electrofishing (SR-18EH, 6.0-7.0 A, 60Hz, 340V DC, Smith-Root, Inc., Vancouver, WA). After capture, each fish was held in the boat livewell and transported to a shore-based surgery site. Post-surgery, all tagged fish were released at their original capture location. Fish were immobilized using either a Portable Electroanesthesia System (PES; Trushenski et al., 2012, Rous et al., 2015) or using the boat's e-fishing electrodes methods that have previously been used to immobilize fish for surgeries (Jennings and Looney 1998; Vandergoot et al. 2011; Brooks et al. 2018). For transmitter implantation, fish were moved from the livewell with a wetted net onto a padded surgical table with the fish in a supine position. During implantation, lake water was continuously passed through the gills of the fish. Each individual was measured for total length. Prior to implanting an acoustic transmitter into an individual, the transmitter and all surgical tools were disinfected in an iodine solution and rinsed. An incision (< 20 mm) was made with a sharp scalpel on the ventral surface of the fish. Curved forceps were used to lift the skin and body wall to avoid any injury while making the incision. The transmitter was inserted

into the coelomic cavity of the fish based on size differences within and between species; individuals were tagged with either a Vemco V7, V9, or V13 transmitter types (69 kHz, Vemco Ltd., Halifax, Canada).

The VPS tracking period in Embayment C extended for 2 years, from 18 November 2013 until 11 November 2015. Fish detections were filtered to remove any potential false detections (i.e., detections that occurred from the same tag at the same receiver within a period of less than the minimum tag delay. Then, detections of individual tags were plotted over space and time to visually examine stationary tags (i.e., those not tracking live fish due to fish mortality or tag shedding). Ninety-two tagged fish were detected (positioned) in the Embayment C VPS. Four individuals were removed from subsequent analysis because they had too few positions to estimate activity space or they were suspected to be have died.

3.3.3. Data Management

Detections of acoustically tagged fish by at least three acoustic receivers in the Vemco positioning system in Embayment C were used by Vemco to estimate fish positions using hyperbolic positioning (Smith 2013). Estimated fish positions (n = 896 103) were filtered by a maximum horizontal positioning error (HPE) of ten, following the methods of Smith (2013), after which 84% of positions were retained. Fish positions were then visually inspected using GIS software (QGIS 2019).

3.3.4 Kernel Density Estimation and Utilization Distribution Overlap

Fish positions were used to develop a kernel density estimate of the utilization

distribution (KUD) for each individual. From each individual KUD, I estimated the 95% activity space and 50% coreuse space. To test for seasonal effect on each KUD, a separate estimate was constructed for each individual in each season. Seasons were defined as spring (1 March until 31 May), summer (1 June until 31 August), fall (1 September until 30 November), and winter (1 December – 28 February). Utilization distributions are robust to spatial autocorrelation (Swihart and Slade 1997) and bias in estimating home range can actually be reduced at higher levels of autocorrelation (de Solla et al. 1999; Fieberg 2007). To measure the degree of overlap in individual KUDs, I used the Utilization Distribution Overlap Index (UDOI). To qualitatively compare the size and overlap of 95% activity space and 50% core use areas, I calculated the minimum convex polygon (MCP) for each individual in each season and plotted each individual MCP overlaid on a satellite image of Embayment C. All space use metrics and overlap estimates were calculated using the 'adehabitatHR' (Calenge 2006) R package and plotted using the 'ggplot2' (Wickham 2016) R package.

3.3.5 Statistical Analysis

Relative differences amongst seasons in the size of both the 95% activity space and 50% core use estimates were analyzed using linear mixed effects models for each of the three species, separately. Both activity space models included fish identification as a random effect and season and body size as a fixed effect. Data exploration was performed using standard tools including Cleveland dot plots and box and whisker plots following the approach suggested by Zuur et al. (2009). The residuals of activity space models were normally distributed and generated using the 'nlme' R package (Pinheiro et al. 2018). If the model indicated a significant result for seasonal effect, a Tukey post-hoc test using

the 'multcomp' R package (Hothorn et al. 2008) was used to make pairwise comparisons.

3.4 Results

Mean activity space size (95% KUD) in Embayment C ranged from 8.10 ha to 19.15 ha (Table 3.1). Mean core use area size (50% KUD) ranged from 1.63 ha to 4.04 ha (Table 3.1). Northern Pike had significantly smaller mean activity space (Kruskal-Wallis rank sum test, df = 2, p-value = 0.001) than both Largemouth Bass (p-value = 0.02) and Common Carp (p-value = 0.004) and core use areas (Kruskal-Wallis rank sum test, df = 2, p-value = 0.007) than both Largemouth Bass (p-value = 0.04) and Common Carp (pvalue = 0.02).

The size of the 95% activity space and 50% core use area increased with body size for Largemouth Bass and Northern Pike (Table 3.2 and Table 3.3, respectively), but not for Common Carp (Table 3.4). There was no apparent seasonal effect on the size of the 95% activity space or 50% core-use size for Largemouth Bass (Table 3.5). However, there was a rather convincing, although not statistically significant, trend where space-use metrics were reduced in winter (Figure 3.2 and Figure 3.3 for 95% and 50%, respectively). There was a significant, seasonal effect on the 95% activity space for Northern Pike (Table 3.3). It was significantly larger during the spring and summer than in the fall and winter (Table 3.6; Figure 3.4), but there were no apparent differences between spring and summer, or fall and winter. There were no seasonal differences in the 50% core-use area for any of the three species. Notably, the 50% core use areas for Northern Pike followed a similar seasonal pattern as its 95% activity space, although the relationship was not found to be statistically significant (Table 3.6; Figure 3.5)
The Utilization Distribution Overlap Index (UDOI) estimates of 95% activity space and 50% core use were significantly influenced by season for Largemouth Bass and Northern Pike (Table 3.6 and Table 3.7, respectively), but not for Common Carp (Table 3.8.). UDOI was not influenced by body size for Largemouth Bass or Northern Pike; while there was a slight positive influence of body size in Common Carp on the 50% core use area UDOI (Table 3.8). For Largemouth Bass, overlap between individual 95% activity space and 50% core use areas was significantly higher during the summer compared to spring and fall, but not in winter (Table 3.9). There was no apparent difference in the degree of overlap between fall and spring, winter and spring, or winter and fall (Figure 3.6). Similarly, overlap between 50% core use areas for Largemouth Bass was significantly higher during the summer compared to spring and fall, but not when compared to winter (Figure 3.7). There were no apparent differences in the degree of overlap between fall and spring, winter and spring, or winter and fall in Largemouth Bass. For Northern Pike, overlap between 95% activity spaces was quite low in all seasons, with only the overlap estimate in winter being significantly higher than overlap during fall (Table 3.10; Figure 3.8). The seasonal influence on the overlaps of 50% core use areas was different, with only the overlap estimate in spring being significantly higher than overlap during fall for Northern Pike (Table 3.10; Figure 3.9).

Qualitatively, the minimum convex polygon areas illustrate the individual variability within each species, which was at least partially driven by body size, in terms of the size and degree of overlap for both 95% activity space and 50% core use areas. There was a pattern in both the 95% and 50% use areas for Largemouth Bass where they are more restricted to the central portion of Embayment C during winter, while in the

other seasons, activity space uses tended to include more of the available embayment space, particularly in the northeast corner (95% activity space: Figure 3.10; 50% core use: Figure 3.11). Northern Pike predominately used (based on 50% core use areas) the central portion of Embayment C during the winter as well, while in the spring and summer, core use areas expanded in size and were more dispersed throughout the entirety of the embayment (Figure 3.12). This pattern of restricted use is not as clear when comparing the 95% activity space areas (Figure 3.13). Tagged Common Carp were completely absent from Embayment C during the winter. There are no visually striking differences in the pattern of space use for this species during spring, summer, or fall (95% activity space: Figure 3.14; 50% core use: Figure 3.15).

Species	Mean 50%	Mean 95%
	Core us	activity space
	(min – max)	(min – max)
Largemouth Bass	4.04	18.40
(N = 23)	(0.03 – 14.17)	(0.21 - 45.41)
Northern Pike	1.63	8.10
(N = 36)	(0.004 - 5.96)	(0.02 - 24.92)
Common Carp	3.84	19.15
(N = 14)	(0.15 – 10.77)	(1.07 – 42.03)

Table 3.1 Summary of 50% and 95% activity space kernel utilization distribution estimates, in hectares (ha), for tagged individuals.

Table 3.2 Linear mixed effects regression model estimates for the 95% activity space and
50% core use areas of Largemouth Bass in Embayment C of Toronto Harbour. Fixed
effects that are significant at the 0.05 level are bolded.

Response parameter	Model term	Value	SE	df	t-value	p-value
95% Activity space	Intercept	-28.63	8.54	23	-3.35	0.003
	Body size	0.13	0.02	23	5.62	<0.0001
	Spring	-3.44	3.22	15	-1.07	0.30
	Summer	-8.43	3.33	15	-2.54	0.02
	Winter	-1.37	4.08	15	-0.34	0.74
50% Core use	Intercept	-7.45	2.10	23	-3.56	0.002
	Body size	0.03	0.006	23	5.62	<0.0001
	Spring	-0.69	1.13	15	-0.62	0.55
	Summer	-2.17	1.19	15	-1.82	0.09
	Winter	-0.30	1.56	15	-0.19	0.85

Table 3.3 Linear mixed effects regression model estimates for the 95% activity space and 50% core use areas of Northern Pike in Embayment C of Toronto Harbour. Fixed effects that are significant at the 0.05 level are bolded.

Response parameter	Model term	Value	SE	df	t-value	p-value
95% Activity space	Intercept	-0.96	1.92	58	-0.50	0.62
	Body size	0.01	0.003	58	3.73	0.0004
	Spring	4.29	1.63	58	2.64	0.01
	Summer	4.62	1.69	58	2.74	0.008
	Winter	-0.11	1.53	58	-0.07	0.95
50% Core use	Intercept	-0.33	0.45	58	-0.74	0.46
	Body size	0.002	0.0007	58	3.51	0.0009
	Spring	0.96	0.39	58	2.43	0.02
	Summer	0.99	0.41	58	2.41	0.02
	Winter	-0.02	0.37	58	-0.05	0.96

Table 3.4 Linear mixed effects regression model estimates for the 95% activity space and 50% core use areas of Common Carp in Embayment C of Toronto Harbour. Fixed effects that are significant at the 0.05 level are bolded.

Model term	Value	SE	df	t-value	p-value
Intercept	40.54	19.33	15	2.10	0.05
Body size	-0.04	0.03	12	-1.33	0.21
Spring	5.58	6.12	15	0.91	0.37
Summer	10.38	5.69	15	1.82	0.09
Intercept	9.18	5.13	15	1.79	0.09
Body size	-0.01	0.0008	12	-1.22	0.25
Spring	1.83	1.66	15	1.10	0.29
Summer	2.58	1.55	15	1.67	0.12
	Model term Intercept Body size Spring Summer Intercept Body size Spring Summer	Model termValueIntercept40.54Body size-0.04Spring5.58Summer10.38Intercept9.18Body size-0.01Spring1.83Summer2.58	Model term Value SE Intercept 40.54 19.33 Body size -0.04 0.03 Spring 5.58 6.12 Summer 10.38 5.69 Intercept 9.18 5.13 Body size -0.01 0.0008 Spring 1.83 1.66 Summer 2.58 1.55	Model termValueSEdfIntercept40.5419.3315Body size-0.040.0312Spring5.586.1215Summer10.385.6915Intercept9.185.1315Body size-0.010.000812Spring1.831.6615Summer2.581.5515	Model termValueSEdft-valueIntercept40.5419.33152.10Body size-0.040.0312-1.33Spring5.586.12150.91Summer10.385.69151.82Intercept9.185.13151.79Body size-0.010.000812-1.22Spring1.831.66151.10Summer2.581.55151.67

Table 3.5 Post-hoc Tukey pairwise comparisons for the fitted models of the Largemouth Bass 95% activity space and 50% core use area size. Pairwise comparisons that are significant at the 0.05 level are bolded.

Response parameter	Season pair	Estimate	SE	Z value	p-value
95% Activity space	Spr – Fall	-3.45	3.22	-1.07	0.70
	Sum – Fall	-8.43	3.33	-2.54	0.05
	Win – Fall	-1.37	4.08	-0.34	0.99
	Sum – Spr	-4.99	3.87	-1.29	0.56
	Win – Spr	2.08	4.53	0.46	0.97
	Win – Sum	7.07	5.04	1.40	0.49
50% Core use	Spr – Fall	-0.70	1.13	-0.62	0.92
	Sum – Fall	-2.17	1.19	-1.82	0.25
	Win – Fall	-0.30	1.56	-0.19	0.99
	Sum – Spr	-1.47	1.31	-1.13	0.67
	Win – Spr	0.40	1.71	0.23	0.99
	Win – Sum	1.87	1.84	1.02	0.73

Table 3.6 Post-hoc Tukey Pairwise comparisons for the fitted models of the Northern Pike 95% activity space and 50% core use area size. Pairwise comparisons that are significant at the 0.05 level are bolded.

Response parameter	Season pair	Estimate	SE	Z value	p-value
95% Activity space	Spr – Fall	4.29	1.63	2.64	0.04
	Sum – Fall	4.62	1.69	2.74	0.03
	Win – Fall	-0.11	1.53	-0.07	0.99
	Sum – Spr	0.34	1.78	0.19	0.99
	Win – Spr	-4.39	1.68	-2.62	0.04
	Win – Sum	-4.73	1.76	-2.69	0.03
50% Core use	Spr – Fall	0.96	0.39	2.43	0.07
	Sum – Fall	0.99	0.41	2.41	0.08
	Win – Fall	-0.02	0.37	-0.05	1.00
	Sum – Spr	0.03	0.43	0.07	0.99
	Win – Spr	-0.98	0.41	-2.40	0.08
	Win – Sum	-1.00	0.43	-2.36	0.09

Table 3.7 Linear mixed effects regression model estimates for the Utilization Distribution Overlap Index (UDOI) of the 95% activity space and 50% core use areas of Largemouth Bass in Embayment C of Toronto Harbour. Fixed effects that are significant at the 0.05 level are bolded.

Response	Model term	Value	SE	DF	t-value	p-value
parameter						
95% Activity	Intercept	-0.04	0.28	21	-0.13	0.90
space						
	Body size	0.0001	0.0007	21	0.14	0.89
	Spring	-0.0007	0.15	17	-0.004	0.99
	Summer	0.60	0.16	17	3.80	0.001
	Winter	0.16	0.21	17	0.79	0.44
50% Core	Intercept	-0.002	0.006	21	-0.34	0.74
use						
	Body size	0.000006	0.00002	21	0.25	0.73
	Spring	-0.0001	0.003	17	-0.03	0.98
	Summer	0.013	0.004	17	3.50	0.003
	Winter	0.0006	0.00002	17	0.13	0.89

Table 3.8 Linear mixed effects regression model estimates for the Utilization Distribution Overlap Index (UDOI) of the 95% activity space and 50% core use areas of Northern Pike in Embayment C of Toronto Harbour. Fixed effects that are significant at the 0.05 level are bolded.

