Freshwater fish populations in eastern Ontario benefit from long standing protected areas

By

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Dedication

I would like to dedicate this thesis to my stepfather, Paul, who has been a central pillar of support, encouragement, and guidance throughout my life. I would not be where I am today if not for his mentorship, care, and love. His endless support of my endeavours and goals has proved to be invaluable in my development, not only academically but as a human being, and for this, I am eternally grateful.

Abstract

Research has identified numerous conservation benefits attributed to the use of protected areas (PAs), yet the effectiveness of spatial protection in freshwater systems (FPAs) remains unclear. In this thesis, I assessed multiple longstanding (>70 years active) intra-lake FPAs within the Rideau Waterway system (Ontario, Canada) to evaluate their potential conservation value. Initially, these FPAs were established to protect exploited populations of largemouth bass (*Micropterus salmoides*). However, since their inception, there has been no empirical data collected to evaluate their effectiveness for protecting bass or the broader fish community. To address this, I conducted a series of comparative assessments to evaluate how these FPAs influence largemouth bass space-use dynamics, capture vulnerability, and physiology. I also evaluated potential indirect benefits at the community level through measuring differences in fish community structuring between FPA and non-protected areas.

The FPAs evaluated strongly benefitted largemouth bass through increased population densities within the protected area boundaries. These FPAs also indirectly benefitted several non-target fish species by supporting increased population densities and species richness, with evidence of fish spillover occurring into adjacent non-protected waters. Acoustic telemetry data revealed that largemouth bass displayed high occupancy, particularly during the spring-summer seasons, within a designated FPA. This space-use behaviour was repeatable across years, and also positively correlated to fish size, with larger individuals utilizing the FPA more extensively relative to smaller individuals. Beyond serving as a mechanism to benefit fish community structure, FPAs were also found to protect key phenotypes linked to angling vulnerability in largemouth bass, suggesting a potential for FPAs to provide evolutionary-enlightened benefits. The results presented in this dissertation are novel and showcase a host of biological benefits associated with the use of FPAs. Moreover, the consistency in results across all FPAs suggests an effective and transferable resource management tool, which may help to enhance freshwater conservation efforts. As challenges facing freshwater systems continue to mount, the need for effective management strategies has never been greater. As such, the data presented here provides a stronger understanding of how FPAs can offset anthropogenic impacts on freshwater fish communities, which may have far-reaching implications for contemporary fisheries management practices.

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Last, but certainly not least, I would like to thank my wife, Oliva. Of all the people who have taken part in getting me to the finish line, you have undoubtedly assisted me the most. Your constant belief in me and your unwavering support throughout the good, the bad, and the very bad, has kept me sane and moving forward. For this, I am truly grateful. This thesis greatly benefitted from funding provided by a Queen Elizabeth II Graduate Scholarship in Science and Technology from the Ontario Graduate Scholarship program, an Ontario Graduate Scholarship, the Carleton University Graduate Student Travel/Research Bursary, and a Research Assistantship from Carleton University.

Thesis Format and Co-authorship

This thesis consists of five chapters, three of which are written in manuscript format. Chapter 1 outlines a general introduction and background of information relevant to my thesis work including thesis objectives and hypotheses. Chapter 2 characterizes the community ecology benefits associated with FPAs through the evaluation of fish species abundance, biomass, and richness inside and outside of protected areas. Chapter 3 quantified the protective capacity of a designated FPA through monitoring the spatial movement patterns of largemouth bass across seasons. Chapters 4 evaluated the differences in capture vulnerability and physiology between largemouth bass residing inside and outside of FPAs. Chapter 5 summarizes my general conclusions, the relevance of my research, and proposes future experiments that may be conducted to support to results observed from the various experiments conducted in the current thesis. This thesis contains all of my own research but was conducted in collaboration with a number of other researchers to which a summary of their contributions is listed below.

Chapter 1: General introduction, thesis objectives and hypotheses.

Chapter 2 (published): Evidence of fish spillover from freshwater protected areas in lakes of eastern Ontario

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All authors contributed to the design of the experiment. Data collection was conducted by A.J.Z., A.E.I.A, and C.H.R. Data analyses were performed by A.J.Z. with assistance by C.D.S., C.H.R., and J.D.M. The manuscript was written by A.J.Z. with all authors contributing to revisions.

Chapter 3 (unpublished): Space use and residency patterns of largemouth bass within a freshwater protected area

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Chapter 4 (unpublished): Freshwater protected areas can increase angler catch rates and preserve high-performance phenotypes in a popular sportfish

Zolderdo AJ, Abrams AEI, Lawrence MJ, Reid CH, Suski CD, Gilmour, KM, Cooke SJ Freshwater protected areas can increase angler catch rates and preserve high-performance phenotypes in a popular sportfish (unpublished).

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Chapter 1: General Introduction

In this thesis I will address the role that spatial protection can play in mitigating humanuse impacts on freshwater fish communities. More specifically, it will quantify the effectiveness of single-resource (i.e., designed for one species) freshwater protected areas (FPAs) to protect wild fish populations from selective and exploitive recreational fisheries practises. This general introduction provides all of the necessary and relevant information for understanding the development of the ideas, hypotheses and predictions that I present in this thesis. The first section addresses the mechanistic processes of how recreational fisheries can impart selection pressures on fish populations (Section 1.1), and its potential effects at a physiological level (Section 1.2). I then describe the role of aquatic protected areas in resource management (Section 1.3), and how spatial protection may protect against fisheries-induced selection pressures (Section 1.4). Finally, I introduce the focal study species, the largemouth bass, and discuss the corresponding cultural and biological significance of this species as it relates to the objectives, hypotheses, and predictive framework for this thesis (Section 1.5 – 1.7).

1.1 Selectivity of recreational fisheries

Recreational angling is an important sport and leisure activity practiced globally in both freshwater and marine environments, and accounts for an estimated 12% of annual global fish harvest (Cooke and Cowx, 2004). However, as of late there has been concern regarding the potential evolutionary consequences imposed by recreational angling on wild fish populations. Similar to commercial fishing, recreational angling has the selective potential to alter the phenotypes/genotypes of highly pressured populations, a phenomena referred to as fisheriesinduced evolution (FIE; Heino and Dieckmann, 2009). FIE occurs as a result of intensive selection pressures on specific individuals of a population (Kuparinen and Merilä, 2007; Heino and Dieckmann, 2008). Selection in this context arises through selective harvesting of individuals using technique-specific fishing gear and tactics to target fish of a particular size class, sex, life-history stage, or behaviour (Conover and Munch, 2002; Wang *et al.*, 2016; Diaz Pauli and Sih, 2017). This type of selection can induce evolutionary changes among fish populations including, which, in the case of size-selective commercial fisheries, can result in reduced age and size at maturity, growth rate, and reproductive investment (Conover *et al.*, 2009; Philipp *et al.*, 2009).

Selective pressures on behavioural and physiological traits can differ greatly between recreational and commercial fisheries based on differences in capture techniques and practices (Diaz Pauli and Sih, 2017). For example recreational angling relies on fish *choosing* to eat or attack a fishing lure, which can impose selection pressure against certain behavioural phenotypes (i.e., more bold and aggressive behaviours) and their underlying physiological drivers (i.e., metabolic rate) (Redpath et al., 2009; Hessenauer et al., 2015; Wilson et al., 2015). Recreational anglers also have a greater capacity to manipulate terminal tackle and lure presentation to capture specific individuals or to intercept a particular life-history stage (e.g., nest-guarding male centrarchids), which can select against essential reproductive and parental care behaviours (Suski and Philipp, 2004). There is concern regarding the impacts of FIE in natural systems due to the opposing affects that FIE has on natural selection processes in wild populations (Diaz Pauli and Sih, 2017). For example, practises for some recreational fisheries select for individuals of a population that are large, mobile, and exhibit aggressive/bold behaviours, which often strongly correlate with superior reproductive capabilities (e.g., larger females produce higher quantity and quality of eggs per spawning bout), which can result in directional selection for suboptimal phenotypes (Kuparinen and Merilä, 2007; Philipp et al., 2009; Sutter et al., 2012). To date, the

majority of research pertaining to FIE from recreational angling has been focused on behaviour (i.e., changes in aggression and personality), largely using captive animals under experimental conditions (reviewed in Philipp et al., 2009). Although this research has been effective in developing a mechanistic understanding of FIE, there has been a paucity of research pertaining to the potential selective impacts of recreational fisheries on wild fish populations.

For FIE to occur in natural systems, two factors must be present; (1) there must be heritable variation in the genotype of the population that is targeted, and (2) the fishing practises employed must cause differential reproduction of the different genotypes (Policansky, 1993; Law, 2000; Heino and Dieckmann, 2009). To date, there are many phenotypic traits that have been shown to be influenced/altered by genotypic variation in fishes including, vulnerability to angling capture (Philipp et al., 2009a), age and size at maturation (Kinghorn, 1983), female egg size (Gall, 1975), and colour patterns (Endler, 1980). As commercial and recreational fisheries are non-random in the fishes targeted, differential selection for specific phenotypes as a result of fisheries practises has been well documented (Heino and Dieckmann, 2008). However, differentiating phenotypic plasticity from FIE is particularly challenging given the suite of biotic and abiotic processes that can influence a populations phenotypic response to fisheries. The major difficulties in the detection and quantification of FIE in wild fish stocks is the disentanglement of environmentally based changes from genetically based ones including, but not limited to, compensatory growth (e.g., reduced competition for resources; Eikeset et al., 2016), migration (e.g., source-sink population dynamics; Dunlop et al., 2009), and environmental changes (e.g., introduction of invasive species; Gobin et al., 2018). These inherent confounding factors, coupled with the lack of pre-fisheries data associated with heavily fished stocks, combine to create a challenging system to isolate evolution from plasticity.

1.2 Physiological consequences of FIE

The interaction between FIE on specific physiological processes (e.g., metabolism and stress-responsiveness) has been gaining significant attention within the scientific community as of late (Conover and Munch, 2002; Hessenauer et al., 2015; Louison et al., 2017). As an animal's physiology can be altered naturally (e.g., environmental changes) and/or though human intervention (e.g., selective harvesting), selection for suboptimal physiological responses to homeostatic perturbations could result in negative fitness consequences at a population level (Heino and Dieckmann, 2008; Hollins et al., 2018; Søgaard Jørgensen et al., 2019). Moreover, selection pressure for/against a specific phenotype may result in indirect changes to other highly correlated traits through pace-of-life syndrome (POLS) processes (Lankford et al., 2001; Réale et al., 2010; Polverino et al., 2018). Specifically, POLS hypothesis suggests that if closely related populations of the same species are subjected to differing ecological conditions, then they should differ, predictably, in a suite of physiological (i.e., metabolic, hormonal, and immunity) traits that are linked to the life-history particularities of the population (Réale et al., 2010; Binder et al., 2016; Montiglio et al., 2018). As such, these traits may be influenced through genetic correlation, whereby selection pressure on a specific trait indirectly alters various interconnected phenotypes, which may correspond to changes predicted along the fast-slow pace of life spectrum (Brodie, 1992; Sinervo and Svensson, 2002; Polverino et al., 2018). For example, selection pressure favouring longer lifespans should also favour low growth rates and delayed onset of sexual maturation. However, it is important to note that POLS can be context dependent resulting in mixed support for the utility of this hypothesis to generalize shifts in interconnected phenotypes associated with abiotic/biotic changes at a population level.

In fish, metabolic rate (MR) comprises a particular set of measurable parameters including standard metabolic rate (SMR), maximum metabolic rate (MMR), and aerobic scope (AS) (Chabot et al., 2016; Treberg et al., 2016). These metabolic parameters are linked to various life-history particularities and can influence bioenergetic processes at all organizational levels (e.g., swimming performance) within an animal (Norin and Malte, 2012; Auer et al., 2018; Biro et al., 2018). SMR represents the basal energy requirements to maintain homeostasis (e.g., cellular maintenance and repair) in a resting/fasting state (Chabot et al., 2016), whereas, MMR represents the maximum rate of oxygen consumption, which sets the upper limit for aerobic exercise that can be performed by an animal (Norin and Clark, 2015). AS is the difference between SMR and MMR, which sets the aerobic capacity for an animal to perform work, and limits the aerobic processes (i.e., growth, maintenance, digestion) that can be performed simultaneously (Hansen and Hunt Von Herbing, 2009; Auer et al., 2015b). Collectively, these parameters form a general metabolic phenotype of the animal (Metcalfe et al., 2016). Moreover, these parameters are heritable and show repeatable intraspecific variation amongst individuals (Redpath et al., 2010; Norin and Malte, 2012; Hessenauer et al., 2015), and may play a key role in determining angling vulnerability in fish (Philipp *et al.*, 2015). Specifically, fish with greater metabolic demands have a higher propensity to forage/feed due to increased nutritional requirements, which may increase their likelihood of interacting with fishing gear (Redpath et al., 2010; Hessenauer et al., 2015; Killen et al., 2015a). Experimental FIE literature has shown that angling-induced selection can negatively alter metabolic phenotypes in both freshwater and marine species. For example, high-performance metabolic phenotypes have been identified in fish populations sourced from unexploited lakes (Hessenauer et al., 2015), as well as marine protected areas (MPAs; Duncan et al., 2019). Furthermore, experimental populations of

largemouth bass bred for high angling vulnerability were also found to have high-performance metabolic phenotypes relative to low vulnerability individuals (Redpath *et al.*, 2010). Collectively, this research highlights the concern regarding the evolutionary potential imposed by fisheries-induced selection processes on metabolic phenotypes. Specifically, that a reduced metabolic capacity can restrict the ability of a population to resist and recover from homeostatic perturbations, resulting in a reduced resiliency to natural and/or anthropogenic challenges.

Hormonal responsiveness to stress is another physiological process that may increase the probability of a fish being captured by angling gear and/or surviving a post-capture release event (Øverli et al., 2005; Louison et al., 2018; Koeck et al., 2019). For example, fish that are less sensitive to external stimuli and/or stressors (e.g., fishing gear), may indirectly increase their exposure to angling capture through a reduced fear or caution towards fishing lures (Louison et al., 2017; Hollins et al., 2018). Alteration to the stress-axis as a result of fisheries practises is of particular concern, as an animal's ability to respond appropriately to a stressor(s) can be imperative to its survival and longevity. Response to a stressor(s) can be energetically demanding as it elicits a suite of physiological and behavioural changes for the animal to maintain homeostasis. However, these homeostatic changes (both physiological and behavioural) can fluctuate temporally (i.e., seasonal adjustments) and with life history stage (i.e., spawning and reproduction). In fish, the initial reaction to a stressor elicits a neuroendocrine response cascade, involving the release of catecholamines from the chromaffin tissue, and the activation of the hypothalamic-pituitary-interrenal (HPI) axis (Schreck et al., 2001; Barton, 2002). Activation of the HPI axis stimulates the release of adrenocorticotrophic hormone (ACTH) from the anterior pituitary region. ACTH is a promoter hormone responsible for triggering the release of corticosteroids (i.e., cortisol) into circulation (Mommsen et al., 1999; Barton, 2002). Cortisol

elicits the secondary physiological responses which include energy mobilization and relocation via catabolism of carbohydrates, proteins, lipids, and the liberation of ions into the blood stream (Barton, 2002). These secondary responses can directly impact aspects of animal performance (i.e., tertiary responses) by altering their metabolic activity and respiration (Mommsen *et al.*, 1999). Collectively, an acute stress response is an adaptive and beneficial reaction to homeostatic perturbations, however, under chronic conditions, the stress response can become maladaptive resulting in whole-animal impairments (e.g., immunoincompetence), and even death. Currently, research linking angling vulnerability with the stress response axis is limited, but recent experimental research has shown that angling targets the most stress-resilient individuals of a population (Øverli *et al.*, 2005; Louison *et al.*, 2017). As such, selection for altered stressresponsiveness may result in fish populations exposed to intense fisheries pressure.

Consequently, selection pressure resulting in changes to the HPI-reactivity and/or metabolism, may also indirectly select for phenotypic changes in essential life-history traits (e.g., reproductive investment), potentially through POLS processes, resulting in fitness level impacts at the population level. To date, research into the selective capabilities of fisheries practises on physiology has been conducted under laboratory conditions, using experimental/hatchery bred fish stocks (Hessenauer *et al.*, 2015; Philipp *et al.*, 2015; Hollins *et al.*, 2018). Although this research has been paramount in shaping our current mechanistic understanding of FIE and its impacts on physiology, we still do not fully understand how this translates into wild fish stocks, under natural conditions.

1.3 Aquatic protect areas

In light of the potential of FIE from fisheries practises, there has been advocation for the development of 'evolutionary-enlightened' management strategies such as the creation of

protected areas within aquatic systems where angling is strictly prohibited, thus providing a protected sanctuary area for fish communities to re-establish a natural state (Ashley et al., 2003; Abell et al., 2007). The use of aquatic protected areas (APAs; a generic term referring to protected areas in either marine or inland waters) as a means to protect against human-induced evolutionary change is a relatively new concept. However, the implementation and use of APAs as a conservation tool (i.e., to protect and promote biodiversity) is a well-established management technique that has been used for decades, largely within marine systems (i.e., Marine Protected Areas; MPAs) (reviewed by Di Lorenzo et al., 2016; Hermoso et al., 2016). The use of APAs are largely considered beneficial as they reduce human-mediated resource uses (e.g., overfishing), reduce negative anthropogenic disturbances (e.g. habitat alteration or destruction), and allow damaged ecosystems to recover (Ashley et al., 2003; Abell et al., 2007; Suski and Cooke, 2007). Furthermore, APAs can greatly benefit the biological communities that inhabit them by increasing species diversity, population size, mean size of individuals within protected populations, and increased assemblage abundances (Watson et al., 2007; Harmelin-Vivien et al., 2008; Chu et al., In Press). Economically, APAs can also directly benefit commercial fisheries through the export of recruitment subsidies (i.e., eggs and larva) and spillover of harvestable fish to fishable waters (reviewed in Di Lorenzo et al., 2016).

In light of these benefits, global commitments, such as the Convention on Biological Diversity Aichi target 11 (CBD, 2010), have been made to increase the coverage of APAs at local, regional, and global scales in an effort to halt biodiversity loss. However, the establishment and use of APAs is largely focused within marine environments (approximate coverage area within marine environments: 2.2 million km²) as compared to freshwater environments (approximate coverage area within freshwater environments: 7989 km²), which is concerning given the fact that freshwater ecosystems are one of the most imperilled worldwide (Chape et al., 2003; WWF Global Programme, 2005). Roughly 90% of freshwater species listed on the 2004 IUCN Red List are largely under threat due to human-mediated resource uses (e.g., overfishing) and habitat degradation (IUCN, 2004; Abell at al. 2007), and greater than 70% of freshwater fish extinctions to date have been related to habitat alterations (Harrison and Stiassny, 1999; Abell et al., 2007). With continued human population growth coupled with a decline of intact/pristine freshwater ecosystems, the need for freshwater conservation efforts are at an all-time high.

Although the use of protected areas is more common in marine environments, freshwater protected areas (FPAs) have been sporadically used throughout inland lake and river systems (Abell et al., 2007; Demille 2010; Hermoso et al., 2016). However, the effectiveness and utility of FPAs are still largely debated (Abell et al., 2007; Hedges et al., 2010a; Acreman et al., 2020). Unlike marine reserves, FPAs are often small in size, active only during specific seasonal time periods, and/or are haphazardly placed within lakes and rivers without full consideration of the movement behaviours and habitat requirements of the target fish species to be protected. These factors have resulted in mixed resource management outcomes, and as a consequence, have created a paucity in the use of FPAs in resource regulation (reviewed in Acreman et al., 2020). Often the intention of FPAs is to protect biodiversity within entire ecosystems, however resource-based FPAs that target a single species are common (Hedges et al., 2010a). Specifically, the generation of FPAs to protect economically valuable species (e.g., black bass in North America) are among the most common (Demille, 2010). In Ontario, there are over 600 established FPAs, with the majority of these being seasonally active (i.e., during the black bass spawning and parental care period: May-June) (2020 Ontario Recreational Fishing Regulations

Summary). However, there are several that are active year-round, providing year-round protection.