Response parameter	Model term	Value	SE	df	t-value	p-value
95% Activity space	Intercept	0.02	0.02	58	1.22	0.23
	Body size	-0.00005	0.00003	58	-1.54	0.13
	Spring	0.02	0.02	58	1.43	0.16
	Summer	0.02	0.02	58	1.40	0.17
	Winter	0.04	0.02	58	2.59	0.01
50% Core use	Intercept	0.0004	0.0002	58	1.54	0.13
	Body size	-0.0000008	0.0000004	58	-1.98	0.05
	Spring	0.0006	0.0002	58	2.67	0.01
	Summer	0.0006	0.0002	58	2.31	0.02
	Winter	0.00009	0.0002	58	0.40	0.69

Table 3.9 Linear mixed effects regression model estimates for the Utilization Distribution Overlap Index (UDOI) of the 95% activity space and 50% core use areas of Common Carp in Embayment C of Toronto Harbour. Fixed effects that are significant at the 0.05 level are bolded.

Response	Model term	Value	SE	df	t-value	p-value
parameter						
95% Activity	Intercept	-0.73	0.37	15	-2.00	0.06
space						
	Body size	0.001	0.0006	12	2.08	0.06
	Spring	0.18	0.12	15	1.50	0.15
	Summer	0.25	0.11	15	2.17	0.05
50% Core use	Intercept	-0.02	0.01	15	-2.28	0.04
	Body size	0.00004	0.00002	12	2.35	0.04
	Spring	0.004	0.004	15	1.00	0.34
	Summer	0.007	0.003	15	2.08	0.06

Table 3.10 Post-hoc Tukey Pairwise comparisons for the fitted models of the Largemouth Bass Utilization Distribution Overlap Index (UDOI) of the 95% activity space and 50% core use areas. Pairwise comparisons that are significant at the 0.05 level are bolded.

Response parameter	Season pair	Estimate	SE	Z value	p-value
95% Activity space	Spr – Fall	-0.0006	0.15	-0.004	1.00
	Sum – Fall	0.60	0.16	3.80	<0.001
	Win – Fall	0.16	0.21	0.79	0.86
	Sum – Spr	0.60	0.17	3.45	0.003
	Win – Spr	0.16	0.23	0.72	0.89
	Win – Sum	-0.44	0.25	-1.79	0.27
50% Core use	Spr – Fall	-0.0001	0.003	-0.03	0.99
	Sum – Fall	0.01	0.004	3.50	0.003
	Win – Fall	0.0006	0.005	0.13	0.99
	Sum – Spr	0.01	0.004	3.20	0.007
	Win-Spr	0.0007	0.005	0.14	0.99
	Win – Sum	-0.01	0.006	-2.14	0.13

Table 3.11 Post-hoc Tukey Pairwise comparisons for the fitted models of the Northern Pike Utilization Distribution Overlap Index (UDOI) of the 95% activity space and 50% core use areas. Pairwise comparisons that are significant at the 0.05 level are bolded.

Response parameter	Season pair	Estimate	SE	Z value	p-value
95% Activity	Spr – Fall	0.02	0.02	1.43	0.48
space	Sum – Fall	0.02	0.02	1.40	0.50
	Win – Fall	0.04	0.02	2.59	0.04
	Sum – Spr	0.0004	0.02	0.02	1.00
	Win – Spr	0.02	0.02	0.98	0.79
	Win – Sum	0.02	0.02	0.92	0.79
50% Core use	Spr – Fall	0.0006	0.0002	2.67	0.04
	Sum – Fall	0.0006	0.0002	2.31	0.09
	Win – Fall	0.00009	0.0002	0.40	0.98
	Sum – Spr	-0.00006	0.0003	-0.24	0.99
	Win – Spr	-0.0005	0.0002	-2.21	0.12
	Win – Sum	-0.0005	0.0003	-1.88	0.24



Figure 3.1: Satellite image of Embayment C in Toronto Harbour. White circles represent the location of acoustic telemetry receivers. Text represents the locations of hydrologically connected regions of the Toronto Harbour.



Figure 3.2: Boxplot showing Kernel Utilization Distribution estimates of the 95% activity space of Largemouth Bass by season. Each boxplot shows the median values (horizontal line), 25 and 75% quartiles (box), values < 1.5 times the interquartile range (whiskers), and outliers (circles).



Figure 3.3: Boxplot showing Kernel Utilization Distribution estimates of the 50% core activity space of Largemouth Bass by season. Each boxplot shows the median values (horizontal line), 25 and 75% quartiles (box), values < 1.5 times the interquartile range (whiskers), and outliers (circles).



Figure 3.4: Boxplot showing Kernel Utilization Distribution estimates of the 95% activity space of Northern Pike by season. Each boxplot shows the median values (horizontal line), 25 and 75% quartiles (box), values < 1.5 times the interquartile range (whiskers), and outliers (circles).



Figure 3.5: Boxplot showing Kernel Utilization Distribution estimates of the 50% activity space of Northern Pike by season. Each boxplot shows the median values (horizontal line), 25 and 75% quartiles (box), values < 1.5 times the interquartile range (whiskers), and outliers (circles).



Figure 3.6: Boxplot showing Utilization Distribution Overlap Index values of the 95% activity space of Largemouth Bass by season. Each boxplot shows the median values (horizontal line), 25 and 75% quartiles (box), values < 1.5 times the interquartile range (whiskers), and outliers (circles).



Figure 3.7: Boxplot showing Utilization Distribution Overlap Index values of the 50% core activity space Largemouth Bass by season. Each boxplot shows the median values (horizontal line), 25 and 75% quartiles (box), values < 1.5 times the interquartile range (whiskers), and outliers (circles).



Figure 3.8: Boxplot showing Utilization Distribution Overlap Index values of the 95% activity space of Northern Pike by season. Each boxplot shows the median values (horizontal line), 25 and 75% quartiles (box), values < 1.5 times the interquartile range (whiskers), and outliers (circles).



Figure 3.9: Boxplot showing Utilization Distribution Overlap Index values of the 50% activity space of Northern Pike by season. Each boxplot shows the median values (horizontal line), 25 and 75% quartiles (box), values < 1.5 times the interquartile range (whiskers), and outliers (circles).



Figure 3.10: Visualization of the seasonal 95% full use activity space for Largemouth Bass during winter (top left), spring (top right), summer (bottom left), and fall (bottom right) estimated by a minimum convex polygon method. Each colour represents an individual tagged fish.



Figure 3.11: Visualization of the seasonal 50% core use activity space of Largemouth Bass during winter (top left), spring (top right), summer (bottom left), and fall (bottom right) estimated by a minimum convex polygon method. Each colour represents an individual tagged fish.



Figure 3.12: Visualization of the seasonal 95% full use activity space for Northern Pike during winter (top left), spring (top right), summer (bottom left), and fall (bottom right) estimated by a minimum convex polygon method. Each colour represents an individual tagged fish.



Figure 3.13: Visualization of the seasonal 50% full use activity space for Northern Pike during winter (top left), spring (top right), summer (bottom left), and fall (bottom right) estimated by a minimum convex polygon method. Each colour represents an individual tagged fish.



Figure 3.14: Visualization of the seasonal 95% full use activity space for Common Carp during spring (top right), summer (bottom left), and fall (bottom right) estimated by a minimum convex polygon method. Each colour represents an individual tagged fish.



Figure 3.15: Visualization of the seasonal 50% full use activity space for Common Carp during spring (top right), summer (bottom left), and fall (bottom right) estimated by a minimum convex polygon method. Each colour represents an individual tagged fish.

3.5 Discussion

The primary objective of this study was to compare and contrast the size and degree of overlap in space use among a group of coexisting, freshwater fish species in a sheltered embayment in the Toronto Harbour. The results suggest that the majority of tracked individuals used Embayment C in all seasons (except Common Carp in winter). There were seasonal differences in the size of the individual activity spaces and the degree of overlap between their activity spaces. Given the small size of Embayment C, the estimated activity spaces were deemed to be moderate in size since, on average, the 95% activity space areas covered between a quarter and half of the available space in Embayment C, while the 50% core use areas generally only covered less than fifteen percent of the available space. The degree of overlap between the activity spaces was generally low between individuals within each species, although there was an increase in the overlap during summer. Based on the conceptual model proposed by McLoughlin et al. (2000), it can be inferred that the habitat in Embayment C is intermediate in quality (i.e. moderately sized home ranges with low levels of overlap).

The 95% activity space, commonly referred to as a home range, and the 50% core use areas estimated from the acoustic telemetry data in Embayment C corroborate well with home range and core use estimates for each species reported in the literature. Of the species included in the current study, the home range size and core use areas of Largemouth Bass have been studied the most extensively. For Largemouth Bass, in a variety of systems, home ranges can vary from as small as <0.1 ha to 50 ha (Fish and Savitz 1983; Mesing and Wicker 1986; Minns 1995; Sammons and Maceina 2005). The mean estimate for the 95% activity space of 18 ha fits well within this range. Notably, the

size of the 95% activity spaces varied considerably among individual Largemouth Bass (0.21 ha - 45 ha). Individuals with the largest activity spaces essentially covered the entire area of Embayment C, while those with the smallest activity spaces were confined to very small pockets within the embayment. It is common for Largemouth Bass to stay in relatively small areas when part of larger systems (Sammons and Maceina 2005), although Hanson et al. (2007) also found considerable individual variation in activity spaces. In their study of Largemouth Bass activity and space use in a small Eastern Ontario lake, even though most individuals held discrete home ranges, some individuals in the population were quite transient and would cover large parts of the lake in the span of a few days (Hanson et al. 2007). In an embayment of a large U. S. reservoir, Largemouth Bass displayed a common pattern in the division of daily space use. The pattern consisted of resting in offshore regions (near woody structure, with low individual activity levels) primarily during the day and moving to the nearshore area, presumably to forage during low light periods (Sammons and Maceina 2005). Largemouth Bass tracked in my study held small core use areas, suggesting that even though some individuals were more exploratory, individuals restricted the majority of their habitat use and movement behaviour to discrete pockets that presumably provided sufficient habitat to support growth and survival.

Reported home range sizes for Northern Pike are generally quite small (0.01 – 0.05 ha; Vehanen et al. 2006). Indeed, they did have the smallest mean 95% activity space and 50% core use areas (8.10 ha and 1.63 ha, respectively) of the three species in this study, however these activity spaces are considerably larger than estimates from the literature. Northern Pike may be using larger areas in Embayment C to move among

limited patches of high quality habitat (e.g., submerged aquatic vegetation) or to access preferred water temperatures, both of which can be quite variable in the central waterfront. Northern Pike are solitary predators that depend on submerged aquatic vegetation or other cover for their ambush style sit-and-wait foraging strategy (Webb and Skadsen 1980; Chapman and Mackay 1984). If there are only a few patches, and they are distributed in a clumped pattern, rather than evenly distributed, then Northern Pike would have larger activity spaces if they frequent multiple patches (Nilsson 2006). Alternatively, in systems without sufficient submerged aquatic vegetation cover, Northern Pike have been observed to exhibit behavioural flexibility in foraging strategies; switching to a more active hunting tactic, particularly in response to decreased prey resources (Kobler et al. 2009) or under environmental conditions that would reduce capture efficiency such as high turbidity (Andersen et al. 2008). It is also possible space use behaviours of Northern Pike in Embayment C are driven by active thermoregulation. The activity spaces of tagged Northern Pike were largest during the summer, when Embayment C water temperatures can reach at least 24°C, exceeding the thermal optimal range for Northern Pike (thermal optima = 19°C to 21°C; Casselman and Lewis 1996). Northern Pike may be required to increase their activity space in order to find and access deeper, colder areas (Pierce et al. 2013; Peat et al. 2016). Many tracking studies of Northern Pike have observed the presence of distinct behavioural types in populations of Northern Pike (Mann 1980; Jepsen et al. 2001), including a type that has highly restricted ranges and a type that moves extensively. Indeed, companion studies tracking Northern Pike throughout the entire Toronto Harbour have found evidence that, while most tagged Northern Pike restrict their movements to a few core areas, a number of tagged

individuals can move quite extensively within geographically close regions and between geographically distant regions of the harbour (Midwood et al. 2019).

Common Carp have been described in the literature as both sedentary and highly mobile (Otis and Weber 1982; Penne and Pierce 2008; Jones and Stuart 2009; Butler and Wahl 2010). The high variability in the 95% activity space and 50% core use areas in Embayment C reflect these disparate observations. Of note, all tagged Common Carp were completely absent from Embayment C during the winter. Common Carp form large overwintering aggregations in deep water (García-Berthou 2001; Penne and Pierce 2008; Bajer and Sorensen 2009; Midwood et al. 2019). Their complete absence from Embayment C during this season suggests that this relatively shallow embayment does not contain preferred overwintering habitat or at least that there is preferred overwintering habitat elsewhere in the Toronto Harbour. Midwood et al. (2019) reported that tagged Common Carp in Toronto Harbour were more resident in deeper, more open coast regions during the winter.

The sizes of the activity space and core use areas of the species were influenced by season. The activity space and core use areas were smallest for Largemouth Bass and Northern Pike during the winter; Common Carp were completely absent. Activity space and Core use area expanded during the spring, generally reaching their largest sizes in the summer, followed by a reduction in size during fall again. This pattern of activity space contraction during fall and winter and expansion during spring and summer has been observed in a number of freshwater littoral species (Sakaris et al. 2005; Sammons and Maceina 2005; Hanson et al. 2007; Kobler et al. 2008; Penne and Pierce 2008). Largemouth Bass tend to stay in close proximity to their initial point of capture. Even

after spending winter in offshore locations, marked Largemouth Bass displayed a remarkable tendency to reside in the same segment of shoreline in successive summers (Lewis and Flickinger 1967). Small winter activity spaces are often the product of reduced metabolism and reduced foraging behaviour, whereby restricted movement is a strategy to minimize energetic costs during this period (Suski and Ridgway 2009). The environmental conditions that lead to selection of specific locations as overwintering sites are not well understood, but Largemouth Bass tend to overwinter in deeper areas and dissolved oxygen levels may influence selection of overwintering sites (Hasler et al. 2009). In the relatively shallow Embayment C, the general pattern was for all tagged individuals to constrict their activity spaces to the deepest sections in the center of the embayment. Increased activity space during the summer period can be the product of warmer water temperatures driving increased metabolism and increased growth during maximal foraging. To support these processes, fish increase their activity space in order to access greater food resources.

The size of activity space and core use areas were influenced by body size. Larger sized individual Largemouth Bass and Northern Pike had larger activity spaces in Embayment C. I did not detect an influence of body size on the space use of Common Carp. This may be a consequence of having a narrower size range of tagged Common Carp (range tagged: 470 - 710 mm), compared to the other species. For Largemouth Bass and Northern Pike, the size range of tagged individuals would have included juvenile and adult individuals (Largemouth Bass size range tagged: 201 - 490 mm; Northern Pike size range tagged: 250 - 972 mm). Largemouth Bass and Northern Pike are known to exhibit size-structured habitat use differences (Werner et al. 1977; Casselman and Lewis 1996).

Furthermore, the smaller individuals would most certainly be vulnerable to predation in the embayment. Individuals in this size range are less likely to have different levels of vulnerability to predation in this embayment. Home range size is also strongly influenced by metabolic requirements (McNab 1963) such that larger individuals require more resources to meet their greater energetic demands. As such, it is often necessary for larger individuals to traverse larger areas to gain the needed resources. Minns (1995) demonstrated that home range sizes increase allometrically with body size in temperate freshwater fishes. In a study of movement behaviour and habitat use in coastal wetlands of Georgian Bay, Midwood and Chow-Fraser (2015) found that the majority of wetland dependent fish species remain within a single wetland throughout the year, although large piscivores can use multiple wetlands over larger areas in order to satisfy their metabolic requirements.