The majority of these full-year FPAs in Ontario are located throughout the Rideau Waterway system (Ontario, Canada), and in most cases, have been active for over 70 years. Initially, these year-round FPAs were established as an experimental means to promote growth and recruitment back into declining largemouth bass populations, and protect the viability of the largemouth bass fishery that was suffering from heavy exploitation through excessive catch-andharvest (Ontario Department of Game and Fisheries Monthly Bulletin 1939). Resource managers worked with the angling community (i.e., fishing guides) to select key locations to establish FPAs within select lakes. One of the key criteria for determining where to establish an FPA was based on local knowledge of largemouth bass spawning locations (Fleming 1947; Ontario Department of Game and Fisheries Monthly Bulletin 1939). However, the usefulness of these protected areas is still highly debated. In 2006, the Fish and Wildlife Branch of the Ontario Ministry of Natural Resources (OMNR) released guidelines pertaining to the use and implementation of fish sanctuaries (i.e., FPAs), suggesting that year-round black bass FPAs are excessively restrictive and should have a standardized 'active' date (May 15-June 30) if they are needed at all (Demille 2010). However, the effectiveness of these year-round FPAs to protect black bass has remained relatively unexplored. Furthermore, the utility of these FPAs to provide indirect benefits to other fish species and/or the fish community as a whole has also largely been neglected. Thus, determining the effectiveness and utility of these long-established FPAs to provide conservation benefits is paramount to understanding their potential role as a resource management tool, and whether their continued presence is of conservation value.

To date, there has been limited investigation into the conservation benefits associated with the Rideau Waterway FPAs. Moreover, all of the research that has been conducted has focused solely on two specific FPAs (i.e., the Murphy's Bay and Darling's Bay fish sanctuaries) within one particular Rideau Waterway lake, Opinicon Lake (Elgin, Ontario). Of the few studies conducted, DeMille (2010) utilized manual radio telemetry tracking techniques in an effort to quantify the protective capacity of the Murphy's Bay FPA. More specifically, DeMille (2010) followed 12 adult largemouth bass outfitted with radio transmitters for up to 79 days during the summer open water period. Of the 12 individuals tracked, 10 received complete or partial protection throughout the monitoring period, however, 2 individuals were not found within the FPA throughout the entire monitoring period. These results highlight that the Murphy Bay FPA does not provide holistic protection to all largemouth bass inhabitants, as several of the telemetered bass exited the protective boundaries during the monitoring period. Although the radio-telemetry study conducted by DeMille (2010) was the first known study to address the fundamental question pertaining to the protective capacity of a Rideau Waterway FPA, the data were limited in scope due to the challenges associated with manual radio telemetry monitoring. Furthermore, several questions still remain regarding how protection varies with life-history stage (e.g., body size, sexual maturity, reproductive period) and across seasons, as well as within other Rideau Waterway FPAs.

Despite telemetered largemouth bass exiting the protective boundaries, some degree of protection at a population level must still occur, as more recent research has identified behavioural differences between populations of largemouth bass residing within and outside of the Opinicon Lake FPAs. Specifically, Twardek et al. (2017) observed that parental male largemouth bass within the FPAs displayed increased parental aggression during the reproductive period, and consequently, had higher angling vulnerability relative to parental males nesting within the main-lakes areas. Furthermore, outside of the reproductive period, largemouth bass inhabiting the Opinicon Lake FPAs were found to have a greater diversity of behavioural traits relative to main-lake individuals (Cooke *et al.*, 2017). Collectively, these behavioural differences have been previously identified as markers of FIE (Philipp *et al.*, 2015; Hollins *et al.*, 2018), which suggests that the FPA populations may indeed be benefitting from fisheries protection within the reserve boundaries. As such, the Rideau Waterway FPAs provide a unique opportunity to investigate the evolutionary consequences from past and current recreational fisheries practises, as well as the effectiveness of long-term FPAs to provide indirect conservation benefits to non-target species.

1.4 Largemouth bass and recreational angling

In North America, the largemouth bass (*Micropterus salmoides*) is the most highly sought after sport fish based on its reputation of being an aggressive, strong fighting, and easily accessible game fish (Siepker *et al.*, 2007). These characteristics have resulted in its rising popularity among anglers over the past century and has led resource managers to create single-resource FPAs (temporary and/or permanent) in an effort to protect largemouth bass from unsustainable fisheries exploitation. In Ontario alone, catch rates of black bass have risen greatly from 1,400,000 in 1970 to 5,189,620 in 2000 (Funnell, 2012; Hogg et al., 2010). Historically, recreational angling for largemouth bass has been primarily catch-and-harvest up until the 1970's when catch-and-release practises began to establish in Ontario (Siepker *et al.*, 2007; Funnell, 2012). Since then, catch-and-release has gained significant traction amongst the angling community, especially among sport anglers, with catch-and-release rates reaching as high as 90% in some lake systems (Hogg *et al.*, 2010; Funnell, 2012). Although catch-and-release is

widely accepted and practised today, legacy FIE effects from decades of catch-and-harvest and unmanaged exploitation could have artificially altered largemouth bass populations in heavily pressured lake and river systems (Hessenauer *et al.*, 2015; Twardek *et al.*, 2017). In addition to artificial selection from harvest, FIE may also occur in systems where catch-and-release is actively practised due to unintentional mortality and sublethal physiological consequences (e.g., osmotic imbalance and stress) associated with fish capture (Cooke et al., 2003; Siepker et al., 2007; Arlinghaus et al., 2008). FIE can also result from angling exploitation during the reproductive and parental care period of largemouth bass (Sutter *et al.*, 2012).

1.5 Habitat requirements

Largemouth bass are warm-water ambush predators that conceal themselves underneath/with habitat structure (e.g., coarse-woody debris) and wait for prey to swim by/near them before explosively engaging and consuming the prey (i.e., ram-feeding) (Brown *et al.*, 2009). Aa such, largemouth bass have a relatively small home range size (e.g., < 1 km²) that varies predictably with habitat complexity, life-stage, and body size (Lewis and Flickinger, 1967; Fish and Savitz, 1983a). Generally, the active home range size for adult largemouth bass decreases as habitat complexity (e.g., course-woody debris and vegetation) increases (Ahrenstorff *et al.*, 2009). Largemouth bass are known to emigrate out of the shallow complex littoral habitat areas into deep water basins during the cold weather months (Raibley *et al.*, 1997; Brown *et al.*, 2009). Specifically, largemouth bass are known to congregate in select deep water locations during the cold-water period, as water temperatures are warmer with higher oxygen concentrations relative to the shallow littoral habitat regions(Raibley *et al.*, 1997; Hasler *et al.*, 2009; VanLandeghem *et al.*, 2013). During the spring lake turnover, adult largemouth bass will transition back in the shallow littoral habitats in preparation for the reproductive period. Parental male largemouth bass are known to exhibit high nest-site fidelity, and can return to the same nesting locations each season, especially if the parental males were successful in raising offspring to independence in previous season(s) (Twardek *et al.*, 2016). Furthermore, female largemouth bass remain in close proximity to spawning areas and nesting sites during the reproductive period (May-June in the Rideau Waterway system; Cooke *et al.*, 2006), as females forage in the shallow littoral regions to replenish energetic reserves post-spawning. As such, it is possible for distinct subpopulations of largemouth bass to exist isolated across large lake areas (Gillis, 2018).

1.6 Parental care

The largemouth bass provides parental care (PC), where the male is solely responsible for rearing his young from the egg stage up to free-swimming independent fry; the parental care period can last up to four weeks depending on water temperatures (Cooke *et al.*, 2006). Nest-site selection is very important for brood success, if parental males choose a hostile nesting location (e.g., high predator densities, excessive light pollution, close proximity to conspecifics, etc.) the likelihood of premature nest abandonment increases (Zuckerman and Suski, 2013; Foster *et al.*, 2016; Twardek *et al.*, 2016). However, high nest-site fidelity can occur if parental males successfully rear a brood to independence (Twardek *et al.*, 2016). During this crucial life-history period, the developing brood is completely defenseless against predators and rely entirely on the nest guarding male to provide protection. Thus, parental males are required to be extremely protective of their brood, as reproductive success (i.e., brood reaching independence) is positively correlated with increased boldness and aggressive behaviours (Suski and Philipp, 2004). Research has shown that parental males can swim upwards of 40 km a day chasing nest predators without actively leaving the nest site area (i.e., 10 m² area) (Hanson et al., 2007). If the

nest-guarding male prematurely abandons his brood, or is removed temporarily, predators will enter the nest-site and consume the developing young (Zuckerman and Suski, 2013). Angling of nest-guarding males is particularly problematic for this, as angling exhaustion coupled with time off nest can increase the likelihood of premature nest abandonment events (Suski and Philipp, 2004; Zuckerman *et al.*, 2014). This can have selective impacts at the population level, resulting in parental males that are less bold and aggressive not only to fishing lures but also to potential nest predators the enter into the nest site (reviewed in Philipp et al., 2009).

1.7 Hypothesis and objectives

To date, several knowledge gaps exist pertaining to the usefulness of FPAs to provide conservation benefits. As such, the primary objective of this dissertation will be to define how spatial protection, in the form of FPAs, can influence the ecology and physiology of a heavily targeted sportfish, the largemouth bass, while concurrently investigating the utility of FPAs to provide indirect benefits to the fish community as a whole. Given that global declines in freshwater environments, and the biodiversity they support, are increasing, the need for stronger and more rigorous resource management strategies to reverse current declining trends are at an all-time high. Furthermore, the potential for unnatural selection processes through humanmediated activities may threaten the viability and resiliency of wild populations to adapt to changing environmental conditions. Thus, quantifying the conservation value associated with FPAs is of high importance from a resource management perspective. As such, this thesis will look to enhance our understanding of how spatial protection through FPAs can have populationand community-level impacts through eliminating fisheries pressure on a keystone species, the largemouth bass. Moreover, the methodological framework, as well as the conclusions derived in this thesis, could provide resource managers with a more integrative and diverse toolset to address when, where, and how best to use FPAs to benefit aquatic biodiversity.