Additionally, home range size could be influenced by abiotic environmental conditions such as thermal conditions (Jackson et al. 2001). Peat et al. (2016) found that Largemouth Bass and Northern Pike in Toronto Harbour exhibited evidence of behavioural thermoregulation. Below water temperatures of 20°C, both species were observed to be in water temperatures warmer than those recorded by nearby temperature loggers, while above water temperatures of 20°C, tagged Northern Pike moved into deeper, cooler areas (Peat et al. 2016). Thermal optima for adult Largemouth Bass ranges from 24°C to 30°C (Stuber et al. 1982), but throughout Toronto Harbour water temperature rarely exceeds 25°C, except in very shallow, protected embayments over relatively short durations in mid to late summer (Hlevca et al. 2015). Largemouth Bass activity spaces in Embayment C are likely driven in part by active thermoregulation behaviour to exploit optimal

temperatures to support growth. Additionally, home range size can be influenced by intra- and interspecific interactions (Jackson et al. 2001). For example, predation risk can restrict the movements of prey species, by actively avoiding areas that are heavily used by predators and hence reduce the size of an animal's activity space (Hampton 2004; Laundre et al. 2010; Gallagher et al. 2017).

Individual animals must share space as they perform their day-to-day activities. This inevitably leads to countless intra- and inter-specific interactions. Pearce et al. (2013) reviewed home range overlap in populations of primates and uncovered two consistent relationships. First, overlap of space use increases with body size – because bigger animals have bigger ranges, and second, overlap increases with declining habitat productivity – because unproductive habitats have less energetic value so individuals need to spend more time and space foraging in unproductive habitats. Although territoriality and aggression are common in primates (Pearce et al. 2013), birds (Mazerolle and Hobson 2004), and some species of marine fish (Low 1971), it is less documented in populations of freshwater fishes. Territorial aggression has been well documented by nest-guarding smallmouth bass (Ridgway et al. 1991), but fewer examples of territorial behaviour outside the spawning period exist. However, competition for optimal food patches is consistent with the ideal dominance model of habitat selection (Fretwell and Lucas 1970). For populations of freshwater fish sharing space in habitats with patchy and dynamic food resources, individuals are likely to concentrate in areas of higher prey availability. Northern Pike in Embayment C showed the lowest levels of space use overlap. Northern Pike are solitary, ambush predators and despite demonstrated ability to swallow large prey items, Northern Pike of all sizes prefer small shallow-bodied prey items (Nilsson 2006). They are also known to be cannibalistic, particularly when prey availability decreases (Grimm 1981). As such, individual Northern Pike should avoid their conspecific neighbours through low overlap in their activity spaces. Indeed, individual Northern Pike have shown signs of substantial overlap in activity spaces in some highly preferred areas although they generally avoided overlap in their core use (Vehanen et al. 2006). Further, Nilsson (2006) showed that individual Northern Pike spatially avoided larger conspecifics, which led to a size-specific distribution of individuals that reduced overlap in an effort to minimize risky, agonistic interactions. Overlap may be higher in the winter because reductions in foraging behaviour can minimize the need to defend territories (Suski and Ridgway 2009). Winter aggregations of individuals (high overlap) may occur because minimizing energy expenditure and maximizing survival from freezing becomes more important than protection from predators or access to food resources (Cunjak 1996; Suski and Ridgway 2009).

The space use behaviour of fish in nearshore areas is driven by trade-offs between predation risk and other life history requirements (e.g., foraging, digestion, spawning / reproduction, etc.; He and Kitchell 1990; Lima and Dill 1990). Home range size can decrease with increasing physical habitat complexity (Ahrenstorff et al. 2009) because it promotes concentration of prey items in favourable locations, so fish do not need to be as active compared to more homogenous habitats that would promote a more uniform distribution of prey (Eklov 1997; Radabaugh et al. 2010). Food resources are often cited as in important limiting factor determining the size of animal home ranges (McLoughin and Fergusen 2000), so it reasonably follows that home range size can be indicative of
habitat feeding quality (McLoughlin et al. 2000).

An animal's home range is commonly defined as being the area an animal uses during the course of a year for normal activities (Burt 1943). What I capture in this study does not constitute a home range according to this definition. Despite Embayment C having high estimates of residency for tagged fish in previous studies (Midwood et al. 2019), I found that there are still substantial levels of transiency. As such, the activity space areas do not capture all of the area a tagged fish uses because the tagged fish were free to move outside of the positioning array (i.e., into adjacent Cell 3 or into the outer harbour). For that reason, I do not refer to these estimates as home ranges and I compare 95% activity spaces to home range estimates in the literature for comparative purposes only. Furthermore, I was unable to capture the fine-scale temporal component of overlap (e.g., I look at seasonal overlap, but not hourly or instantaneous overlap) and temporal partitioning is known to be important (Ross 1986). These estimates of space use overlap may overestimate true encounters if individuals or species are avoiding areas of overlapping space by partitioning habitat temporally. Nonetheless it shows they use the same space even if not at the same time.

Based on the species complexes classified by Jude and Pappas (1992), Largemouth Bass belong to the 'wetlands' or 'coastal' taxocene, which are either permanent residents or highly dependent on these habitats for nursery, spawning, or shelter. Northern Pike and Common Carp fit under the 'transitional' or 'intermediate' taxocene, which utilize both open water and nearshore areas, and depend on wetlands for spawning and/or nursery habitat. Further, Wei et al. (2004) found that Largemouth Bass,

Northern Pike, and Common Carp were all significantly correlated with wetlands. Tommy Thompson Park is intended to be a "center of biological organization" for the Toronto Harbour (TRCA 2000; Toronto Waterfront Aquatic Habitat Restoration Strategy). Embayment C is a 'created' sheltered embayment designed and engineered directly in terms of shape, depth, shoreline gradients, and location of some elements of physical habitat (e.g., boulders, coarse woody debris, vegetation) and indirectly in terms of exposure and water temperature (TRCA 2000). Understanding the ecological functionality of created or restored habitats is an essential aspect of evaluating the success of ecological restoration (Lindell 2008). For example, a mismatch between the human perceptions of improved habitat quality and the reality if the habitat is unsuitable for target animals can lead to ill-suited habitat restoration activities, or worse, ecological traps (Hale et al. 2015; Hale and Swearer 2017). For example, Veilleux et al. (2018) investigated the timing and duration of occupancy of seven species in four large urban slips areas in Toronto Harbour. Two of the slip areas were located in close proximity to more natural vegetated habitats and had undergone habitat enhancement activities, while the other two had no habitat enhancements and were located in close proximity to deep and turbid channelized regions. Overall, there was no reliable evidence that the majority of the seven adult fish species frequented either the enhanced or degraded slips, suggesting that there may be a mismatch between the smaller scale habitat enhancement efforts and overall habitat suitability for target fish.

Freshwater aquatic systems are some of the most impacted systems globally (Dudgeon et al. 2006; Reid et al. 2019). Although physical modification is only one of many threats for freshwater aquatic systems, human development generally reduces

habitat heterogeneity in impacted lakes (e.g., removing aquatic macrophytes and/or coarse woody debris and other structure and shallow areas). As the systems become more homogeneous (in physical structure) and degraded in environmental conditions, refuge from predation is lost and the potential for habitat segregation is reduced, and thus overlap in search patterns is increased (Jackson et al. 2001). Agencies responsible for the conservation and restoration of aquatic habitats are faced with decisions to balance the preservation of high quality habitat with ongoing development or create (including enhancement) habitats of sufficient quality and diversity to offset the impacts of habitat loss and degradation.

Chapter 4. Habitat-specific variation in annual locomotor activity behaviour of two teleost fish residing in a set of coastal embayments of the Laurentian Great Lakes 4.1 Abstract

Different habitats impart unique challenges for organisms. Sub-optimal habitat is associated with fewer resources and often increases an organism's energy expenditure. Animals make frequent localized movements on the scale of seconds to hours to days, and these locomotor activities constitute a substantial portion of an animal's energy budget. In the Laurentian Great Lakes, coastal wetlands provide important habitat for the vast majority of fish species. However, many wetlands have been lost, and the remaining wetlands have declined in habitat quality. I captured high-resolution positional telemetry data, and acceleration-derived locomotor swimming behaviour, to test how ecological factors relate to the activity patterns of two ecologically and economically important fish species. The system studied was coastal embayments with existing and ongoing habitat restoration and enhancement along the Toronto waterfront. There was habitat-specific variation in average locomotor activity. Generally, Largemouth Bass (Micropterus *nigricans*) activity levels were greater than Northern Pike (*Esox lucius*) activity levels, however, there was considerable variability in activity levels among tagged individuals of both species. There was also variation in the activity levels across habitats, seasons, and diel periods, as well as interactions between the explanatory variables. The greatest differences in activity between species occurred in colder, exposed habitats separating sheltered, vegetated and wetland habitats. Higher activity rates in Largemouth Bass suggested avoidance of these cold, exposed habitats. The high costs of longer movements associated with navigating large or highly unsuitable gaps between smaller, but higher

quality habitat patches can lead to spatial and temporal structuring of populations.

4.2 Introduction

Animals make decisions to move for a variety of reasons – to find food or mates, for shelter or protection – and across a gradient of spatiotemporal scales. The causes and consequences of long distance migrations have received great attention in the literature (Dingle and Drake 2007). However, most animals make frequent movements that are localized and smaller-scale in nature (Demers et al. 1996; Wilson et al. 2008; Wearmouth and Sims 2009), as part of what could be considered a daily routine (e.g., foraging movements within an area of core use), or less frequent movements that may involve longer distance travel over the course of days (e.g., ranging between territories). This locomotory activity, on the scale of seconds to hours to days, influences the activity costs that can account for a substantial portion of an animal's energy budget (Boisclair and Leggett 1989; Christian et al. 1997; Cooke et al. 2004).

Animal movement is the outcome of interactions between an individual (internal state, navigation capacity, and motion capacity) and the environment (external factors; Nathan et al. 2008). Theoretically, animals move to acquire energy at a greater rate than they expend it, in order to have a surplus to allocate to fitness-enhancing processes. Heterogeneity in environmental characteristics across habitats can influence animal energetics in meaningful ways (Ellis et al. 2012; Shepard et al. 2013; Tomlinson et al. 2014; Brownscombe et al. 2017). Activity will vary spatiotemporally as the distribution of food, temperature, predation risk, and the cost of movement are not homogeneous across the landscape (Lima and Zollner 1996; Wilson et al. 2012; Shepard et al. 2013; Gallagher et al. 2017). For example, in suboptimal lakes with smaller or less accessible

prey, predators rested less frequently, experienced higher energetic costs when active, and had higher overall daytime activity costs (Cruz-Font et al. 2019). As such, animals should respond to variation in landscapes by optimizing energy expenditure differently on an hourly or a daily basis – and their locomotor activity should reflect this. Living in small fragmented or suboptimal habitats can be more costly for organisms because of increased energy demands associated with longer movements between select habitats (e.g., gap crossing) on a daily, or seasonal basis (Ellis et al. 2012). If there are high costs of movement across gaps between higher quality habitat areas can lead to spatial and temporal structuring of populations (Shepard et al. 2013).

The proliferation of field-based biotelemetry is providing researchers everexpanding insight into the physiology and behaviour of wild, free-moving animals (Cooke at al. 2004; Hussey et al. 2015). Researchers have used acceleration sensors in biotelemetry to understand the activity and energetics of several taxa including humans (Halsey et al. 2008) and other mammals (Hindle et al 2010), birds (Wilson et al. 2006) and fish (O'Toole et al. 2010; Payne et al. 2011; Wilson et al. 2013; Landsman et al. 2015; Cruz-Font et al. 2016; Brownscombe et al. 2017). It has become a popular tool for fisheries researchers to measure activity levels (O'Toole et al. 2010; Landsman et al. 2015) and energetics (Wilson et al. 2013; Brownscombe et al. 2017) of fish species across a variety of aquatic environments and habitats. Because choices of habitat can have energetic consequences for organisms, animals that occupy suboptimal habitats may experience increased expenditure of energy, which can cause negative outcomes for individuals and populations in those areas (Huey 1991; Jeffrey et al. 2015). Estimating locomotor activity in the wild enables comparisons of habitat use, its inferred quality, and

differential use based on habitat variables. Ultimately, identifying critical aspects that make a habitat suitable, or not, for a particular species (Lindell 2008).

Without direct observation of the free-ranging animal, interpreting precise behaviours associated with given acceleration measurement is challenging (Brown et al. 2013). Increased activity can reflect increased foraging activity (Brownscombe et al. 2017), increased predator avoidance (Gallagher et al. 2017), avoidance of environmental conditions (e.g., cold water intrusions; Hlevca et al. 2015), or ranging behaviour between habitat patches, for spawning for example. While decreased activity levels could reflect station-keeping behaviour for refuge or digestion or ambush or nest guarding. The use of biotelemetry tags and associated sensors reveal how actively habitats are used and their associated energetic costs or benefits (Lapointe et al. 2013).

Largemouth Bass (*Micropterus nigricans*) is classified as a warmwater species throughout its North American range. Adult Largemouth Bass typically prefer shallow (<6m deep) areas that support submergent aquatic vegetation or other submerged cover (i.e., logs, brush piles, and root wads). Largemouth Bass tend to require deeper areas (up to 15m) for overwintering habitat (Stuber et al. 1982; Suski and Ridgway 2009). They are most abundant in areas with 40-60% cover, as too much cover can limit prey capture (Stuber et al. 1982). Adult Largemouth Bass are primarily piscivorous (Brown et al. 2009). They employ a variety of foraging strategies, including actively searching for prey (Savino and Stein 1989; Ahrenstorff et al. 2009), as well as sit-and-wait "ambush" style predation (Savino and Stein 1982).

Northern Pike (*Esox lucius*) is considered a mesothermal or 'coolwater', apex

predator throughout most of its circumpolar range. The specific habitat requirements of Northern Pike are well documented (Inskip 1982; Casselman and Lewis 1996 Lane et al. 1996a, b, c). Adult Northern Pike are generally found in relatively shallow water in summer, usually < 4 m, and sometimes as deep as 12 m in relatively clear, cool, and well oxygenated areas (Headrick and Carline 1993). In winter, Northern Pike tend to move to deeper areas with the inshore onset of ice cover (Diana et al. 1977; Casselman 1978; Cook and Bergersen 1988). In general, they are most abundant at intermediate (30-80%) cover) vegetation densities (Casselman and Lewis 1996; Randall et al. 1996). However, the smallest Northern Pike tend to be found in the densest vegetation, while the largest individuals tend to be found in the least dense areas (Casselman and Lewis 1996). Additionally, aquatic macrophytes provide refuge from predation for young pike and forage fish of all sizes (Inskip 1982). In lakes and reservoirs, the movements of Northern Pike have been investigated in several studies using telemetry (e.g., Diana et al. 1977; Diana 1980; Cook & Bergersen 1988; Lucas 1992; Jepsen et al. 2001, Koed et al. 2006; Kobler et al. 2008; Baktoft et al. 2012).