This thesis is arranged in a logical pattern whereby I first address the community ecology benefits of long-established FPAs (Chapter 2). More specifically, I test the hypothesis that protection from fisheries pressure afforded by FPAs would result in ecological benefits to the fish community as a whole. Here, I predicted that fish abundance, biomass, and richness would be highest within FPAs relative to open-access main-lake areas. Once I had characterized the community structuring dynamics within protected and non-protected lake areas, I quantified how largemouth bass utilize an FPA by evaluating how space-use varied with body size and across seasons (Chapter 3). I tested the hypothesis that FPAs should provide a refuge area for largemouth bass due to protection from fisheries exploitation. I predicted that occupancy rates within the reserve boundaries would be highest amongst larger individuals, especially during the open-access fishing seasons. Finally, I tested the hypothesis that, due to long-term protection from fisheries pressure, certain physiological phenotypes associated with increased angling vulnerability would be present within largemouth bass population inhabiting FPAs (Chapter 4). I predicted that largemouth bass inhabiting FPAs would have greater metabolic scope, as well as lower HPI-reactivity, to an angling capture and air exposure stressor.

Chapter 2: Evidence of fish spillover from freshwater protected areas in lakes of eastern Ontario

2.1 Abstract

Research has identified numerous conservation benefits attributed to use of marine protected areas (MPAs), yet comparatively less is known about the effectiveness of freshwater

protected areas (FPAs). Here, I assessed multiple longstanding (>70 years active) intra-lake FPAs in three lakes in eastern Ontario, Canada, to evaluate their potential conservation benefits. These FPAs were initially intended to protect exploited largemouth bass (*Micropterus salmoides*, Lacépède, 1802) populations, but since their establishment there has been no empirical data collected to evaluate their effectiveness for protecting bass or the broader fish community. A comparative biological census of fish species abundance, biomass, and species richness was conducted using snorkeling surveys within FPAs, along the bordering transitions zones, and in more distant non-protected areas of the lake that had similar habitat to the FPAs. In general, the FPAs yielded benefits that were most obvious (in terms of abundance and biomass) for the focal protected species (i.e., largemouth bass) as well as several shiner species. Largemouth bass and shiner abundance and biomass was highest in the FPA, lowest in the distant non-protected areas, and intermediate in the transition zone. Species richness was also highest in the FPAs in two of the three lakes. Collectively, these results support the use of FPAs as a viable and effective conservation strategy that extends beyond simply limiting exploitation of a target species. Beyond benefits afforded to fish within the FPA, I also observed evidence of spillover in adjacent areas which is promising. Additional research is needed on the effectiveness of FPAs in a variety of regions and waterbody types facing different threats in an effort to understand when, where and how to best use FPAs to benefit aquatic biodiversity.

2.2 Introduction

Threats to freshwater habitats and the biodiversity they support are mounting in magnitude and complexity, making freshwater ecosystems among the most imperilled worldwide (Ricciardi and Rasmussen, 1999; Jenkins, 2003; Arthington *et al.*, 2016a). As such, immediate management action and regulatory intervention is needed to improve freshwater conservation,

and reverse current declining trends (Cowx, 2002; Nilsson, Reidy, Dynesius, & Revenga, 2005). One conservation strategy, commonly used within marine environments, is the establishment of protected areas (MPAs; marine protected areas) (Di Lorenzo *et al.*, 2016). MPAs are largely considered beneficial as they reduce/eliminate human-mediated resource uses (e.g., overfishing), reduce negative anthropogenic disturbances (e.g. habitat alteration or destruction), and allow for the rehabilitation of ecosystems disturbed or damaged from human-use activities (reviewed in Di Lorenzo et al., 2016). Furthermore, MPAs can greatly benefit the biological communities that inhabit them (e.g., increased biodiversity), while providing economic benefits to local commercial and recreational fisheries through the export of recruitment subsidies (i.e., eggs and larva) and spillover of harvestable fish to fishable waters (Ashworth and Ormond, 2005; Tupper, 2007; Harmelin-Vivien *et al.*, 2008).

Despite the apparent benefits of protected areas (PAs) in marine systems, they remain comparatively uncommon in the freshwater realm (Saunders *et al.*, 2002; Abell *et al.*, 2007; Cucherousset *et al.*, 2007), particularly throughout North America. However, the use of PAs in European freshwater systems has received more attention, and application, in recent years due to the European Communities Council Directives, requiring more rigorous habitat protection measures (Council of the European Communities, 1992; Bouchet, Falkner, & Seddon, 1999; Paavola, 2004). Nevertheless, the global application of freshwater protected areas (FPAs) as a conservation tool is still limited, and as a result, understudied. Indeed, there is relatively little research pertaining to the effectiveness of freshwater protected areas (FPAs) which creates uncertainty regarding their application (Finlayson, Arthington, & Pittock, 2018; Harrison et al., 2016). With declining trends in freshwater biodiversity and the rapid degradation of pristine/intact freshwater ecosystems (Dudgeon et al., 2006; Reid et al., In Press), action in the form of FPAs could be an effective conservation strategy (Abell et al., 2007; Harrison et al., 2016; Suski & Cooke, 2007).

Although the use of FPAs are relatively limited throughout inland lake and river systems of North America (Abell *et al.*, 2007; Hermoso *et al.*, 2016), their application(s) have resulted in successful outcomes (Suski & Cooke, 2007; Zuccarino-crowe, Taylor, Hansen, Seider, & Krueger, 2016). Often the intention of FPAs is to protect biodiversity within entire ecosystems, however resource-based FPAs that target a single species are common (Hedges *et al.*, 2010a). Specifically, the establishment of FPAs to protect economically valuable species (e.g., largemouth and smallmouth bass [(Micropterus dolomieu, Lacépède, 1802)] in North America; Sztramko, 1985; Suski & Cooke, 2007; Twardek et al. 2017) are among the most common applications (Watson *et al.*, 2014).

The Rideau Waterway system (Eastern Ontario, Canada) is a unique freshwater system that is comprised of multiple lakes and rivers that span from Ottawa Ontario, to the St. Lawrence River system. The majority of lakes within the Rideau Waterway system support one or multiple long-term (>70 years) single-resource FPAs. These FPAs are closed to all fisheries activities 365 days a year and were initially established as an experimental means to protect the viability of the largemouth bass fishery that was suffering from heavy fisheries exploitation through excessive catch-and-harvest (Ontario Department of Game and Fisheries, 1946). The FPAs were intended to provide an exclusion zone to promote growth and recruitment back into the declining largemouth bass populations. However, since their establishment, the effectiveness of these yearround FPAs to satisfy their primary objective (i.e., protect largemouth bass and promote recruitment) has remained relatively unexplored. Furthermore, the utility of these FPAs to provide indirect benefits to other species of fishes and/or the fish community as a whole has also largely been neglected. As such, the Rideau Waterway FPAs provide a unique opportunity to investigate the direct effects of long-term protection on an economically and culturally significant fish species (i.e., largemouth bass), as well as the potential indirect benefits of protection on the fish community as a whole.

One way to assess the benefits associated with protection is to quantify differences between the biological communities that reside inside and outside of designated PAs (Watson et al., 2014) and, as an example, spillover of fish species outside of PAs is often considered a biomarker of successful protection (Goñi et al., 2010). Previous research evaluating the effectiveness of MPAs has focused on quantifying various biological parameters including density dependent spillover of fish biodiversity, abundance, and biomass across a spatial gradient emanating outward from the MPA up to several kilometers from the protected area boundaries (Rakitin and Kramer, 1996; Ashworth and Ormond, 2005). Often, successful MPAs show gradient effects (i.e., spillover), where fish diversity, abundance, and biomass decrease as distance from the MPAs increases (Tupper, 2007; Harmelin-Vivien et al., 2008). From a fisheries perspective, spillover of fishes (juveniles and/or adults) is considered a key feature of an effective and successful protected area, where the export of economically valuable species of fishes outside of MPAs can result in a continuous and renewable source population(s) for commercial and recreational fisheries (Di Lorenzo et al., 2016). Through direct comparisons of fish community parameters between PAs and adjacent non-protected areas, one can accurately quantify benefits at the individual, population, and community levels that may be linked, directly or indirectly, with the protection provided.

Employing techniques previously used to evaluate PAs in marine systems, the objective of this study was to evaluate the effectiveness of long-standing (i.e., since the 1940s) FPAs
evidenced by direct assessment of spillover of species of fishes into fishable waters. I hypothesized that fish abundance, biomass and richness would be highest in the FPAs, lowest in areas of similar habitat but distant from FPAs, and intermediate in the areas immediately outside of PAs, indicative of spillover effects similar to PAs in the marine environments. Assessments were replicated across three interconnected lakes with similar fish communities, each containing a combination of PAs and non-protected waters.

2.3 Methods

2.3.1 Study sites:

Three interconnected lakes throughout the Rideau Waterway system, Ontario, Canada, were used for this study: Lake Opinicon, Newboro Lake, and Big Rideau Lake. Each of these lakes have one or more long-standing (i.e., >70 year) intra-lake FPA that provide year-round protection from fishing activity (Figure 2.1). The placement of the FPAs within each of the study lakes were based upon historic knowledge of spawning locations for largemouth bass, provided from anecdotal observations by local fishing guides and resource managers (Ontario Department of Game and Fisheries, 1946). All lakes have active recreational fisheries (both catch and release and harvest) for a variety of species of fishes including, but not limited to, black basses (i.e., collective term for both smallmouth bass and largemouth bass), northern pike (*Esox lucius*, Linnaeus, 1758), bluegill (Lepomis macrochirus, Rafinesque, 1810), and yellow perch (Perca flavescens, Mitchill, 1814). These lakes are also subject to intermittent small-scale commercial fishing activity that targets mainly 'pan-fish' (e.g., bluegill and pumpkinseed (Lepomis gibbosus, Linnaeus, 1758), yellow perch, black crappie (Pomoxis nigromaculatus, Lesueur, 1829) and brown bullhead (Ameiurus nebulosus, Lesueur, 1819)(Hogg et al., 2010; Larocque et al., 2012) all such fishing activities, both commercial and recreational, are prohibited inside the FPAs, and

have been since their inception. Lake Opincon (~8.66 km²) houses two separate FPAs with an approximate combined protection area of 1.0 km². Newboro Lake (~17.01 km²) also has two separate FPAs with an approximate combined protection area of 3.33 km². Big Rideau Lake (~45.36 km²) has one designated FPA with an approximate protection area of 0.57 km² (Figure 2.1). These long-standing protected areas are easily identifiable from the water (i.e., well maintained signage posted at each entrance way and along the bordering transition zones between the FPAs and neighbouring waters, as defined below), as well as from navigation and/or fishing maps. Furthermore, these FPAs are actively patrolled and enforced by the Ontario Ministry of Natural Resources and Forestry (OMNRF) with assistance in reporting of infractions by the public to ensure fishing activity does not occur within their boundaries.

2.3.2 Visual censuses:

Fish species richness, abundance, and size (estimated to within a \pm 2cm error) were recorded by snorkelers conducting visual surveys along standardized transects within the littoral regions of each study lake. Transects were established within three zones of each lake. The three lake-zones were designated as (1) entirely within the FPAs, (2) within the bordering transition zone immediately adjacent to the FPA boundaries, which I defined as the area of water/habitat extending outward up to 2 km from a FPA border, and (3) outside in fished areas, which I defined as lake area that extended beyond the transition zone (i.e., >2 km from FPAs). Establishing the transition zones as a 2 km lake/habitat area enabled us to account for the home range size of largemouth bass (i.e., <1 km²; Lewis and Flickinger, 1967; Ahrenstorff *et al.*, 2009), reducing the potential confound of quantifying transient fish that may be long-term inhabitants of either the FPA or outside fish lake area. Establishing three distinct lake-zones to survey in this manner allows for informative evaluations of the effectiveness of these FPAs as a conservation tool, through the assessment of ecological spillover and/or changes in fish community structure between lake-zones.

All snorkeling surveys were conducted within the month of July, 2017. July was selected as the ideal time period to evaluate the protective potential of the FPAs for several reasons; (1) largemouth bass have completed their spawning and parental care period by the end of June in the Rideau Waterway system (Cooke et al., 2006), reducing the potential bias associated with nest site habitat preferences (i.e., increased abundance of reproductively active fishes in the shallow littoral regions; Brown, Runcimen, Pollard, Grant, & Bradford, 2009) and associated nest-site fidelity (Twardek et al., 2017); (2) recreational fisheries pressure is greatest during the month of July throughout the Rideau Waterway system (Hoyle, 1990; Sheridan & Krishka, 1995), so the effect of protection afforded by the FPAs should be most detectable during this time period (i.e., catch-and-harvest and post-release mortality rates should be highest during July). To minimize any potential biases in sampling locations, all transects were established within the shallow littoral regions of each of the lake-zones. Furthermore, survey times were systematically randomized between lake-zones, following a specified temporal sampling effort per lake-zone approach. Specifically, lake-zones were surveyed in 4 hour time blocks (i.e., morning [8:00am - 12:00pm], afternoon [12:00pm - 4:00pm], and evening [4:00pm - 8:00pm]) starting in a randomly selected lake-zone and alternating through the remaining lake-zones systematically. Randomizing survey times and locations in this manner reduces any potential spatial and temporal effects that may influence fish behaviour and habitat selection (Cooke, Steinmetz, Degner, Grant, & Philipp, 2003). Collectively, 173 transects were surveyed across the three replicate lakes. In Big Rideau Lake, 62 transects were surveyed (n=25 within the FPA, n=17 within the transition lake-zone, and n=20 within the outside fished lake-zone). In Lake

Opinicon, 46 transects were surveyed (n=15 within the FPAs, n=17 within the transition lakezone, and n=14 within the outside fished lake-zone). In Newboro Lake, 63 transects were surveyed (n=24 within the FPAs, n=23 within the transition lake-zone, and n=16 within the outside fished lake-zone). All surveys were conducted under strict pre-set criteria to standardize observation effort and duration. Specifically, all transect dimensions were standardized to be 100 m in length × 5 m in width, snorkeler observation effort was restricted to 10 minutes per transect, and the same snorkelers were used throughout the duration of the study. In addition, all snorkelers validated observations under 'practise' conditions which entailed comparative survey assessments of species identification, length estimations of fishes (various species) to within a \pm 2 cm error, vegetation complexity assessments to within \pm 10% variance, water depth to within \pm 10 cm variance, and consistent substrate composition assessment.

During each transect survey, all fishes encountered were identified to species except for certain species of Cyprinidae that were too difficult to accurately differentiate underwater from a distance (e.g., blackchin shiners [*Notropis heterodon* (Cope, 1865)] vs. blacknose shiners [*Notropis heterolepis* (Eigenmann & Eigenmann, 1893)]). Based on the underwater visual identification difficulty of Cyprinidae and their known diversity within each of the study lakes, the identification of species of Cyprinidae was broken down as such: shiner (including common shiner [*Luxilus cornutus*, (Mitchill, 1817)], golden shiner [(*Notemigonus crysoleucas*, (Mitchill 1814)], blackchin shiner, and blacknose shiner); common carp (*Cyprinus carpio*, Linnaeus, 1758), dace (*Chrosomus* spp.); and chub (*Semotilus spp. & Couesius* spp.). Grouping the members of the Cyprinidae family in this way allowed for a coarse assessment of their diversity, abundance, and biomass across lake zones. Furthermore, fishes that were observed during a transect survey, but were unable to be identified to a definitive genus or family group, were

recorded and categorized as '*unknown*'. This group of fish were included in abundance analyses; however, they were not included in species richness or biomass assessments.

Actual numbers of fishes were counted and recorded individually, however when large schools of fish were encountered, snorkelers would estimate abundance using count intervals of 10, a method similar to what has been proposed in the literature (Harmelin-Vivien et al., 2008). The size of each fish observed was recorded to within a 2 cm error. Snorkelers calibrated fish size by estimating the lengths of fishes along practise transects (i.e., visually estimating stationary and mobile fishes), and estimating the lengths of known objects (e.g., PVC tubing, submerged logs, etc.). Furthermore, snorkelers drew measuring sticks (15 cm in length) on data slates (i.e., ~ 30 cm x 15 cm CPVC sheets that enabled underwater data recording), to provide a reference for measurements during surveys if needed. Surveys only commenced once size estimation error was consistently within + 2 cm between snorkelers. Validating sampling error in this manner allowed for consistency in the fish parameter data collected, reducing any potential biases between snorkeler observations. Inherent biases and sampling error can arise from visual estimates of fish parameters (e.g., length and abundance), especially when fishes are mobile or staged at a distance from the observer making accurate visual assessments difficult (Jennings and Polunin, 1995). However, underwater visual censes (UVC) can produce relatively accurate data (e.g., 86% accuracy in length measurements, and 91.6% accuracy in abundance counts; St John, Russ, & Gladstone, 1990), especially when observers standardize visual sampling error and effort. As such, UVC methods can produce consistent and reliable data for comparative evaluations (St John et al., 1990; Macpherson et al., 2002; Harmelin-Vivien et al., 2008).

Due to the high proportionality between length and weight within most freshwater fishes (Schneider *et al.*, 2000), fish biomass for select species was calculated using pre-established

length-weight data generated from existing Rideau Lakes population data as well as Great Lakes populations (Lawrence, Godin, & Cooke, 2018; Schneider et al., 2000; see Appendix A for details). Specifically, weight (g) data for largemouth bass, pumpkinseed, bluegill, yellow perch, and shiners was calculated for biomass comparisons. Due to difficulties in accurate underwater identification of certain shiner species, all shiners were grouped and analyzed collectively for biomass and abundance assessments. The length-weight ratio for common shiner was used as a proxy ratio to calculate shiner biomass (g) in order to provide a quantifiable, and comparable, index biomass score between lake-zones. The length-weight ratio for common shiner was chosen based on the ubiquity of this species throughout each of the replicate study lakes. It is important to note that the grouped shiner species are not monophyletic in origin. As such, grouping shiner species in this manner may create bias in the biomass values between lake-zones depending on the true diversity of shiners observed within each transect/lake-zone. However, the length-weight relationship for common shiner within the study region is well described in the literature (Schneider et al., 2000), whereas length-weight data for other shiner species (i.e., blackchin and blacknose shiners) were not available. Therefore, grouping and analyzing the biomass data for the grouped shiner species in this manner, using the common shiner length-weight data as a proxy, enabled for a coarse scale evaluation of shiner assemblage biomass between lake-zones.

Habitat structure and complexity was also assessed within each transect surveyed, as these factors can influence small-scale temporal and spatial variability of fish species (Randall *et al.*, 1996). Several habitat features were measured including: vegetation complexity comprising emergent vegetation, submergent vegetation, and coarse woody debris (CWD) coverage (based on percent scale out of 100), water depth (m), and substrate composition. Substrate was categorized as organic matter (OM), rock (R), sand (S), and gravel (G). If mixed substrates were present during the survey, they would be denoted to reflect the combination of substrate materials present (e.g., organic material and rock = OM/R). All habitat features were measured at three standardized locations including 0 meters (beginning of transect), 50 meters (middle of transect), and at 100 meters (end of transect) along each transect surveyed. At each of these locations, habitat parameters were measured within the immediate vicinity of the snorkeler (~5 m^2); vegetation complexity and CWD were measured as the percent coverage of macrophytes, and CWD within the water column, respectfully (e.g., 50% = half of water column filled by macrophytes and CWD). Substrate composition and water depth were analyzed directly below the snorkeler.