Rarely have telemetry studies, in their design and analyses, tracked the activity and behaviour of fish in northern temperate lakes for their full annual cycle (Marra et al. 2015, but see Hanson et al. 2007 and Baktoft et al. 2012). Here, I capture high-resolution, positional telemetry data with associated acceleration-derived insight on locomotor activity. These data provide novel insight into the locomotory and activity patterns of these ecologically and economically important fish species (i.e., Largemouth Bass and Northern Pike) in a system of embayments with existing and ongoing habitat restoration and enhancement in the Laurentian Great Lakes. I use these two species of fish as models

for how locomotor activity patterns vary across habitat types. The objective of this paper is to understand the pattern of annual activity of fish species from different thermal guilds across multiple habitat types in a set of coastal embayments. I test how ecological factors may drive the activity patterns of Largemouth Bass and Northern Pike. I hypothesize that variation in the activity patterns for both species will be dependent on distinct habitat use because of the heterogeneous distribution of abiotic and biotic resources in the area (Doka et al. 2018). Specifically, I predict that individuals exhibit higher locomotor activity patterns in habitats that are deeper, more exposed and have lower levels of submerged aquatic vegetation, possibly due to increased effort required for foraging (Ahrenstorff et al. 2009; Kobler et al. 2009). I further hypothesize that activity patterns will differ between the species, primarily in foraging behaviour and home range size (Ahrenstorff et al. 2009; Kobler et al. 2009). Specifically, I predicted that Largemouth Bass would exhibit higher locomotor activity patterns than Northern Pike because they exhibit less sit-and-wait foraging tactics.

4.3 Methods

4.3.1 Study Site

The central Toronto waterfront, including Toronto Harbour, is partly a set of large coastal embayments (~15 km²) connected to Lake Ontario situated directly along the downtown core of Toronto, ON, Canada. Historically, the eastern side of Toronto Harbour was an expansive marsh complex at the mouth of the Don River known as Ashbridge's Bay. After this wetland area was drained and reclaimed to serve as industrial port lands, only a fragment of this original bay remains (separated from the current

Toronto Harbour by the reclaimed land). The harbour is divided into inner and outer harbour areas (Figure 4.1). Two zones dominate the inner harbour: the city waterfront (urban and industrial landscape with hardened shorelines) and the Toronto Islands (a series of channels and islands with more naturalized shorelines). The outer harbour is bounded by industrial and recreational uses, and an interconnected series of largely, renaturalized embayments known as Tommy Thompson Park (TTP). The eastern gap (a channel) joins the inner and outer harbours, and both harbours are directly connected to Lake Ontario proper: one lake connection is via the western gap channel connecting the inner harbour to Humber Bay and the open lake, while the outer harbour is open to the Lake. TTP is a man-made peninsula that was started in the early 1970's and construction is ongoing. The peninsula is made from infill materials and has been modified to naturalize portions of Toronto Harbour, and restore lost coastal features, as well as house contained disposal facilities (CDFs) until they are capped and enhanced naturally. This large aquatic and terrestrial park projects 5 km into Lake Ontario and covers a total surface area of over 250 ha (TRCA 2000). To create a more thermally and structurally complex system, the aquatic portions of the park are functionally divided into three cells (two prior CDFs and one ongoing) and four embayments (TRCA 2000; Figure 4.1). In addition to providing aquatic habitat, the cells in the park have functioned as deposition sites for dredged material from the active shipping areas and the mouth of the Don River; cells are then capped when active dumping is considered complete. Construction in Cell 1 was completed in 2006, and the Cell 2 CDF stopped receiving dredged material in the mid-2000s. Cell 3 continued to receive dredge material (deposited by barges) during the study period, however the telemetry receiver in Cell 3 was placed outside of the area

where sediment material was being deposited.

Habitat restoration activities in Embayments A, B and C, Cell 1, portions of the Toronto Islands and slips have used a variety of techniques (Barnes et al. 2020), including but not limited to: i) shoreline modification (slope profile and linear complexity) and creation (spawning channels, and island crests and peninsulas), ii) coastal vegetation planting and creation of areas to facilitate vegetation establishment (riparian, emergent and submergent), iii) structural habitat addition (e.g., anchored log tangles, boulder clusters, submerged log cribs and stump fields, reefs and shoals), and iv) passive control of non-target species (e.g., Common Carp exclusion gates; Wilcox and Whillans 1999).

4.3.2 Acoustic Telemetry Array

To track the activity of tagged fish in Toronto Harbour, I deployed a passive acoustic telemetry array (see Donaldson et al. 2014 for an overview of acoustic telemetry methods and terminology). For this study, 39 acoustic telemetry receivers (Vemco VR2W, 69 kHz, Vemco Ltd., Halifax) were strategically positioned throughout the harbour to cover a variety of habitat types, as well as key movement corridors (Figure 4.1). In shallow areas (<5 m), acoustic receivers were attached to a rope approximately 1 m above a steel or concrete anchor with a Castro float at the top to keep the receiver positioned vertically. Anchors were tethered to the nearest attachment point on shore by submerged steel cable. In deeper water (up to 10 m), the anchor was connected by floating rope to an additional weight approximately 20 m away from the primary anchor weight. Receivers were retrieved every 6 months to offload data, to remove any accumulated biofouling and check receiver condition. Receivers were then redeployed in

the same locations. Range testing (see Kessel et al. 2014) was conducted at a subset of receivers in different habitat types and in different seasons to inform receiver placement, and varied from 400 to 1500 m (see Veilleux 2014).

4.3.3 Fish Tagging

All fish in this study were captured via boat electrofishing (SR-18EH, 6.0–7.0 A, 60 Hz, 340V DC, Smith-Root, Inc., Vancouver, WA) between August and September 2014 and 2015. After capture, each fish was held in a live well until the crew could safely dock the boat and set up for transmitter implantation. Fish were immobilized by holding each individual in a wetted mesh net between the boat electrofisher electrodes (Smith-Root, Inc., Vancouver, WA) – a method that has previously been used to immobilize fish for surgeries (Jennings and Looney 1998; Vandergoot et al. 2011; Brooks et al. 2019). For transmitter implantation, fish were moved from the live well with a wetted net onto a padded surgical table with the fish in a supine position. Each individual was measured for total length. Prior to implanting an acoustic transmitter into an individual, the transmitter and all surgical tools were disinfected in an iodine solution and rinsed. An incision (<20 mm) was made with a sharp scalpel on the ventral surface of the fish. Curved forceps were used to lift the skin and body wall to avoid any internal injury while making the incision. The transmitter was inserted into the coelomic cavity of the fish. The incision was closed using two simple, interrupted sutures (Ethicon PDS II, 3/0, FSL needle). Post transmitter implantation, all fish were immediately released at their original capture location.

I tagged 42 individual fish over the course of the study (Table 4.1). In 2014, I

tagged 15 Northern Pike and 13 Largemouth Bass. In 2015, I tagged 10 Northern Pike and 6 Largemouth Bass. Fish detections were filtered to remove any potential false detections (i.e., detections that occurred from the same tag at the same receiver within a period of less than the minimum tag delay. Then, detections of individual tags were plotted over space and time to visually examine stationary tags (i.e., those not tracking live fish due to fish mortality or tag shedding). Four Northern Pike (three tagged in 2014 and one tagged in 2015) and one Largemouth Bass (tagged in 2014) were removed from the dataset prior to any analysis because they were suspected to have died immediately after release. All individuals were tagged with Vemco V13A transmitters (69kHz, 90 s transmission delay, ± 3.43 g acceleration range, 5 Hz sampling frequency, Vemco Ltd., Bedford, Nova Scotia). These transmitters function by measuring acceleration (g, 9.8 m/s²) in three axes (x = lateral, y = forward, and z = vertical) and processing the information before transmission. The root mean square (RMS) of acceleration (a) is calculated as:

$$a = A_{x}^{2} + A_{y}^{2} + A_{z}^{2};$$

where *A* represents acceleration in each axis. The RMS is averaged over each sampling period (25 s) and stored in memory until transmission. Acceleration is considered a good proxy for swimming activity (i.e., locomotion) and therefore will subsequently be referred to as activity (Wilson et al. 2013).

4.3.4 Data analysis

Receivers were either treated as a unique station (N = 14) or the individual

receivers were combined into arrays (N = 9), which represented locally homogeneous areas with respect to habitat features but also increased the total detection area relative to a single receiver (Figure 4.1). For example, at the connection point between the outer harbour and Lake Ontario, there were seven receivers deployed as a gate to track fish that may exit the telemetry array for the open lake. These receivers covered a similar habitat type (deep, open water) and were in close proximity to each other, which resulted in single-transmitter pings frequently being detected at all seven receivers. Data from all of these receivers were therefore integrated into a single receiver array to represent this "curtain" of receivers (Figure 4.1). Herein, both the unique stations and arrays of receivers are collectively referred to as "receiver arrays".

The full detection database was filtered into separate events using the 'event_filt' function in the 'GLATOS' R package. The event filter uses spatial and temporal criteria to assign each detection to a unique event. I applied a temporal criterion of 3600 seconds (60 minutes) and a spatial criterion that uses receiver arrays to differentiate between events. For example, an individual fish that had sequential detections on a different array, regardless of the time interval between detections, were assigned as separate events. Alternatively, if an individual fish had sequential detections on the same receiver array but detections were separated by 3600 seconds or more, those were assigned as separate events; within the hour all detections were included in the same event.

The median acceleration values per event were fit using a linear mixed-effects model; log-transformed median acceleration value was the response variable, and total length, species, habitat type, season, diel period, and all two-way interactions, as predictors. Individual fish ID was included as a random intercept. A constant variance

function was assumed for heterogeneity among factor levels in species and seasons. Habitats were classified by integrating spatial habitat layers (see Midwood et al. 2019 for full details). Briefly, Fisheries and Oceans Canada provided a digital elevation model (DEM) for Toronto Harbour. From this DEM, the elevation gradient (slope) was calculated in ArcMap 10.2 (Environmental Systems Research Institute, Redlands, CA, USA). Mean exposure (i.e., effective fetch) was calculated for the entire harbour at a 10 m^2 grid cell size using a wind-fetch model developed by the United States Geological Survey (Rohweder et al. 2012). An estimate of SAV percent cover (calculated using DEM, slope and mean exposure) was generated from an equation developed for Hamilton Harbour, an urban harbour located approximately 40 km southwest of Toronto Harbour on Lake Ontario (Doolittle et al. 2010). Finally, mean benthic water temperature during stratification (June to September) was used for the temperature variable. Generally, during the pre- and post-stratified periods, the water had fairly uniform temperatures, with minimal variations with depth or spatially throughout the harbour. During the stratified summer period, there was much greater spatial and temporal variability (Hlevca et al., 2015).

An integrated measure of habitat conditions was developed using a k-means cluster analysis (using the 'cluster' R package) with four input parameters: mean exposure, submerged aquatic vegetation cover, mean water temperature during the stratified season (derived from Hlevca et al. 2015), and depth (Midwood et al. 2019). Input data were first scaled so that the distribution of each parameter had a mean of zero. Using this integrated habitat measure, each receiver array was placed into one of five distinct habitat types that can be described as: 1) wetlands (shallow, low fetch, warm,

vegetated), 2) coastal vegetated (moderate depth, moderate fetch, cool-warm, vegetated), 3) shallow un-vegetated (shallow, low fetch, cool-warm, no SAV), 4) deep un-vegetated (deep, moderate fetch, cool, no SAV), and 5) exposed (moderate-deep, high fetch, coolwarm, no SAV). Within Toronto Harbour, there was a clear, clustering of these habitat types, with wetland areas concentrated in the Toronto Islands, Cell 1, and Embayment D and more coastal vegetated areas along the Inner Harbour margin of the Toronto Islands and in the Outer Harbour Marina.

Seasons were defined as spring (1 March until 31 May), summer (1 June until 31 August), fall (1 September until 30 November), and winter (1 December – 28 February). Diel periods were defined as dawn (06:00 until 08:00), day (08:00 until 18:00), dusk (18:00 until 20:00), and night (20:00 until 06:00). All statistical analyses were conducted using RStudio version 1.1.383 (RStudio Team 2015) and R version 3.5.1 (R Core Team 2013). Models were fit using the R package 'nlme' (Pinheiro et al. 2018). Model selection was conducted using the drop1 command to compare full models to reduced models with log ratio tests. Models were validated using the procedures outlined in Zuur et al. (2009).

4.4 Results

Throughout the study, I resolved over 1.3 million detections with associated acceleration estimates. Northern Pike represented approximately 76% of the total detections (1,023,132) while Largemouth Bass represented approximately 24% (312,371). Individuals were tracked for an average of 60% of the days in the tracking window (range = 44 - 321 days; Table 4.1). The number of detections per tagged individual varied from 1,414 – 101,704 detections (mean = 36, 024 detections per tagged

individual). On average, tagged individuals were detected on seven receivers; from a minimum of one and a maximum of twenty receivers. The event filter reduced the full detection database down to 139,039 distinct detection events, with a mean of 10 detections per event.

Overall, the swimming patterns for both species ranged from stationary to bursts of high activity; the vast majority of the recorded observations were characteristic of stationary or very low activity behaviour (Figure 4.2). The maximum recordable acceleration value of the transmitter is $3.43 \text{ m}^2/\text{s}$. As such, the cluster of measurements at the tail of the histogram could represent bursts that equal or exceed $3.43 \text{ m}^2/\text{s}$. These events could represent one or more behaviours (i.e., foraging attempt, angling event, escape event), however I do not have the resolution in the data at a scale to tie those recordings to such events.

There was considerable variability in activity levels among tagged individuals of both species (Figure 4.3). In general, mean Largemouth Bass activity levels were always greater than Northern Pike activity levels. There was variation in the locomotor activity across body size, seasons, habitats, and diel periods, with significant interactions between these explanatory variables (Table 4.2). In all habitat classes, both species were most active in late summer and early autumn. The increased activity began in early spring and continued to increase throughout the warmer months, reaching a peak in August (Figure 4.4). Activity levels were generally lower throughout the winter season, but neither species was completely quiescent. Average activity levels were slightly higher for Largemouth Bass compared to Northern Pike in winter; however, Northern Pike did exhibit a greater number of isolated high-activity events, consistent with their overall

behavioural pattern. Largemouth Bass swimming activity was significantly higher than Northern Pike in all habitat types, except in coastal vegetated and wetland habitats (Figure 4.5). The greatest differences in activity between species occurred in colder, exposed habitats (shallow un-vegetated, deep un-vegetated, and exposed), where Largemouth Bass activity was much higher than that of Northern Pike. During summer and fall periods, Largemouth Bass activity was highest during day and dusk periods. During the winter period, there was no difference in the activity patterns between the diel periods (Figure 4.6).

Table 4.1 Summary information for tagged Largemouth Bass and Northern Pike individuals. Tracking window represents the number of days that a fish was at large in the system. Day detected represent the percentage of those days that a fish was detected on a receiver array.

Fish ID	Number of Detections	Number of Arrays	First Detection	Last Detection	Tracking Window (Days)	Days Detected (%)
Bass 326	20803	3	2014-08-07	2015-03-15	220	81.8
Bass 334	18544	3	2014-08-10	2015-07-29	353	41.9
Bass 365	1414	13	2015-08-25	2016-09-03	375	11.7
Bass 392	16943	3	2014-08-16	2015-08-09	358	42.2
Bass 393	21782	9	2014-08-07	2015-03-14	219	79.5
Bass 403	8643	2	2015-08-31	2016-06-01	275	38.5
Bass 403b	3260	1	2015-08-31	2016-09-05	371	16.4
Bass 404	2759	3	2015-08-31	2016-09-08	374	1.5
Bass 405	22952	3	2014-08-07	2015-03-13	218	76.6
Bass 415	15963	4	2014-08-05	2015-08-02	362	48.3
Bass 417	21908	7	2015-09-10	2016-08-27	352	43.8
Bass 453	30908	3	2014-09-04	2015-09-04	365	50.1
Bass 457	11345	3	2014-09-05	2015-03-16	192	83.3
Bass 462	41353	20	2014-08-08	2015-08-12	369	61.2
Bass 466	6500	2	2014-08-09	2015-08-10	366	31.4
Bass 473	17318	15	2014-08-11	2015-08-05	359	51.5
Bass 490	27992	15	2014-08-07	2015-07-28	355	51.8

Bass 495	19387	2	2015-08-27	2016-09-05	375	46.9
Pike 434	28934	3	2014-08-08	2015-07-31	357	44.3
Pike 458	15419	3	2014-08-08	2015-02-25	201	71.6
Pike 468	40712	4	2014-08-08	2015-06-09	305	83.6
Pike 469	33348	3	2014-08-07	2015-02-05	182	71.4
Pike 504	22895	3	2014-08-07	2015-03-15	220	73.6
Pike 538	73883	5	2014-08-07	2015-08-12	370	71.9
Pike 567	67206	7	2015-08-25	2016-08-29	370	80.5
Pike 630	73470	4	2015-08-25	2016-08-29	370	77.6
Pike 641	101744	3	2014-08-07	2015-08-12	370	67.3
Pike 680	57596	15	2014-08-06	2015-08-10	369	66.4
Pike 684	97626	8	2015-08-25	2016-08-28	369	87.0
Pike 690	38772	13	2015-08-26	2016-08-28	368	48.4
Pike 713	38760	8	2014-08-08	2015-07-18	344	77.6
Pike 735	52045	13	2015-08-24	2016-08-28	370	84.6
Pike 790	5647	5	2014-09-04	2015-07-11	310	21.3
Pike 817	84809	9	2015-09-05	2016-08-31	361	70.4
Pike 828	47940	11	2015-08-26	2016-08-29	369	77.2
Pike 829	45892	17	2015-08-26	2016-07-26	335	72.5
Pike 967	96434	13	2014-08-05	2015-08-07	367	87.2

Predictor	df	F value	<i>p</i> value
Total length	1	95.02	< 0.0001
Species	1	102.30	< 0.0001
Habitat type	4	266.28	< 0.0001
Season	3	760.82	< 0.0001
Diel period	3	96.40	< 0.0001
Total length : Habitat type	4	184.91	< 0.0001
Total length : Season	3	124.96	< 0.0001
Total length : Diel period	3	35.33	< 0.0001
Species : Habitat type	4	22.58	< 0.0001
Species : Season	3	97.44	< 0.0001
Species : Diel period	3	25.94	< 0.0001
Habitat type: Season	12	37.05	< 0.0001
Habitat type : Diel period	12	4.08	<0.0001
Season : Diel period	9	5.88	< 0.0001

Table 4.2 Significant predictors of activity by the top model estimated with a linear mixed effects model. Animal ID was included as a random effect.



Figure 4.1: Map of the Toronto Harbour Acoustic Receiver Array and habitat categories. Red circles represent the locations of acoustic receivers (N=39).



Figure 4.2: Histogram of the median acceleration values from all detection events. The maximum measured value of the transmitters is $3.43 \text{ m}^2/\text{s}$.



Figure 4.3: Boxplots of event filtered acceleration sensor values for each individual Largemouth Bass (N=18) and Northern Pike (N=19). Within species, animals are ordered by increasing body size (total length). Each boxplot shows the median values (solid horizontal line), 25 and 75% quartiles (box), values < 1.5 times the interquartile range (whiskers), and outliers (circles). The maximum measured value of the transmitters is $3.43 \text{ m}^2/\text{s}.$



Figure 4.4: Boxplots of event filtered acceleration sensor values for each species by month of the year. Each boxplot shows the median values (solid horizontal line), 25 and 75% quartiles (box), values < 1.5 times the interquartile range (whiskers), and outliers (circles). The maximum measured value of the transmitters is $3.43 \text{ m}^2/\text{s}$.



Figure 4.5: Boxplots of event filtered acceleration sensor values for each habitat type by season. Each boxplot shows the median values (solid horizontal line), 25 and 75% quartiles (box), values < 1.5 times the interquartile range (whiskers), and outliers (circles). The maximum measured value of the transmitters is $3.43 \text{ m}^2/\text{s}$.



Figure 4.6: Boxplots of event filtered acceleration sensor values for each season by diel period. Each boxplot shows the median values (solid horizontal line), 25 and 75% quartiles (box), values < 1.5 times the interquartile range (whiskers), and outliers (circles). The maximum measured value of the transmitters is $3.43 \text{ m}^2/\text{s}$.

4.5 Discussion

A central tenet in ecological energetics is that different habitats impart different energetic challenges for organisms (Tomlinson et al. 2014). As such, animals should differ in their behavioural responses across different habitats since the distribution of resources, competitive interactions, predation risk, and costs of movement vary spatiotemporally in heterogeneous environments (Lima and Zollner 1996). Moreover, the structural components of habitat affect intra- and interspecific interactions (Yeager and Hovell 2017). Energy gain can be maximized through diverse behavioural strategies involving movement, habitat use, foraging, and predator avoidance. Fewer resources and increased threat of predation can characterize sub-optimal habitat, which often leads to increased intraspecific and interspecific competition (Jeffrey et al. 2015). Use of suboptimal habitat is known to increase an organism's energy expenditure; ultimately affecting individual fitness (Ricklefs and Wikelski 2002). The data support the hypothesis of habitat-specific variation in annual locomotor activity behaviour of two teleost fish residing in a system of coastal embayments of the Laurentian Great Lakes.

The results support my prediction that Largemouth Bass exhibit higher average locomotor activity patterns than Northern Pike. This general pattern is in agreement with a number of studies of Largemouth Bass and Northern Pike activity patterns, however I believe this is the first study to evaluate the locomotor-derived activity patterns of these two piscivores simultaneously. Northern pike are generally considered sit-and-wait predators while Largemouth Bass are generally considered to be more active foragers (Savino and Stein 1989; Ahrenstorff et al. 2009). Animals often expend greater amounts of energy foraging, although this depends on the foraging mode (Anderson and Karasov

1981; Arnould et al. 1996). A sit-and-wait strategy is characterized by substantial portions of time moving minimally, or not at all, accented by infrequent periods of high activity. However, studies have revealed that Northern Pike also exhibit active hunting behaviours (Turesson and Bronmark 2004) and regularly perform active movements (Diana 1980; Jepsen et al. 2001; Kobler et al. 2008). Largemouth Bass are equally known to exhibit station-keeping behaviour, particularly in locations near emergent or submergent cover. In a very small Danish lake (~1 ha), Baktoft et al. (2012) estimated that Northern Pike moved an average of 621 - 1248 m/day, whereas in a much larger Canadian lake (~5700ha), Diana et al. (1977) found that daily pike movements ranged from 0 - 4000m, however, most daily movements were less than 1000m. In contrast, Hanson et al. (2007) estimated daily movement rates for Largemouth Bass in an 18 ha lake to range from 2000 - 7000m/day, depending on the time of year. Although I could not calculate mean distance swam per day for tagged fish in this study, the activity data are consistent with the general consensus in the literature that Largemouth Bass are more active than Northern Pike.

I observed substantial individual variation in the activity levels within both species. This was most striking for Largemouth Bass, where some individuals had average acceleration values below 0.1 m²/s, while others had average acceleration values over 0.5 m²/s. Hanson et al. (2007) found that daily movement rates varied by as much as 25 fold among individual Largemouth Bass. They attributed the differences in the daily movement rates to the spatial range of the individual, suggesting that individuals that occupied discrete areas and made only localized movements, moved less, in terms of total distance, than other individuals that made lengthier journeys covering much of the lake in

periods of as little as one day. Previous studies have posited that fish movements at spatial and temporal scales not captured by most tracking study designs likely underestimate a significant portion of daily activity (Lucas et al. 1991; Demers et al. 1996, Hanson et al. 2007). For example, in an electromyogram tracking study of Largemouth Bass, the majority of their positional estimates were localized within the littoral zone, suggesting limited positional changes, however the underlying muscular activity from the EMG biotelemetry indicated significant levels of activity (Demers et al. 1996). These frequent short-duration, but localized swimming events can represent a high activity cost (Lucas et al. 1991) even though spatial ranges are small.

Largemouth Bass swimming activity was significantly higher than Northern Pike in all habitat types, except in coastal vegetated and wetland habitats (Figure 4.5). The greatest differences in activity between species occurred in colder, exposed habitats (shallow un-vegetated, deep un-vegetated, and exposed) that separate regions of coastal vegetated and wetland habitat. Largemouth Bass activity was very high in these habitat gaps, suggesting they are actively swimming through these areas without spending much time, before reaching more optimal habitat where activity decreases. Midwood et al. (2019) found very low residence values for Largemouth Bass in these exposed habitats. In Toronto Harbour, Largemouth Bass and Northern Pike had similar thermal experiences throughout the year, except during the summer, when Northern Pike were consistently observed in cooler waters (Peat et al. 2016). Depth use was also different between species throughout the entire year, with Northern Pike consistently selecting deeper habitat (Peat et al. 2016). Largemouth Bass and Northern Pike both showed evidence of active thermoregulation, where both species were observed at temperatures higher than what

was being recorded at acoustic receiver stations in the near vicinity, up until 20°C, when Northern Pike began to actively seek cooler areas (Peat et al. 2016). Northern Pike generally prefer shallow vegetated areas (Diana et al. 1977; Inskip 1982; Chapman and Mackay 1984; Cook and Bergersen 1988), however, there may be an advantage to exhibiting flexibility in habitat selection, depending on availability of prey locally. Indeed, Northern Pike may abandon preferred habitat when surface temperatures become too high (Headrick and Carline 1993), thus making the habitat less preferred. Kobler et al. (2009) noted searching behaviours characterized by higher activity in Northern Pike inhabiting open water. Indeed, my data support this, as on average, Northern Pike activity was highest in cool, moderate depth habitats. Large Northern Pike occupy the macrophyte-open-water interface, while small individuals do not (Chapman and Mackay 1984; Midwood et al. 2019). There are bioenergetic reasons for flexibility in foraging behaviour because relationships between habitat structure, predation risk, and foraging efficiency are strongly influenced by body size and agility (Werner and Gilliam 1984; Bartholomew et al. 2000; Yeager and Hovell 2017). Indeed, Brownscombe et al. (2017) found that energy expenditure in a bonefish population was highly influenced by fishhabitat interactions. And that energy expenditure was primarily driven by activity, rather than temperature, as the bonefish were observed to be moderating against temperature extremes. Bonefish expended the most energy in shallow, nearshore environments that are used for feeding (Brownscombe et al. 2017). Similarly, the variation in Largemouth Bass activity estimates were greatest in wetland and coastal vegetated habitats. These habitat types are primarily present in Cell 2 and 3 of TTP, and the southwest portion of the Toronto Islands. The wide variation in swimming activity suggests that these habitats

are being utilized for multiple functional activities (e.g., active foraging and resting). Sammons and Maceina (2005) observed that Largemouth Bass divide their day, resting offshore (near woody structure, moving little) primarily during the day and moving to nearshore areas, presumably to forage during low light periods. Furthermore, Largemouth Bass are known to converge and overwinter in aggregations (Carlson 1992; Karchesky and Bennett 2004). There are a limited number of these over-wintering locations in the Toronto Harbour (Rous et al. 2017; Midwood et al. 2018; Midwood et al. 2019), such that fish subpopulations from different embayments might tend to congregate and mix there. Together with the observation that most of the Largemouth Bass captured and tagged spent the entire tracking period without leaving the study area suggests that these locales are providing sufficient physical and ecological habitat and food required to fulfill their needs on an annual basis.

For Northern Pike, the relationship between activity and season has been wildly inconsistent in the literature. To illustrate this, consider that Diana et al. (1977) and Baktoft et al. (2012) found that Northern Pike activity was similar between seasons, although Diana et al. (1977) did find that longer distance movements (>1000 m) occurred more frequently in winter, and others have found winter activity was even higher than summer activity levels (Cook and Bergersen 1988; Koed et al. 2006; Pankhurst et al. 2016). Conversely, Kobler et al. (2008) found a decrease in activity levels of Northern Pike during winter.

My activity data demonstrate that both species exhibit clear activity patterns across seasons. Each species exhibited decreased activity levels during the winter months although neither species were completely quiescent. Average activity levels were slightly

higher for Largemouth Bass compared to Northern Pike during this period, however, Northern Pike did exhibit a greater number of isolated, high-activity events, consistent with their overall behavioural pattern throughout the rest of the year. There was a marked shift in the activity level for both species in the early spring, although that shift was more pronounced for Largemouth Bass.

Increased activity in spring may be in preparation for reproductive activities. During this time fish will actively seek out food and warmer water temperatures to enable gonad development needed for spawning. As submerged aquatic vegetation can be sparse during spring, Northern Pike and Largemouth Bass could be quite active as they search for suitable areas to forage after ice-out. Activity levels continued to increase throughout the spring and into the summer months, peaking in late summer (August). They decreased substantially in November as fish resumed low levels of activity as water temperatures became cold and isothermal. Fish may show increased activity levels during late summer and early fall in an attempt to increase overwinter energy reserves (Miranda & Hubbard, 1994; Mackereth et al., 1999) when food is plentiful, or to locate overwintering regions with suitable water quality conditions (e.g., Raibley et al., 1997).

In the Laurentian Great Lakes, Largemouth Bass are primarily considered resident wetland species that rarely make substantial movements between wetland complexes (Midwood and Chow-Fraser 2015). Of the 18 Largemouth Bass tagged in the Toronto Harbour, only 3 made cross-harbour movements. In two of these instances, the individual was captured and tagged in the Toronto Islands region and moved to the cells and embayments of Tommy Thompson Park before returning back to the Toronto Islands area. Murphy et al. (2012) found evidence from otolith microchemistry that Largemouth

Bass existed as a metapopulation in the coastal embayments of Toronto Harbour, and as juveniles were found in embayments different than their natal habitats after their first winter. They suggested that these fish may move among embayments after dispersing from their overwintering habitats each spring. Although I did see some dispersal between regions in these tagged fish, there was no clear seasonal pattern (e.g., after overwintering). Bass 473 initiated this dispersal behaviour in mid-October and spent much of the winter in Cell 2 before returning to the same region in the Toronto Islands in late May. Bass 462 spent eight months post-tagging in the southwest region of the Toronto Islands before initiating a cross-harbour movement to the cells and embayments of Tommy Thompson Park in mid-May, only to return to the same region of the Toronto Islands after one month. In contrast, Bass 490 was captured and tagged in Cell 2 of Tommy Thompson Park, but left shortly after, reaching the Toronto Islands area in mid-October. Throughout the remainder of the tracking period, this individual made local movements between regions in the islands and the western portion of the central waterfront, but did not return to Tommy Thompson Park. These individuals were some of the largest tagged Largemouth Bass in the study, supporting the positive relationship between body size and home range for temperate freshwater fishes (Minns 1995). The remainder of the tagged Largemouth Bass showed high fidelity to their capture site. Half of the individuals were captured and tagged in Tommy Thompson Park and were only detected on receivers in, or in very close proximity, to Tommy Thompson Park, while the other half were captured and tagged in the Toronto Islands or Exhibition Place and were only detected in close proximity of their capture locations.