2.3.3 Data analysis; fish community composition and species richness

To define differences in fish communities between lake-zones (i.e., FPAs, transition zones, and outside fished zones), a multivariate approach was employed. Due to the potential differences for fish communities between each of the replicate study lakes (as a result of differing abiotic/biotic factors), community composition and species richness were analyzed independently btween lake zones within each replicate study lake. Specifically, non-metric multidimensional scaling (NMDS) ordination with analysis of similarities (ANOSIM) and similarity percentages (SIMPER) were used to compare fish community composition scores between lake-zones (following similar methods employed by Midwood *et al.*, 2016). Mean abundance scores of observed fish species per transect/per zone were used for community composition, as species abundance can vary greatly due to density dependent/independent processes (i.e., predator burden and exploitation). The NMDS ordination allowed for visualization of the data, whereas the ANOSIM determined whether statistically significant

differences occurred in community composition between lake-zones. The SIMPER provided a species-specific (except for shiner species as they were grouped together prior to analysis) *post-hoc* analysis to evaluate which species were driving the differences in community composition detected based on their mean abundance. Following the methodology of Midwood *et al.*, 2016, only species that exhibited an arbitrary dissimilarity proportion greater than 5% were interpreted and evaluated further, as this cut off percentage reflected a meaningful dissimilarity proportion from an analytical perspective. A Bray-Curtis distance measure was applied to the non-transformed mean abundance data for all analyses conducted, as the Bray-Curtis function is designed to find a stable solution based on the global optima using numerous random starting points (Oksanen et al., 2013).

The input matrix contained the total abundance data for 13 species/species groups from each lake-zone including largemouth bass, bluegill, pumpkinseed, yellow perch, shiner, black crappie, brown bullhead, dace, common carp, rock bass (*Ambloplites rupestris*, Rafinesque, 1817), northern pike, chub, and unknown. For species of fishes that were determined to contribute to differences in community composition, a non-parametric Kruskal-Wallis (KW) test paired with a Mann-Whitney *post-hoc* analysis was conducted to determine if there were statistically significant differences in mean abundances between lake zones. Species richness between lake-zones was analyzed using a one-way analysis of variance (ANOVA) comparing the mean number of species detected per transect within each lake-zone. A Tukey's *post-hoc* analysis was used to differentiate statistically significant differences. The ANOSIM and SIMPER analyses were conducted using the statistical software package PAST 3.14 (Hammer *et al.*, 2009), whereas the NMDS was completed using the metaMDA function in the *vegan* package (Oksanen *et al.*, 2013) in RStudio (RStudio: Integrated Development for R. RStudio, Inc., Boston, MA). ANOVA, KW, Tukey and Mann-Whitney *post-hoc* analyses were completed using the statistical software package JMP 13 (SAS Institute, Cary, NC, USA). Statistical significance was set at (α) = 0.05 for all analyses and all values are reported as mean <u>+</u> standard error (SEM) where appropriate.

2.3.4 Data analysis; fish parameter evaluations

To evaluate the effectiveness and utility of the Rideau Waterway FPAs, fish abundance and biomass data were compared across zones (i.e., FPAs, transition zones, and outside fished zones) using a Residual Maximum Likelihood (REML) fitting of a mixed model regression. Separate models were run for fish abundance and biomass, and each model contained zone as a single fixed effect (FPA, transition zone, and outside fished zone), along with lake [Big Rideau Lake (BR), Newboro Lake (NB), and Opinicon Lake (OP)] as a random effect. This use of 'lake' as a random effect allowed us to compare patterns in response variables (e.g., fish abundance) across the three zones, while accounting for inter-lake differences (Zar, 1999). Post-hoc analyses using a Tukey's test were conducted to differentiate statistical trends in the abundances and biomass of species of fishes between lake-zones. Abundance data were analyzed as a continuous data-type with a Poisson distribution as abundance data were counts. Biomass data were analyzed as a continuous data-type with a normal distribution. All analyses were completed using the statistical software package JMP 13 (SAS Institute, Cary, NC, USA). Statistical significance was set at (α) = 0.05 for all analyses, and all values are reported as mean \pm standard error (SEM) where appropriate.

2.3.5 Data analysis; habitat analyses

To understand the potential mechanisms underpinning differences in fish community parameters it was necessary to determine whether habitat, and temporal sampling effort, were consistent across the zone-specific transects. Sampling time blocks within and between lakezones (within each replicate lake) were compared using a Wald Chi-Squared Test. The proportion of vegetation (i.e., vegetation complexity) and water depth were compared within and between transects across lake-zones using Generalized Linear Models (GLMs). Nominal Logistic Regression analyses were used to analyze substrate composition between lake-zones, as substrate composition was collected as categorical data. For these GLMs and Nominal Logistic Regression analyses, lake-zone (i.e., within the FPA, transition zone, and outside fished zone) and location of habitat score (i.e., 0, 50, and 100 m) were entered as dependent variables, and proportion vegetation and transect water depth were entered as independent variables. Also, because the data type for vegetation measurements were proportions, GLMs for habitat analyses were run using a binomial distribution. Conversely, the data type for depth was continuous, and, as such, depth GLMs were run under a normal (Gaussian) distribution. Both habitat and depth GLMs were constructed to account for potential overdispersion in the datasets. Due to the habitat variability that naturally occurs between lake systems, all habitat data were analyzed on an individual lake level.

2.4 Results

2.4.1 Fish community comparisons

The NMDS output suggests there are distinct communities among replicate lakes, particularly Big Rideau Lake relative to Lake Opinicon and Newboro Lake (Figure 2.2). Within Big Rideau Lake, fish community composition was significantly different across all lake-zones (ANOSIM, P<0.001; R²=0.183; Table 2.1), whereas no differences in community composition across lake zones were detected within Newboro Lake or Lake Opinicon (ANOSIM, P>0.05 for all analyses). The SIMPER analysis for Big Rideau Lake suggests fish species differences were mainly driven by the mean abundance of shiners, bluegill, yellow perch, and pumpkinseed between all zone pairings, and mean abundance of largemouth bass only between the FPA and outside fished lake-zone pairing (Table 2.1). However, statistically significant differences were only detected between shiners, largemouth bass, and bluegill (KW; $X^{2}_{(3)}$ = 15.09, *P*<0.0001; $X^{2}_{(3)}$ = 36.17, *P*<0.0001; $X^{2}_{(3)}$ = 8.638, *P*<0.05, respectively). *Post-hoc* analyses reveal that shiner abundance was significantly higher within the FPA zone, as compared to the outside fished zone. Similarly, both largemouth bass and bluegill abundance were significantly greater both within the FPA and the bordering transition zone, as compared to the outside fished zone (Figure 2.3).

Species richness was found to be significantly different between lake-zones across Big Rideau Lake, Newboro Lake, and Opincion Lake (ANOVA, df=2, F=9.447, P<0.001; df=2, F=4.210, P<0.05; df=2, F=3.252, P<0.05, respectively; Table 2.2). For Big Rideau Lake, posthoc analyses indicate that species richness was significantly greater within the FPA and bordering transition zones, as compared to the outside fished zone. Conversely, within Newboro Lake, post-hoc analyses reveal species richness to be greater within the outside fished lake-zone as compared to within the FPAs. Within Opinicon Lake, post-hoc analyses reveal a greater species richness within the FPAs, as compared to the outside fished lake-zone (Figure 2.4).

2.4.2 Fish abundance and biomass comparisons

Abundance and biomass of both largemouth bass and shiners was found to be significantly different between FPAs and outside fished lake-zones (Fixed Effect Test, F = 5.013, P<0.01; F = 4.556, P<0.05 for abundance; F = 10.993, P<0.0001; F = 4.624, P<0.05 for biomass) across all replicate lakes. *Post-hoc* analyses indicate that largemouth bass abundance was significantly greater within FPAs, as compared to outside fished zones (Figure 2.5 a). Similarly, largemouth bass biomass was found to be significantly greater within FPAs, as compared to both the bordering transition zones as well as the outside fished zones (Figure 2.5 b). Shiner abundance and biomass were significantly greater within FPAs, as compared to both the bordering transition zones as well as the outside fished zones (Figure 2.5 a, b). No statistically significant differences in the abundance or biomass were detected between lake-zones for pumpkinseed, yellow perch, or bluegill (Fixed Effect Test, P>0.05 for all analyses).

2.4.3 Habitat and sampling effort comparisons

Results produced from the Wald Chi-Squared analyses indicate no differences in temporal sampling effort between lake-zones within any of the replicate lakes (P>0.05 for all analyses; Table 2.3). No differences were found in the proportion of vegetation cover between lake-zones within any lake (P>0.05 for all analyses; Figure 2.6 a, Table 2.4). Furthermore, no differences in lake-zone transect depths were detected within Big Rideau Lake (P>0.05 for all analyses; Figure 2.6 b, Table 2.5). However, small differences in transect depth were detected within Newboro Lake and Opinicon Lake. Within Newboro Lake, transect depth was approximately 0.25 m deeper within the transition zone compared to the depths within both the FPA and outside fished zones (GLM, $X_2^{(3)}=17.002$, Prob> $X_2^{(3)}= 0.030$; Figure 2.6 b, Table 2.5). Within Opinicon Lake, transect water depth was approximately 20 cm deeper in the outside fished zones as compared to the FPAs and transition zones (GLM, $X_2^{(3)}=18.020$, Prob> $X_2^{(3)}$ <0.001; Figure 2.6 b, Table 2.5). Based on nearly all substrate measurements consisting of primarily OM, no differences were detected for substrate composition between lake-zones (P>0.05 for all analyses; Table 2.6).

Zone Species Avg. B Contributio Avg. Avg. A **Comparisons** Dissimilarity n (A) Transition 72.97 Shiner 55.5 15.8 23.78 (B) Outside Bluegill 45.1 13.4 19.46 fished Yellow perch 21.5 3.85 17.43 (A) FPA 71.11 Shiner 83.7 15.8 35.85 (B) Outside Bluegill 32.6 13.4 13.61 fished Yellow perch 14.1 3.85 8.72 Largemouth 11.2 0.9 6.65 bass Pumpkinseed 10.8 6.95 5.42 (A) FPA 83.7 63.74 Shiner 55.5 28.98 (B) Transition Bluegill 32.6 45.1 13.65 Yellow perch 14.4 21.5 11.49

Table 2.1: Output from similarity percentages (SIMPER) analyses for Big Rideau Lake showing overall dissimilarity of mean species abundances between each zone pairing. Note that only species with contributing dissimilarity values greater than 5.0% are represented. Zone pairings are organized from highest to lowest for dissimilarity scores.