Conversely, Northern Pike are considered to be more migratory. Midwood and

Chow-Fraser (2015) found it was common for Northern Pike to move among wetlands approximately 2 km apart. In the Toronto Harbour, 6 of the 19 tagged Northern Pike made cross-harbour movements. All of these mobile individuals followed similar patterns. They were captured and tagged in the western portion of the Toronto Islands or central waterfront (e.g., Spadina Slip) and spent the entire tracking period making repeated movements along the central waterfront slip area, including the Keating Channel, and then returning to the Toronto Islands. Very infrequently, did any of these individuals travel through the eastern gap and get detected in any of the cells and embayments of Tommy Thompson Park. Of the remainder of the tagged Northern Pike, all but one individual was captured and tagged in TTP, and showed very high site fidelity in this area over the entire year. Mann (1980) suggests that Northern Pike populations consist of two distinct behavioural types; one type that has highly restricted ranges and one type that moves extensively, while Jepsen et al. (2001) identified a further 'intermediate' behavioural type; i.e., individuals that move between a few "favourite areas". While the majority of the tagged Northern Pike in Toronto Harbour appear to display the restricted area strategy, this tracking data do suggest that some individuals display the "favourite areas" strategy as well.

The data support that there is habitat-specific variation in annual locomotor activity behaviour of two teleost fish. Tagged Largemouth Bass and Northern Pike individuals were highly associated with habitat that had considerable submerged aquatic vegetation. This type of habitat is both limited (by quantity) and area restricted to a few regions within the Toronto Harbour. Furthermore, these preferred habitats are separated by large areas of suboptimal habitat (i.e., deep, cold, and un-vegetated). Limitation of

high quality habitat may force individuals in the population to use otherwise lower quality habitat or search out areas (an expend more energy) of comparably higher quality habitat. Reducing the area of contiguous habitat below a species' home-range size reduces resource availability, meaning individuals must either increase energy expenditure and employ a strategy of multiple patch use, or suffer consequences of resource limitation (Hinsley 2000; Ellis et al. 2012). Living in fragmented habitats can be more costly for organisms because of increased energy demands associated with movements (e.g., gap crossing) on a daily or seasonal basis (Ellis et al. 2012). Indeed, Hinsley et al. (2008) found that structural and functional habitat gaps significantly increased the daily energy expenditure of breeding birds, and ultimately increased the cost of rearing young. High-cost movement associated with navigating gaps that connect higher-quality habitat areas can lead to spatial and temporal structuring of populations (Shepard et al. 2013). In fragmented habitats, including those that have received restoration and rehabilitation actions, habitat managers must account for the existence of these metapopulations, as they require broader ecosystem-based management approaches that consider how the biotic and abiotic characteristics of the environment impact the movement energetics of animals (Nawrocki et al. 2019). A better understanding of an organism's activity levels, at the scale of an entire year, and increased recognition of variable energy landscapes can uncover functional mechanisms underlying seasonal habitat use (Wilson et al. 2012; Shepard et al. 2013).
5.0 Synthesis and Future Directions

5.1 Summary of thesis findings

The overarching goal of this thesis was to examine the drivers of space use and movement behaviour of multiple freshwater fish species to provide insight into the fishhabitat interactions in an urban locale that is the subject of ongoing habitat management activities.

In Chapter 2, I found that daily site fidelity estimates in different habitats in the Toronto Harbour area were influenced by the restoration status of the sites, and status interactions with species and body size, as well as season and its interactions with species and body size. Northern Pike (Esox lucius) and Yellow Perch (Perca flavescens) had higher daily site fidelity in restored versus non-restored areas, while Common Carp (Cyprinus carpio) had lower daily site fidelity in restored versus non-restored areas (Figure 2.2). Largemouth Bass (*Micropterus nigricans*) also had lower daily site fidelity in restored areas, but the effect was influenced by body size. Smaller individuals had lower daily site fidelity in restored areas, whereas larger individuals exhibited higher daily site fidelity in restored areas. Larger Northern Pike had lower site fidelity estimates than smaller individuals, whereas, larger Yellow Perch exhibited higher site fidelity than smaller individuals. All species exhibited the highest daily site fidelity during the summer period and the lowest during the fall period. There was a clear spatial pattern in the daily site fidelity of tagged fish throughout the Toronto Harbour area. Daily site fidelity estimates were highest in sheltered regions of the harbour, including Embayment C and Cells 2 and 3 of Tommy Thompson Park and the backwater regions of the Toronto Islands (Figure 2.3).

In Chapter 3, I found that size and degree of intraspecific overlap in activity spaces within Embayment C was influenced by season and fish body size. Activity spaces were largest in the summer and smallest in the winter (e.g., Figure 3.3 and Figure 3.5). Interestingly, the degree of overlap between individual activity spaces was greater during both of these seasons (e.g., Figure 3.6 and Figure 3.8). Larger individuals had larger activity spaces, but the degree of overlap in activity spaces was not influenced by body size. In general, the estimated activity spaces were moderately sized. Whereas, the degree of overlap between individual activity spaces was quite low.

In Chapter 4, I found that variation in locomotor activity behaviour was influenced by species, habitat, season, diel period, and body size, as well as interactions between these variables. Generally, Largemouth Bass exhibited greater activity levels compared to Northern Pike, however, there was considerable variability among both species (Figure 4.3). The greatest differences in the activity levels between species were observed in colder, more exposed habitats, whereas in coastal, vegetated and wetland habitats, the differences were less pronounced (Figure 4.5). Both species exhibited similar seasonal patterns of activity. Activity levels were highest during late summer and early fall and much reduced during the winter months (Figure 4.4).

Space use represents the expression of animal behaviours, which can provide information on underlying ecological processes (Borger et al. 2008). Space use behaviour captures the broad scale individual movements and patterns of habitat use and site fidelity. These behaviour patterns can be highly informative because the environment may select for specific space use behaviours (McLoughlin et al. 2000). Indeed, the size of activity spaces can be affected by body size (McNab 1963; Minns 1995), population

density (Wolff and Schauber 1996), risk of predation (Desy et al. 1990), food availability (Lurz et al. 2000; McLoughlin and Ferguson 2000), and habitat patchiness (McLoughlin et al. 2003). Since behavioural patterns can often reflect habitat quality (Brown 1988; Persson and Stenberg 2006), quantifying the space use patterns of animals offers information on the relative quality of habitats, including restored ecosystems (Lindell 2008). Understanding the variation in space use behaviour among individuals, one can infer space use of populations, and the variation in space use behaviour among species can scale up to communities (Allen et al. 2016). This can be critically important because the environmental factors that influence individual-level or species-level space use can vary substantially (Avgar et al. 2013; Allen et al. 2016). Our anthropocentric definition of animal habitat is often based on elements that we perceive to have importance or value to the animal, but this may represent a mismatch with habitat from the perspective of organisms (Van Dyck 2012). As such, Van Dyck (2012) argued that it is time for ecologists to integrate the 'Umwelt' concept – that different animals live in different perceptual worlds – into our approach to animal conservation and habitat restoration. Behavioural studies of animal habitat, including space use behaviour, have the potential to improve our ability to predict responses to environmental change, including habitat degradation and habitat restoration. In this thesis, I use the space use behaviour of multiple species of fish at multiple spatial and temporal scales to infer the aquatic habitat quality in a heterogeneous landscape. I believe this approach has merit and can be applied across a wide variety of taxa and ecosystems in order to study the effects of habitat use and management from the perspective of the organism.

5.2 The importance of full annual cycle research

Marra et al. (2015) published an important call to researchers to increase full annual cycle research in animal ecology. They highlighted a severe research bias towards breeding period research. Notably, fish were not included as one of the four classes of vertebrates they reviewed; however, I contend that fish research has not escaped the seasonal bias revealed by Marra et al. (2015). Fish are inherently challenging to study in the wild because of their aquatic lifestyles (Hussey et al. 2015), and this is further exacerbated for fish in northern lakes that are wholly or partly covered by ice for varying durations during the winter season (Campbell et al. 2005). In 1935, Hubbs and Trautman called for fisheries researchers and agencies to explicitly recognize the importance of winter conditions in influencing fisheries productivity, and concomitantly to put a stop to the annual migration of fisheries professionals indoors to their offices for the winter. Modern biotelemetry offers a clear technological advantage over traditional fisheries assessment techniques (e.g., netting) or direct observational techniques (e.g., snorkeling), in that it can provide observations during the "ice-on" period (Marsden et al. 2021) and during periods of adverse environmental conditions (e.g., high flow, storm periods or low water levels; Cooke et al. 2013; Lapointe et al. 2013). Furthermore, it permits studies investigating habitat use and movement behaviour during critical periods, such as spawning in winter or shoulder seasons, or without interference by direct observation or collection of individuals from spawning locations (Cooke et al. 2004). Seasons represent regular and periodic changes in the abiotic and biotic conditions. These changes (e.g., temperature, photoperiod, resource availability) are among the most important variables driving spatial and temporal distributions of animals over a variety of scales (Fretwell

1972). I delve into fish-habitat associations and movement behaviour for each season. *Winter*

Winter is a critical period for animals (Shuter et al. 2012). In addition to direct mortality, the indirect seasonal effects can carry over and have important individual-level and population-level consequences (Hurst 2007; O'Connor and Cooke 2015). A portion of animals make annual long-distance migrations to wintering habitats that may closely resemble the environmental conditions they experience throughout their summer habitats (Dingle and Drake 2007). Alternatively, animals that remain during the winter season in regions that experience temperatures at or near the freezing point, broadly employ one of three strategies: i) hibernate, ii) tolerate, or iii) maintain activity and behaviour (Shuter et al. 2012). There exists a pervasive myth that the winter season represents a period of negligible biological activity (Campbell et al. 2005). However, a growing body of research indicates that most freshwater fish species, including warmwater species in temperate lakes, are not quiescent during the winter (Suski and Ridgway 2009; Baktoft et al. 2012), albeit with reduced activity and metabolism as they are poikilothermic. Indeed, I found a considerable reduction in the swimming activity levels of Largemouth Bass and Northern Pike during the winter (Chapter 4). Furthermore, the size of individual 95% activity space and 50% core-use areas for Largemouth Bass (0.47 ha and 0.08 ha, respectively) and Northern Pike (4.39 ha and 0.85 ha, respectively) overwintering in Embayment C were comparatively smaller during the winter season (Chapter 3). During winter, fish tend to have lower activity levels to conserve energy and would be less likely to move large distances between habitats, but will make movements in response to prey availability and oxygen concentrations, especially Northern Pike (Casselman and Lewis

1996; Baktoft et al. 2012). All of the Common Carp exited Embayment C prior to winter and therefore I am unable to discern whether those individuals travelled to a preferred overwintering area, or what size the activity spaces were compared to other seasons. However, winter residency estimates for Common Carp in Toronto Harbour were reasonably high in some deeper open-coast areas (Midwood et al. 2019), suggesting that once Common Carp reach their overwintering habitat, they may use a smaller activity space than during other seasons. In fact, daily site fidelity estimates for Common Carp, Largemouth Bass, Northern Pike and Yellow Perch were all reasonably high, across all regions of the Toronto Harbour during the winter (Chapter 2), suggesting that individuals have preferred overwintering areas. Importantly, there was clear evidence that a substantial number of the tagged fish in Toronto Harbour are concentrated in a small number of areas during the winter (e.g., Cell 2, Cell 3, and Embayment C of Tommy Thompson Park and the southwestern region of the Toronto Islands near a wetland area known as Trout Pond). These areas should be managed and protected with explicit consideration of the role they play in providing overwintering habitat to multiple species in the fish community.

Spring

As water temperature begins to steadily increase in early spring, this represents a marked shift in the behaviour for many freshwater fish species. Overwintering aggregations break-up and individuals begin to disperse throughout lakes and streams (Hall and Werner 1977). In general, daily site fidelity was lower in the spring relative to winter and summer for Largemouth Bass and Yellow Perch (Chapter 2). For Northern Pike, daily site fidelity was depressed during spring relative to summer levels but was not

appreciably different than daily site fidelity in winter. I found evidence that the spring season coincided with activity space expansion for both Largemouth Bass and Northern Pike using Embayment C (Chapter 3). In addition, the activity levels for both Largemouth Bass and Northern Pike increased compared to winter levels (Chapter 4). As submerged aquatic vegetation can be sparse during spring and food availability may be low, Northern Pike, Largemouth Bass, and Yellow Perch could be quite active as they search for suitable areas to forage (Rennie et al. 2005) as temperature increases and spawning begins. For smaller individuals and for prey species, including Yellow Perch, this may represent a period of high vulnerability to predation as reduced structural vegetated habitat limits refuge areas. Additionally, spring represents the onset of the spawning period for many freshwater, wetland-dependent species, particularly earlyspawning species, like Northern Pike and Yellow Perch (Casselman and Lewis 1996; Robillard and Marsden 2001). Increased activity in spring may be in preparation for spawning activities. During this time fish will actively seek out abundant food resources and warmer water temperatures to enable gonad development needed for spawning and the location of supportive rearing areas.

Summer

The summer season represents the most studied period of freshwater fish behaviour. Much of our understanding of habitat use is based on habitat preferences during the summer period (e.g., Pratt and Smokorowski 2003). During the summer, Largemouth Bass, Northern Pike, Common Carp, and Yellow Perch exhibited the highest daily site fidelity (Chapter 2). This season has increased prey availability (Hall and Werner 1977; Adams et al. 1982) and increased habitat heterogeneity, which promotes

the concentration of prey items in discrete locations. Therefore, fish do not need to be as active compared to more homogenous habitats that would promote a more uniform distribution of prey (Eklov 1997; Radabaugh et al. 2010). For example, once the submerged aquatic vegetation cover is high enough to provide complex habitat for cover and refuge, Largemouth Bass have sufficient habitat for foraging and there is little incentive to move widely among habitats (Hanson et al. 2007; Ahrenstorff et al. 2009). However, for fish using Embayment C during the summer, their activity spaces were not significantly different than spring or fall (Chapter 3). Higher water temperatures in the summer can force coolwater fish species, like Northern Pike and Yellow Perch to seek out the coolest habitats. Throughout Toronto Harbour, water temperature rarely exceeds 25 °C, except in very shallow sections of protected embayments over relatively short durations in mid to late summer (Hlevca et al. 2015). The activity spaces of tagged Northern Pike were largest during the summer, when Embayment C water temperatures reached at least 24°C (Peat et al. 2016), exceeding the thermal optimal range for Northern Pike (thermal optima = 19°C to 21°C; Casselman and Lewis 1996). Thus, Northern Pike may be required to increase their activity space to find and access deeper, colder areas to thermoregulate (Pierce et al. 2013; Peat et al. 2016). In contrast, for a warmwater species like Largemouth Bass (thermal optima = 24°C to 30°C; Stuber et al. 1982), Embayment C water temperatures only reached the lower range of their thermal optima for growth. As such, Largemouth Bass activity spaces in Embayment C were also likely driven in part by active thermoregulation behaviours to exploit the warmest areas to support growth.

Fall

Fall represents a period of substantial change to the environmental and physical components of fish habitat. For all species, daily site fidelity was lowest during this time of year (Chapter 2). Studies have found that higher movement rates occur during autumn for Largemouth Bass (Karchesky and Bennett 2004; Sammons and Maceina 2005; Hanson et al. 2007), Yellow Perch (Radabaugh et al. 2010) and Common Carp (Penne and Pierce 2008), which supports our observation of reduced site fidelity during this season. Cooling water temperatures during the fall months may force fish to move more extensively to seek out remaining areas of warm water, or cue for overwintering shelter. While this may explain the decreased site fidelity for Largemouth Bass and Common Carp, it does not adequately explain decreased site fidelity for coolwater species, like Northern Pike and Yellow Perch. At this time, prey availability may be decreasing or may be moving more extensively (Hall and Werner 1977) and there may be a breakdown of habitat structure, as submerged aquatic vegetation would senesce (Kufel 2001). As such, lower daily site fidelity may be an indication that individuals must expand their space use behaviour in order to find or follow prey resources. Although, tagged fish using Embayment C during the fall did not increase activity space size relative to other seasons (except winter). In fact, Northern Pike activity spaces reduced during the fall, suggesting that Northern Pike may be using multiple areas in close proximity (e.g., Embayment C, Cell 3, Cherry Beach), but their specific space use in Embayment C was concentrated in particular patches. For all species, fall represents a critical foraging period, as individuals were expected to forage heavily to accumulate energy stores for overwinter survival (Suski and Ridgway 2009). Furthermore, fidelity in fall could be lower in locations that

are not used as overwintering habitats, as individuals, particularly for those species that form winter aggregations, may begin movement towards overwintering habitats.

5.3 Aquatic Habitat Restoration

Alteration of physical habitat and degradation of water quality associated with urbanization, industrial activities, agriculture and other development, coupled with introduction of invasive species, and resource exploitation, have had devastating effects on freshwater ecosystems around the globe (Richter et al. 1997; Strayer and Dudgeon 2010). There has been a greater loss of biodiversity in freshwater systems than in any other ecosystem (Dudgeon et al. 2006; Reid et al. 2018). The impact on aquatic systems in urbanized regions has been deemed the "urban stream syndrome" (Walsh et al. 2005) and Toronto Harbour exhibits many of the characteristic symptoms associated with such a syndrome as the recipient of both stream, outfall, and natural lake effects. The Toronto and Region Area of Concern suffers from 8 Beneficial Use Impairments (IJC 2020) including, 'degradation of fish and wildlife populations' and the 'loss of fish and wildlife habitat' (Toronto Region RAP 2007). In response to habitat loss and degradation effects on the productivity of animal populations, habitat restoration (and similarly termed activities such as rehabilitation, remediation, creation, and enhancement) is practiced by nearly every conservation organization (Bernhardt et al. 2005). In the Toronto Harbour area, habitat restoration has used a variety of techniques including: shoreline profile modification, aquatic vegetation planting, and placement of shallow shoals, shoreline aggregates, and log tangles. It is generally accepted that newly restored aquatic areas can contribute positively to the biodiversity and productivity of local animal populations. However, the effects and timelines of aquatic habitat restoration projects are largely

unknown (Block et al. 2001). Ecological restoration of fish habitat has generally focused on restoring the structural components of habitat, including abiotic structure and vegetation. However, it is often assumed that these structural changes will lead to population level responses by animals, such as increases in biodiversity or greater abundances of target species. This "if you build it, they will come" approach is commonly referred to as the "Field of Dreams Hypothesis" (Palmer et al. 1997; Sudduth et al. 2011). There are a number of examples of unsuccessful habitat restoration projects, whereby establishing or altering structural habitat does not lead to increases in biodiversity or abundance (e.g., Baril et al. 2018). Worse, failure to design a monitoring program that captures information on the vital responses by animals in the restored area will surely result in uncertainty over whether the project was successful (i.e. merely redistribution of individuals). Even still, simply collecting presence/absence data on animals fails to capture any information on the ecological reasons for their presence or absence (Lindell 2008). Moreover, collecting information at the population and/or community level (e.g., abundance or richness) may fail to capture important interindividual variability in responses (Lapointe et al. 2013; Ward et al. 2016). For example, Kelso and Minns (1996) inferred that local species richness at AOCs in the Great Lakes is unlikely to improve as a result of habitat restoration, since species richness is more influenced by regional factors. Following an individual's behaviour at these sites allows for comparisons of ecosystem health to an individual's behaviour that has fitness consequences, can identify critical spatial resources, and provide insight into the mechanisms through which species contribute to ecosystem function (Lindell 2008; Lapointe et al. 2013; Brooks et al. 2017).

According to Hale and Swearer (2017), a number of criteria must be met for habitat restoration to be successful for animals: (1) restoration must improve structural habitat, (2) animals must be available to colonize, (3) animals must select the habitat, (4) the restored habitat must provide the resources that the animal needs, and (5) restored sites must enable a net reproductive rate greater than 1. In this thesis, I was able to address two of the five criteria.

The Toronto and Region Conservation Authority (TRCA) has been directly involved in the introduction of physical habitat elements (e.g., coarse woody debris, rock shoals, vegetation, shelter from wind/wave exposure), as well as monitoring in restored areas of the harbour (Toronto Waterfront Aquatic Habitat Restoration Strategy; criterion 1). Further, the Toronto Harbour supports populations of as many as 50 species of fish (Dietrich et al. 2008; Hoyle et al. 2018; criterion 2). I specifically addressed the third and fourth criteria in this thesis. In the Toronto Harbour, I found that Northern Pike and Yellow Perch exhibited higher daily site fidelity in areas with restored habitat compared to areas without restored habitat (Chapter 2; criterion 3). Further, I used activity space size and space use overlap of tagged Largemouth Bass, Northern Pike, and Common Carp to infer that an embayment in the Toronto Harbour that has received extensive restoration provided habitat of sufficient quality for these species (Chapter 3; criterion 4). Management agencies have documented evidence of reproductive success for Northern Pike in restored, spawning habitat in the Toronto Harbour (L. Matos, pers. comm); however, evidence of recruitment has not been evaluated to date (criteria 5). Speculation that spawning does occur in restored areas does not provide sufficient evidence of nursery habitat or recruitment (Veilleux et al. 2018)

Shallow, protected areas of Toronto Harbour that support the establishment of submerged aquatic vegetation appear to be hotspots for tagged fish, in terms of habitat use for many of the species in the community (Chapter 2; Chapter 3; Chapter 4; Midwood et al. 2019). This supports the well-established notion that shallow, protected, warmwater habitat is generally limited, while being highly selected by fish species in the Toronto Harbour (Murphy et al. 2011). Unfortunately, these regions of the Toronto Harbour are spatially isolated, on the order of several kilometers, by a matrix of less suitable habitat for the tagged species (characteristically cold, deep, and homogeneous). Longer movements associated with gaps that connect small, higher quality habitat areas can lead to spatial and temporal structuring or isolation of populations (Shepard et al. 2013). Murphy et al. (2012) used analysis of otoliths to provide evidence of a metapopulation structure for Largemouth Bass, Yellow Perch, and Pumpkinseed between these regions of the Toronto Harbour. Acoustic tracking of seven fish species in the Toronto Harbour also confirms that there are low levels of cross-harbour movement between these spatially distinct warmwater regions (Midwood et al. 2019). Often, a goal of animal-based habitat restoration initiatives is improving functional connectivity in a landscape in order to facilitate movements between habitat patches or to optimize the configuration of restored areas to enhance the population viability (McAlpine et al. 2016); both larger or more connected patches. Given the documented reliance of many of the tracked fishes on warmwater habitat in Toronto Harbour, managers should prioritize protecting and (where possible) expanding warmwater habitat in the system. Furthermore, restoration actions aimed at improving the connectivity between Tommy Thompson Park and the Toronto Islands and/or the Toronto Islands and Spadina or

Exhibition Place could increase the likelihood of regional fish population persistence if independent local extinctions of its subpopulations occurs (Pulliam 1988; Dias 1996; Gonzalez et al. 1998). For fish populations in the Toronto Harbour, Murphy et al. (2011; 2012) noted the possibility of ecological traps that might occur whereby embayments that have requisite structural habitat for spawning and nursery conditions, but where water temperatures do not warm enough to permit growth and survival of young-of-the-year individuals. As such, it may be critically important that habitat for warmwater fishes, take into account the thermal characteristics that are likely to persist in restored sites in addition to physical habitat features.

Ecological traps in managed ecosystems are often the product of a mismatch between human perception of animal habitat and what truly represents functional habitat from the perspective of the animal (Hale et al. 2015). Ecological traps can occur as an unintended consequence of habitat restoration (Sievers et al. 2018) This underscores the importance of understanding habitat functionality from the perspective of the animals in the design and implementation of habitat restoration actions (Lindell 2008; Van Dyck 2012; Hale and Swearer 2017). For example, tracking endpoints such as site fidelity (Chapter 2), space use (Chapter 3), and activity (Chapter 4), to complement presence/absence or abundance data, can help us to understand the environmental conditions that influence individual habitat use and movement behaviour to better assess the results of population or community sampling, and whether restored habitats meet the resource's needs (e.g., Espinoza et al. 2011; Farrugia et al. 2011; Freedman et al. 2016; Veilleux et al. 2018).

From an applied perspective, decisions surrounding delisting the 'loss of fish and wildlife habitat' Beneficial Use Impairments in the Toronto and Region Area of Concern pose a significant challenge for aquatic habitat managers. Using an area-based target alone without monitoring would fail to capture whether the restored habitat is functionally used or results in the overall net reproductive rate being greater than 1. Similarly, using population or community responses (e.g., community composition) can identify whether some species are over- or underrepresented in the community, but again, does not capture whether the restored habitat constitutes functional habitat from the perspective of the animals based on longer term use. For example, the Index of Biotic Integrity (IBI) in Toronto Harbour reported by Hoyle et al. (2018) suggests that the IBI is lower than expected for a comparable nearshore area in the Great Lakes, but that may be because it is surrounded by the largest urban center in Canada on one side and a deep cold upwelling region on the other, therefore, I would argue that a lower IBI is to be expected, even under natural conditions. The authors suggest, "on-going aquatic habitat remediation and creation projects on the Leslie Street Spit (including Tommy Thompson Park) and the Toronto Islands, should ensure maintenance or improvement in IBI scores and aquatic ecosystem health generally". But survey-type assessments only provide snapshots and thus limited evidence about the functionality of the restored habitat, or insight into why continued effort may or may not contribute to the maintenance and improvement of fish habitat in the Toronto Harbour.

For example, Veilleux et al. (2018) investigated the timing and duration of occupancy of seven species in four large urban boat slips on the north shore of Toronto Harbour. Two of the boat slips were located in close proximity to more natural vegetated

habitats and had undergone habitat enhancement activities while the other two had no habitat enhancements and were located in close proximity to deep and turbid channelized regions. Only a few of the seven adult fish species visited either the enhanced or degraded slips, suggesting that there may be a mismatch between the habitat enhancement efforts and habitat suitability for target fish without major changes. Even though unsuccessful or equivocal restoration outcomes are rarely published (Zedler 2007; Hobbs 2009), some general findings coming from the literature suggest that continuing to add spawning habitat may not increase the productivity of a fish populations if that habitat is not the limiting habitat, or a population threshold may be reached when the minimum habitat supply for a particular life stage has been reached in an area (Casselman and Lewis 1996; Minns et al. 1996b). In fact, Minns et al. (1996b) identified that YOY and juvenile-adult habitat was the limiting factor in a population of Northern Pike in the Hamilton Harbour. This was contrary to conventional thinking on habitat management for Northern Pike in many aquatic systems that focused on spawning access; admittedly spawning and nursery areas are many time synonymous.

My thesis identifies environmental and habitat-specific drivers of space use and movement behaviour of multiple freshwater fish species to provide insight into the fishhabitat interactions in an urban aquatic habitat that is the subject of ongoing habitat management activities. This provides evidence of improved functional habitat in the Toronto Harbour and directly guides where and what habitats in future efforts are needed the most. This information can be used to complement traditional fish monitoring methods and guide efforts to rehabilitate fish populations and fish habitat (Brooks et al. 2017; Crossin et al. 2017).

5.4 Acoustic telemetry for fish and fish habitat management

From an applied perspective, a contribution from this thesis is insight into how biotelemetry can be used to inform fisheries and habitat management. Biotelemetry, as a tool, has seen a exponential rise in studies of fish and their habitats (Cooke et al. 2013; Hussey et al. 2015), including in the Laurentian Great Lakes (Landsman 2011; Brooks et al. 2017). There was a delay in ensuring that these emerging biotelemetry studies were relevant to the management agencies in charge of fish and fish habitat. However, recent examples are demonstrating that the scientific contributions from biotelemetry studies are increasingly informing decision-making processes (Cooke et al. 2016; Nguyen et al. 2017; Brooks et al. 2017; Crossin et al. 2017; Brooks et al. 2018; Cooke 2018; Delle Palme 2019). Fish and fish habitat resource managers should strive to incorporate multiple, complementary performance metrics and evaluation criteria into restoration and mitigation monitoring programs (Freedman et al. 2016). However, telemetry is expensive so partnerships to advance restoration science would make it more accessible. In my experience using biotelemetry and the information it generates has been highly regarded by managers within Toronto and Region Conservation Authority, Environment and Climate Change Canada, and Fisheries and Oceans Canada, as part of a suite of regulatory and science agencies that specifically oversee aquatic habitat plans (e.g. Aquatic Habitat Toronto; Prime et al 2013). In fact, preliminary findings from this fish tracking study were directly incorporated into the habitat restoration design of Cell 2 in TTP, based upon the seasonal habitat use by Northern Pike and Largemouth Bass (Cooke et al. 2018). As a consequence, more heterogeneous habitats at a range of depths were added to support both species throughout the year. While acoustic telemetry offers many

opportunities for fish and fish habitat management, it is crucial to understand the technological constraints, including but not limited to small sample sizes (i.e., cost), tag size limitations, tag malfunctions, and detection range.

5.5 Future directions

Each chapter in the thesis revealed patterns in seasonal habitat use, highlighting that subsequent management decisions needed to be cautious in extending fish-habitat interactions, based largely on the summer period, to the full annual cycle of habitat use. This is one of the great benefits of in situ biotelemetry systems. In-water activities, especially those that affect nearshore littoral zones, include water drawdowns (Rogers and Bergersen 1995; Carmignani and Roy 2017), dredging and subsequent deposition of material, and shoreline construction (both small-scale shoreline modifications to large projects like built infrastructure). These activities are often subject to "timing windows", whereby regulatory agencies dictate the time period when these activities can occur (Goodchild 2004). These windows are largely informed by and intended to protect spawning and nursery periods for freshwater fish. However, overwintering periods may be equally critical to local population persistence. Focused research on the spatial ecology and functional habitat requirements of overwintering fish are warranted to ensure that conservation and protection strategies that are seasonally appropriate.

The extent to which predation risk and prey availability varied in the Toronto harbour system are unknown, and are certainly areas deserving of further study. Further research in the Toronto Harbour could quantify predation risk and prey availability in a number of ways. Firstly, one approach would be to pair hydroacoustic surveys of the Toronto Harbour throughout the year, in order to estimate prey availability through the

distribution of prey resources across seasons and habitats. Alternatively, future research could include prey species in the tracking study by simultaneously capturing and tagging small-bodied prey species. New acoustic transmitter technology can detect when an individual has been consumed, and the application of this technology would be beneficial for future studies of small-bodied fishes in the area (Halfyard et al. 2017). In the present tracking study, there were a few suspected cases of predation of tagged fish, but confirmation is not possible (Midwood et al. 2019). Understanding predation risk and prey availability would allow tests of season- and habitat-specific predation risk and prey availability. This could inform habitat restoration's effectiveness by quantifying refugia and forage base.