The Avg. A represents the mean abundance for each species found in the specified zone listed first. The Avg. B represents the same metric for the zone listed second.

Table 2.2: ANOVA of mean species richness of fishes observed per transect within each lake zones across each of the replicate study lakes including Lake Opinicon (OP), Big Rideau Lake (BR), and Newboro Lake (NB).

Lake	Inside FPAs	Transition zone	Outside fished zones	F	Р
OP	4.800	4.588	3.930	3.252	0.048
BR	4.320	3.882	3.150	9.447	<0.001
NB	3.875	4.087	4.812	4.210	0.019

Table 2.3: Output from the Wald Chi-Square analyses testing for temporal differences in survey effort between lake-zones within each of the replicate lakes including Lake Opinicon (OP), Big Rideau Lake (BR), and Newboro Lake (NB). Lake-zones include the freshwater protected areas (FPAs), the transition zone bordering the FPAs, and the outside fished lake areas (>2 km from a FPA border).

Lake	Fixed Effect	Degrees of freedom	Wald X ² (3)	Prob> X ² ₍₃₎	Sig.
OP	Zone	2	3.509	0.173	ns
BR	Zone	4	8.516	0.074	ns
NB	Zone	4	8.794	0.066	ns

Table 2.4: Output from GLM analysis for differences in mean transect vegetation complexity per lake-zone, across each replicate lake. Abbreviations for lakes include Opinicon Lake (OP), Big Rideau Lake (BR), Newboro Lake (NB). For each of the replicate lakes, the Whole Model Test for differences in mean transect vegetation complexity was not significant, thus no post-hoc analyses were conducted.

Lake	Fixed Effect	Degrees of	$X^{2}_{(3)}$	Prob> X ² ₍₃₎	Sig.	
		freedom				

OP	Zone	2	2.797	0.247	ns
	Location	2	0.627	0.730	ns
	Zone x Location	4	0.336	0.987	ns
Whole Model Test		8	3.722	0.881	ns
BR	Zone	2	2.890	0.236	ns
	Location	2	1.533	0.464	ns
	Zone x Location	4	0.711	0.950	ns
Whole Model Test		8	5.472	0.706	ns
NB	Zone	2	1.319	0.517	ns
	Location	2	0.599	0.741	ns
	Zone x Location	4	0.184	0.996	ns
Whole Model Effect		8	2.053	0.979	ns

Table 2.5: Output from GLM analysis for differences in mean transect water depth per lakezone, across each replicate lake. Abbreviations for lakes include Opinicon Lake (OP), Big Rideau Lake (BR), Newboro Lake (NB). As the Whole Model Test for differences in mean transect water depth for both OP and BR were not significant, no post-hoc analyses were conducted. However, for NB the Whole Model Test was significant, thus post-hoc analyses were conducted.

Lake	Fixed Effect	Degrees of freedom	X ² (3)	Prob> X ² ₍₃₎	Sig.
OP	Zone	2	18.020	<0.001	***
	Location	2	0.607	0.738	ns
	Zone x Location	4	1.735	0.784	ns
Whole Model Test		8	20.063	0.010	*

BR	Zone	2	9.029	0.011	*
	Location	2	0.698	0.705	ns
	Zone x Location	4	1.525	0.822	ns
Whole Model Test		8	11.445	0.177	ns
NB	Zone	2	14.619	< 0.001	***
	Location	2	2.457	0.292	ns
	Zone x Location	4	0.135	0.998	ns
Whole Model Test		8	17.002	0.030	*

Table 2.6: Output from Nominal Logistic Regression analysis for differences in substrate composition per lake-zone, across each replicate lake. Abbreviations for lakes include Opinicon Lake (OP), Big Rideau Lake (BR), Newboro Lake (NB). For each of the replicate lakes, the Whole Model Test for differences in mean transect vegetation complexity was not significant, thus no post-hoc analyses were conducted.

Lake	Fixed Effect	Degrees of freedom	X ² (3)	Prob > X ² ₍₃₎	Sig.
OP	Zone	4	7.013e ⁻⁶	1.000	ns
	Location	4	6.873e ⁻⁶	1.000	ns
	Zone x Location	8	9.701e ⁻⁶	1.000	ns
Whole Model Test		16	8.868	0.918	ns
BR	Zone	6	8.696e ⁻⁶	1.000	ns
	Location	6	9.843e ⁻⁶	1.000	ns
	Zone x Location	12	2.767	0.997	ns
Whole Model Test		24	16.187	0.881	ns

NB	Zone	6	5.254	0.511	ns
	Location	6	3.157	0.789	ns
	Zone x Location	12	3.909	0.985	ns
Whole Model Effect		24	20.590	0.662	ns



Figure 2.1: Maps of the three replicate study lakes including Opinicon Lake (a), Big Rideau Lake (b), and Newboro Lake (c). The freshwater protected areas (FPAs) are designated by red shading, with a solid red line delineating the FPAs borders. For Opincon Lake and Newboro Lake that have two designated FPAs each (distinguished by 'A' and 'B', respectively), the data collected from each FPA were pooled together to provide a holistic representation of the protective potential provided by FPAs within each lake system.



Figure 2.2: Non-metric multidimensional scaling output of fish community composition based on species abundance scores. The open circles represent the sample scores. Ellipses represent the 95% confidence intervals. The black ellipses represents the fish community composition score for Big Rideau Lake, whereas the red circle represents Newboro Lake, and the blue ellipses represents Opinicon Lake. Note that Ellipses that do not overlap represent distinct fish community compositions.



Figure 2.3: Differences in species abundances between lake-zones within Big Rideau Lake. Lake-zones include the freshwater protected area (FPA), the transition zone bordering the FPA (<2 km from a FPA border), and the outside fished lake area. The species represented in the figure were selected for Kruskal-Wallis analysis based on their contribution to the dissimilarity of community composition between lake-zones within Big Rideau Lake. Error bars represent the standard error of the abundance means calculated from transect censuses within each zone; n = 25 within the FPA, n = 20 within the outside fished zone, and n = 17 within the bordering transition zone. Dissimilar letters (a and b) above the error bars denote statistically significant differences between groups (P<0.05).



Figure 2.4: Differences in species richness between lake-zones (i.e., outside fished zones, transition zones, and freshwater protected areas [FPAs]) across each of the three replicate lakes including Lake Opinicon (OP), Big Rideau Lake (BR) and Newboro Lake (NB). Using real time visual assessments via snorkeling censes, 62 transects in BR, 63 transects in NB, and 46 transects in OP were evaluated. All transects were located within permanent freshwater protected areas (blue bars), outside of protected areas (red bars) or within bordering transition zones adjacent to freshwater protected areas (<2 km from a FPA border; yellow bars). Dissimilar letters (a and b) above the vertical error bars denote statistically significant differences between groups (P<0.05).



Figure 2.5: Differences in fish species abundance (a) and biomass (b) between lake-zones (i.e., outside fished zones, transition zones, and freshwater protected areas [FPAs]), based on pooled data from all replicate lakes including Lake Opinicon, Big Rideau Lake, and Newboro Lake. Error bars represent the standard error of the abundance (a) and biomass (b) means calculated from pooled transect data; n = 64 within FPAs, n = 57 within transition zones, and n = 50 within outside fished zones. Dissimilar letters (a and b) above the vertical error bars denote statistically significant differences between groups (P<0.05).



Figure 2.6: Vegetation score (a), and transect depth (b), for transects between lake-zones (i.e., outside fished zones, transition zones, and freshwater protected areas [FPAs]) examined by snorkeling census across replicate lakes including Lake Opinicon (OP), Big Rideau Lake (BR) and Newboro Lake (NB). Using real time visual assessments via snorkeling censes, 62 transects in BR, 63 transects in NB, and 46 transect in OP were evaluated. All transects were located within permanent freshwater protected areas (blue bars), the transition zone bordering the FPAs

(<2 km from a FPA border; yellow bars), or within outside fished zones (red bars). Dissimilar letters (a and b) above the vertical error bars denote statistically significant differences between groups (P<0.05).

2.5 Discussion

2.5.1 Fish community composition and species richness

The FPAs in the Rideau Waterway system were initiated in the 1940s to protect a subset of the largemouth bass population from fisheries exploitation, and to promote recruitment, yet, until recently, there has been little effort to assess their effectiveness in protecting the initial focal species (largemouth bass), or the potential benefits afforded to the broader fish community. Here, I quantified the effectiveness of FPAs in three interconnected lakes within the Rideau Waterway system with the goal of defining the potential benefits of FPAs in freshwater temperate systems. The NMDS output suggested that there were distinct fish species assemblages among replicate lakes, particularly Big Rideau Lake relative to Lake Opinicon and Newboro Lake, which supported the independent assessment of fish species composition and richness within each of the three replicate lakes. From the ANOSIM analyses, Big Rideau Lake was the only lake where species composition was statistically different between lake-zones. Specifically, the abundance of shiners, bluegill and largemouth bass were significantly higher inside both the FPA and bordering transition zone, as compared to the outside fished lake-zone, despite no difference in habitat features measured across all sample locations (Figure 2.3). These results indicate a spillover of target (largemouth bass) and non-target fish (bluegill and shiner) species emanating outward from the Big Rideau Lake FPA. Given the relatively small home range sizes of largemouth bass and bluegill, these data would suggest that these populations may be at their maximum density within the Big Rideau Lake FPA. However, a more holistic telemetry-based study tracking space-use patterns of fishes within FPA(s) would be invaluable in providing empirical data to confirm/track residency rates. For fish spillover to occur from a PA, it is a pre-requisite that the PA is 'filled' to facilitate the outflow of fish into non-protected zones (Tupper, 2007; Goñi *et al.*, 2010). Spillover events are largely the result of density-dependent processes (e.g., intra-specific competition for resources), and can reflect, in part, the status and health of an ecosystem (Di Lorenzo et al., 2016).