In this thesis, I confirmed the broadly held belief that shallow, warmwater habitat is generally limited in the Toronto Region's nearshore, and is highly selected by many fish species in the Toronto Harbour. Unfortunately, these zones of the Toronto Harbour are spatially isolated, on the order of several kilometers apart, by a matrix of non-habitat (characteristically cold, deep, and homogeneous). Acoustic tracking of seven fish species in Toronto Harbour confirms that there are low levels of cross-harbour movement between these spatially distinct warmwater regions (this thesis; Midwood et al. 2019). Future research efforts could explicitly quantify the movement rates and the internal and external drivers (Nathan et al. 2008) behind these larger scale movement behaviours. Further, demonstrating the positive demographic effects of connectivity via corridors would provide concrete evidence that population viability is enhanced due to regional connectivity between the Toronto Islands and Tommy Thompson Park (Beier and Noss 1998). Testing the value of movement corridors could be challenging in this system

because there are only two routes that connect the Toronto Islands to Tommy Thompson Park (Eastern Gap and Western Gap). Due to the limited dispersal routes in this system, it may be critically important to identify and preserve the abiotic and biotic conditions that facilitate movements between these two regions of the Toronto Harbour.

In this thesis, I quantified the seasonal and habitat-specific activity and space use behaviour of selected fish species to better understand the functional use (inferred habitat quality) in Toronto Harbour. However, perhaps the most important criteria for evaluating successful habitat restoration for animals is whether or not restored areas contribute to a net reproductive rate greater than 1 (Hale and Swearer 2017). Although the links between individual behaviour, habitat quality, and potential fitness are reasonably strong (Olsson et al. 2002; Lindell 2008), future research should strive to demonstrate and quantify the individual reproductive success and population replacement rate to bolster inferential preferred use statistics. This would provide further evidence to support the delisting of the Beneficial Use Impairments: 'degradation of fish and wildlife populations' and the 'loss of fish and wildlife habitat' in the Toronto and Region Area of Concern.

Appendix A. Abstracts of non-thesis publications during doctoral studies

1. Midwood, J. D., A. M. Rous, S. E. Doka, and S. J. Cooke. 2019. Acoustic telemetry in Toronto Harbour: assessing residency, habitat use, and within harbour movements of fishes. Canadian Technical Report of Fisheries and Aquatic Sciences 3331: xx + 174 p.

The Toronto and Region Area of Concern (AOC) has a long history of development that has resulted in substantial losses of fish habitat. Efforts are ongoing to create new habitat and remediate degraded habitat in the AOC. This report presents high-level results from a five-year acoustic telemetry study of fish movements and habitat use in the AOC. Given the documented reliance of many of the tracked fishes on warmwater habitat, results highlight the importance of protecting and (where possible) expanding warmwater habitat in the system. Results from an assessment of fish residency within the central waterfront of the AOC characterize different species as primarily resident (i.e., Largemouth Bass [Micropterus nigricans]; Northern Pike [Esox lucius]) or migratory (i.e., Common Carp [Cyprinus carpio]; Walleye [Sander vitreus]; White Sucker [Catostomus commersonii]), which can inform both the recovery of target species (i.e., Walleye) and assessments of contaminant burden in fishes captured in the AOC (i.e., Common Carp and White Sucker). Finally, a major product from this report is the development of a data processing and analytical approach that can review, integrate, and summarize extensive acoustic telemetry datasets to support more targeted analyses of fish habitat use. Future efforts will focus on more detailed species- or site-level analysis to provide a better understanding of their core ecology and aid in the development of species-specific habitat remediation strategies not only for the Toronto and Region AOC, but also throughout the Great Lakes.

2. Abrams, A.E.I., A.M. Rous, J.L. Brooks, M.J. Lawrence, S.E. Doka, J.D. Midwood, and S.J. Cooke. 2018. Comparing immobilization, recovery, and stress indicators associated with electric fish handling gloves and a portable electrosedation system. Transactions of the American Fisheries Society 147: 390-399.

Fish sedation facilitates safer handling of fish during scientific research or fisheries assessment practices, thus limiting risk of injury to fish and reducing stress responses. In recent years, there has been growing interest in using electricity to sedate fish; two methods include (1) lower-voltage, non-pulsed-DC fish handling gloves (FHGs) that tend to only sedate fish while the gloves are touching the animal; and (2) a comparatively high-voltage, pulsed- DC Portable Electrosedation System (PES) that leads to galvanonarcosis. This study compared the physiological consequences of exposure to FHGs and PES in teleost fish. Bluegills Lepomis macrochirus and Largemouth Bass Micropterus nigricans were exposed to FHGs, PES, or a handling control for a 3-min simulated surgery. Blood was then sampled at 0.5 and 4.5 h postexposure and was analyzed for blood glucose, blood lactate, and plasma cortisol concentrations. Opercular rates were monitored during surgery, at 2 min post-surgery, and 0.5 h post-surgery. At 24 h post-surgery, time to exhaustion (via a standardized swimming chase protocol) was assessed. Fish exposed to FHGs tended to exhibit lower opercular rates than fish that were sedated with the PES during simulated surgery. Cortisol levels of Largemouth Bass treated with FHGs were higher than those of fish sedated with the PES. Glucose levels recorded for Bluegills at 4.5 h post-surgery were higher with FHGs than with the PES. In both species, lactate was lower for fish treated with FHGs than for those treated with the PES. At 24 h posttreatment, Bluegills sedated with FHGs exhibited a longer time to exhaustion than those subjected to the PES, whereas Largemouth Bass sedated with the PES exhibited a longer time to exhaustion than those sedated with FHGs. Physiological responses to treatments were inconsistent between species. Further investigation to determine the optimal electrosedation method is required.

3. Cooke, S.J., A.M. Rous, L.A. Donaldson, J.J. Taylor, T. Rytwinski, K.A. Prior, K.E. Smokorowski and J.R. Bennett. 2018. Evidence-based restoration in the Anthropocene – From acting with purpose to acting for impact. Restoration Ecology 26: 201-205.

The recognition that we are in the distinct new epoch of the Anthropocene suggests the necessity for ecological restoration to play a substantial role in repairing the Earth's damaged ecosystems. Moreover, the precious yet limited resources devoted to restoration need to be used wisely. To do so, we call for the ecological restoration community to embrace the concept of evidence-based restoration. Evidence-based restoration involves the use of rigorous, repeatable, and transparent methods (i.e. systematic reviews) to identify and amass relevant knowledge sources, critically evaluate the science, and synthesize the credible science to yield robust policy and/or management advice needed to restore the Earth's ecosystems. There are now several examples of restoration-relevant systematic reviews that have identified instances where restoration is entirely ineffective. Systematic reviews also serve as a tool to identify the knowledge gaps and the type of science needed (e.g. repeatable, appropriate replication, use of controls) to improve the evidence base. The restoration community, including both scientists and practitioners, needs to make evidence-based restoration a reality so that we can move from best intentions and acting with so-called "purpose" to acting for meaningful impact. Doing so has the potential to serve as a rallying point for reframing the Anthropocene as a socalled "good" epoch.

4. Brooks, J.L, C. Boston, S. Doka, D. Gorsky, K. Gustavson, D. Hondorp, D. Isermann, J.D. Midwood, T.C. Pratt, A.M. Rous, J.L. Withers, C.C. Krueger, and S.J. Cooke. 2017. Use of fish telemetry in rehabilitation planning, management, and monitoring in Areas of Concern in the Laurentian Great Lakes. Environmental Management 60: 1139-1154.

Freshwater ecosystems provide many ecosystem services; however, they are often degraded as a result of human activity. To address ecosystem degradation in the Laurentian Great Lakes, Canada and the United States of America established the Great Lakes Water Quality Agreement (GLWQA). In 1987, 43 highly polluted and impacted areas were identified under the GLWQA as having one or more of 14 Beneficial Use Impairments (BUIs) to the physical and chemical habitat for fish, wildlife and humans, and were designated as Areas of Concern (AOC). Subnational jurisdictions combined with local stakeholders, with support from federal governments, developed plans to remediate and restore these sites. Biotelemetry (the tracking of animals using electronic tags) provides information on the spatial ecology of fish in the wild relevant to habitat management and stock assessment. Here, seven case studies are presented where biotelemetry data were directly incorporated within the AOC Remedial Action Plan (RAP) process. Specific applications include determining seasonal fish-habitat associations to inform habitat restoration plans, identifying the distribution of pollutantindicator species to identify exposure risk to contamination sources, informing the development of fish passage facilities to enable fish to access fragmented upstream habitats, and assessing fish use of created or restored habitats. With growing capacity for fish biotelemetry research in the Great Lakes, we discuss the strengths and weaknesses of incorporating biotelemetry into AOC RAP processes to improve the science and practice of restoration and to facilitate the delisting of AOCs.

5. Dick, M.*, A.M. Rous*, V.M. Nguyen, and S.J. Cooke. 2016. Necessary but challenging: interdisciplinary approaches to solving conservation problems. FACETS 1: 67-82.

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Contemporary conservation problems are typically positioned at the interface of complex ecological and human systems. Traditional approaches aiming to compartmentalize a phenomenon within the confines of a single discipline and failing to engage non-science partners are outmoded and cannot identify solutions that have traction in the social, economic, and political arenas in which conservation actions must operate. As a result, conservation science teams must adopt multiple disciplinary approaches that bridge not only academic disciplines but also the political and social realms and engage relevant partners. Five reasons are presented that outline why conservation problems demand multiple disciplinary approaches in order to move forward because: (i) socio-ecological systems are complex, (ii) multiple perspectives are better than one, (iii) the results of research must influence practice, (iv) the heterogeneity of scale necessitates it, and (v) conservation involves compromise. Presenting reasons that support multiple disciplinarity demands a review of the barriers that impede this process, as we are far from attaining a model or framework that is applicable in all contexts. Two challenges that impede multiple disciplinarity are discussed, in addition to pragmatic solutions that conservation scientists and practitioners can adopt in their work. Overall, conservation researchers and practitioners are encouraged to explore the multiple disciplinary dimensions of their respective realms to more effectively solve problems in biodiversity and sustainability.

6. Lennox, R., G. Blouin-Demers, A.M. Rous, and S.J. Cooke. 2016. Tracking invasive animals with electronic tags to quantify their ecological impacts and evaluate control options. Biological Invasions 18: 1219-1233.

Invasive species alter ecosystem structure and function when they establish in new habitats. Although preventing or managing invasions is extremely important for maintaining biodiversity, doing so is difficult and requires efficient intervention. Remote monitoring of free-living animals with electronic tags (i.e. tags that transmit data remotely or log them for future retrieval) can contribute important knowledge about invasive animal biology. A quantitative literature review identified instances in which electronic tagging has contributed to studying invasions. Electronic tags were generally used for one of four purposes: (1) characterize spatial ecology; (2) identify interactions; (3) assess risk potential; or (4) evaluate management options. Overall, electronic tags have considerable potential for developing, refining, and evaluating invasion management strategies that con- tribute to conservation efforts. We explore the role of electronic tags as a component of integrated control program design and implementation for invasive animals.

7. Chapman, J.M., D. Algera, M. Dick, E.E. Hawkins, M.J. Lawrence, R.J. Lennox, A.M. Rous, C.M. Souliere, H.L.J. Stemberger, D.P. Struthers, M. Vu, T.D Ward, A.J. Zolderdo, and S.J. Cooke. 2015. Being relevant: practical guidance for early career scientists interested in solving conservation problems. Global Ecology and Conservation 4: 334-348.

In a human-altered world where biodiversity is in decline and conservation problems abound, there is a dire need to ensure that the next generation of conservation scientists have the knowledge, skills, and training to address these problems. So called "early career researchers" (ECRs) in conservation science have many challenges before them and it is clear that the status quo must change to bridge the knowledge-action divide. Here we identify thirteen practical strategies that ECRs can employ to become more relevant. In this context, "relevance" refers to the ability to contribute to solving conservation problems through engagement with practitioners, policy makers, and stakeholders. Conservation and career strategies outlined in this article include the following: thinking 'big picture' during conservation projects; embracing various forms of knowledge; maintaining positive relationships with locals familiar with the conservation issue; accepting failure as a viable (and potentially valuable) outcome; daring to be creative; embracing citizen science; incorporating interdisciplinarity; promoting and practicing pro-environmental behaviours; understanding financial aspects of conservation; forming collaboration from the onset of a project; accepting the limits of technology; ongoing and effective networking; and finally, maintaining a positive outlook by focusing on and sharing conservation success stories. These strategies move beyond the generic and highlight the importance of continuing to have an open mind throughout the entire conservation process, from establishing one's self as an asset to embracing collaboration and interdisciplinary work, and striving to push for professional and personal connections that strengthen personal career objectives.

8. Rous, A.M., A. Forrest, E. Hart McKittrick, G. Letterio, J. Roszell, T. Wright, and S.J. Cooke. 2015. Orientation and position of fish affects recovery time from electrosedation. Transactions of the American Fisheries Society 144: 820-828.

Commercially available electrosedation apparatuses (e.g., the Smith-Root Portable Electroanesthesia System [PES]) are growing in popularity within the fisheries research community. This technology can be used to immobilize fish rapidly and does not require a withdrawal period before fish are released. A number of studies examined how various settings (e.g., duration, frequency, voltage) influence the performance of the PES for fish sedation, but comparatively less is known about the role of fish orientation and position on the efficacy of electrosedation within the PES. We compared recovery times of Bluegill Lepomis macrochirus upon manipulation of three variables: orientation of fish, electric field size (i.e., spacing between the anode and cathode), and fish proximity relative to the anode. Fish were individually exposed to pulsed DC with a standardized frequency (100 Hz), voltage (90 V), and shock duration (3 s). Full recovery time was significantly longer for fish oriented at horizontal angles (0° and 180°) than at acute angles (45° and 135°). Significant interactions were found between orientation and electrode spacing, as well as between orientation and fish proximity. These findings are pertinent to researchers in the field looking to optimize recovery time for a quick release after surgery, tagging, or any other time fish sedation is required.

9. Gutowsky, L.F.G., W. Aslam, R. Banisaeed, L.R Bell, K.L. Bove, J.W. Brownscombe, G.J.J. Burrows, E. Chu, J.M.T. Magel, A.M. Rous, and S.J. Cooke. 2015. Considerations for the design and interpretation of fishing release mortality estimates. Fisheries Research 167: 64-70.

To generate mortality estimates for fish that are captured and released in recreational and commercial fisheries, it is common to temporarily hold fish in captivity. Typically, captured fish are placed in some form of pen, cage or tank with control individuals, yet little is known about how the type of holding environment influences fish condition or mortality. Here we captured freshwater fish (bluegill; Lepomis macrochirus) via angling and fyke net and retained them in one of four holding environments; a round flowthrough tank on shore [TANK], a knotless nylon pen with natural substrate in the lake [PEN], a knot- less nylon floating cage with a rigid structure [RCAGE], and a knotless nylon floating cage that lacked rigid structure [CAGE]. Mortality was low (1%) across both capture techniques and holding environments during the 14-day retention period. All mortalities were associated with capture by fyke net. A chronic stress indicator, blood glucose, was determined for a subset of fish on day 5. Although there were significant differences in blood glucose between angled RCAGE and angled PEN (Tukey, P = (0.047) and angled RCAGE and fyke PEN (Tukey, P = 0.015), the observed levels were generally quite low (range: $1.0-3.9 \text{ mmol } \text{L}^{-1}$) and the differences were likely associated with differences in feeding; fish in the PEN group with access to substrate (and presumably the most food) had slightly higher glucose levels. At the conclusion of the study Fulton's condition factor was similar among all groups (ANOVA, P > 0.05, all terms). However, fish held in the TANK treatment had the highest levels of external protozoan parasite infection by Ichthyopthirius (Tukey, P < 0.05). This study illustrates that in situ holding environments (rather than tanks) may help reduce mortality, stress, and disease during studies that estimate post-release mortality. We encourage additional research to explore how the holding environment can influence inferences made about post-release mortality and sublethal impacts of fishing.

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