As largemouth bass are one of the most highly targeted sport fish in Big Rideau Lake (Hoyle, 1990; Hogg et al., 2010; Sheridan & Krishka, 1995), the decline in fish numbers emanating outward from this FPA could be a direct response to protection, which has been similarly observed in recreationally targeted marine fish (Westera et al., 2003). This trend could also be related to other non-accounted for factors including, but not limited to, increased forage availability (e.g., increased abundance of shiners and bluegill inhabiting the Big Rideau Lake FPA and bordering transition zone). Similarly, bluegill are also popular sport fish within Big Rideau Lake (Hoyle, 1990; Hogg et al., 2010; Sheridan & Krishka, 1995), and greater density of bluegill within the FPA and transition zone could be the result of protection. It is also possible that the higher numbers of both largemouth bass and bluegill could be related to unique predatorprey interactions. Largemouth bass-bluegill assemblages are often held in check by both species, due to a balancing predator-prey dynamic (Savino and Stein, 1982; Hambright et al., 1986). More specifically, bluegill are a fundamental prey resource for largemouth bass, but are also a key nest-predator during their reproductive period (Cooke et al., 2006; Zuckerman and Suski, 2013). If the density of reproductively active largemouth bass is higher within the FPA and transition zone, it could promote a greater abundance of nest predators (i.e., bluegill) due to increased potential food availability. As nest-site fidelity is highly correlated to reproductive success in largemouth bass, coupled with relatively small home range sizes for both largemouth

bass and bluegill (i.e., <250 m² for bluegill, and <1 km² for largemouth bass; Fish and Savitz, 1983; Ahrenstorff *et al.*, 2009), relief from targeted fisheries pressure over time could allow for a greater proportional abundance of both species within the FPA, and also within the bordering transition zone as a result of density-dependent spillover (Abesamis, Russ, & Alcala, 2006; Halpern, Lester, & Kellner, 2010).

Since shiners are not targeted by conventional recreational fisheries (i.e., rod-and-real angling), only via commercial practises (e.g., collected via netting techniques for live-bait markets) within Big Rideau Lake (Hogg *et al.*, 2010; Larocque *et al.*, 2012), it is not certain why this grouped assemblage of species would be in greater abundance within the FPA and transition zone boundaries, especially when risk of predation is significantly higher (i.e., greater density of largemouth bass within FPAs and bordering transition zones; Figure 2.4). In marine systems, fisheries exploitation has been shown to alter community composition and species assemblages (Côté, Mosqueira, & Reynolds, 2001; Dulvy, Freckleton, & Polunin, 2004; Westera, Lavery, & Hyndes, 2003). Specifically, Watson, Harvey, Kendrick, Nardi, & Anderson, (2007) found a variable response in the abundance of non-targeted prey fish species between MPAs and fished areas, indicating that fisheries exploitation of certain top-predator fish species can disrupt food web dynamics. It is also possible that differences in resource availability may occur between these lake-zones but were not accounted for in the present study (e.g., food resources).

The state of shoreline development could also potentially influence species composition and abundances, especially for species sensitive to habitat perturbations (Schneider, 2002; Pusey and Arthington, 2003). Degradation of the terrestrial riparian vegetation zone(s) can reduce a shoreline buffering capacity to inhibit contaminated runoff (e.g., pesticide laden rainwater) from entering lakes and rivers (Wenger, 1999). Extensive shoreline development is prominent throughout the Rideau Waterway area, largely due to infrastructure development (e.g., waterfront cottage/home construction). Through anecdotal observation, the focus of the shoreline development has been concentrated outside of FPAs, which could differentially impact species composition dynamics between zones (Bryan and Scarnecchia, 1992; Scott, 2006; Seitz et al., 2006). However, the relationship between shoreline status (i.e., developed or natural) and fish community dynamics can be context and species dependent. Chu, Ellis, & Kerckhove, (2018) conducted a large-scale evaluation of the conservation benefits provided by terrestrial protected areas (TPAs) on fish communities inhabiting adjacent aquatic systems and found that TPAs provide marginal benefits to lake fish assemblages. Furthermore, small-bodied fishes including common shiner and golden shiner, were found in greater densities outside of TPA boundaries (Chu et al., 2018). Despite standardizing intra and inter-transect habitat variables (i.e., vegetation complexity, depth, and substrate composition) in the current study, shoreline development was not accounted for in the study design. Nevertheless, it is entirely possible that this shoreline development is an important factor in indirectly influencing differences in fish community assemblage dynamics between lake-zones.

Species richness was also found to differ statistically between lake-zones within each replicate lake. Within Opinicon Lake, species richness was highest inside the FPAs, intermediate within the bordering transition zones, and lowest within the outside fished lake-zones (Figure 2.4). A similar trend was also detected within Big Rideau Lake, where species richness was significantly greater both within the FPA and bordering transition zone, as compared to the outside fished lake-zone (Figure 2.4). Similar to community composition differences detected in Big Rideau Lake, it is likely that protection from fisheries afforded by the FPAs played a key role benefitting the fish communities in both Big Rideau Lake and Opinicon Lake. Greater

species richness within PAs have been widely documented (Rodrigues *et al.*, 2004), especially within marine environments (Côté *et al.*, 2001; Edgar *et al.*, 2014). Often the objectives of PAs are to promote habitat recovery, which enables populations/communities to re-establish a natural state (Abell *et al.*, 2007; McLeod *et al.*, 2009), and although this can be particularly challenging to illuminate, especially within the Rideau Waterway system due to a lack of pre-FPA data, it is possible that the habitats within the FPAs in both Opinicon Lake and Big Rideau Lake have achieved a more naturalized state in the absence of fisheries activities, enabling these areas to support a greater, and more consistently diverse, community composition.

Differences in habitat features between lake-zones may have influenced species richness within Opinicon Lake. Transect water depth was on average 20 cm deeper within the outside fished lake-zone, compared to the FPAs and bordering transition zones (Figure 2.6 b). As such, it is possible that variation in species richness could be related to differences in mean transect water depth. Variation in water column depth can directly influence residency patterns of fishes, as shallow water is more easily influenced by abiotic and biotic processes (e.g., UV light exposure and avian predation) (Cooke et al., 2003), whereas deeper water can limit habitat complexity by reducing aquatic vegetation growth (Hudon et al., 2000). However, vegetation complexity is considered a more influential driver of space-use and residency patterns of warm water fishes, as compared to water column depth (Hall and Werner, 1977; Keast and Harker, 1977; Keast et al., 1978). Furthermore, it is important to note that transect water depth varied by a mere 20 cm, and no differences in vegetation complexity were detected between lake-zones across any of the replicate lakes (Figure 2.6 a). As such, it is likely that the differences in mean transect water depth is not biologically significant in terms of influencing the fish community parameters evaluated within Opinicon Lake.

Interestingly, species richness was observed to be lowest within the Newboro Lake FPAs, intermediate within the bordering transition zones, and highest with the outside fished zones (Figure 2.4). Although, the effect of protection was found to benefit target (i.e., largemouth bass) and specific non-target species (i.e., shiners) across all replicate lakes (as indicated from the multifactor analyses using the pooled fish parameter data, discussed in detail below; Figure 2.5 a, b); it is possible that the geographical placement of the Newboro Lake FPAs may be unfavourable for certain fish species based on differences in unaccounted for habitat variables including, but not limited to, unmeasured habitat complexity (e.g., dissolved oxygen) and/or microhabitat variables (e.g., finite differences in macrophyte communities between lake-zones). These types of microhabitat features were not recorded in the present study, but may have influenced space-use dynamics of certain fish species, in particular, small-bodied fishes (e.g., small species and/or juvenile fishes; Paradis, Bertolo, Mingelbier, Brodeur, & Magnan, 2014; Massicotte et al., 2015; Stahr and Shoup, 2016). Similar to Opinicon Lake, differences in mean transect water depth were detected between lake-zones within Newboro Lake and may have also influenced species richness between zones. Specifically, mean transect water depth was 25 cm deeper within the transition zone, as compared to both the FPAs and outside fished zones. However, it is important to note that the differences in transect water depth do not match the trend in species richness between zones (Figure 2.4 & 2.6 a, b). Furthermore, no differences were detected in vegetation communities or substrate composition between zones. These habitat features are considered more influential regarding space-use and residency patterns in warm water fishes, as compared to water column depth (Keast and Harker, 1977; Werner et al., 1977; Keast et al., 1978).

Although collectively the Rideau Waterway FPAs have achieved their primary objective of providing effective protection to the largemouth bass population(s), the indirect benefits of increased species richness (as observed through independent analyses in Opinicon Lake and Big Rideau Lake) is promising in terms of understanding and utilizing FPAs for biodiversity conservation. Maintaining biodiversity is an essential component for optimal ecosystem function(s), as reduced biodiversity can degrade essential ecosystem processes (e.g., nutrient cycling) (Dudgeon et al., 2006; Loreau et al., 2001; Worm et al., 2006). As global freshwater biodiversity is currently in a state of decline (Reid et al., In Press), FPAs may provide a useful tool to promote biodiversity conservation (Abell et al., 2007; Dudgeon et al., 2006; Pittock, Hansen, & Abell, 2008).

2.5.2 Fish parameter evaluations

The effect of protection afforded by the Rideau Waterway FPAs was found to significantly benefit both largemouth bass and shiners across all three replicate lakes. Specifically, largemouth bass abundance and biomass was four- and six-fold greater inside FPAs relative to outside fished lake-zones. Similarly, shiner abundance and biomass were four- and six-fold higher within FPAs relative to the outside fished lake-zones (Figure 2.5 a, b). These results provide evidence that protection offered by FPAs can increase abundance and biomass of both target (i.e., largemouth bass) and non-target (i.e., shiners) species within designated single-resource FPAs. Through direct assessments of species abundances and biomass across lake-zones, the present study is one of the first to provide empirical evidence to allow for a critically objective evaluation of FPAs. Indeed, these types of analyses are common in the marine realm (reviewed in Di Lorenzo et al., 2016), and are used as biomarkers to evaluate population health and status. However, there has been limited quantitative investigations using these assessment

metrics in FPAs (Hermoso et al., 2016), partly due to the lack of PA use within freshwater systems, and the scarcity of research/data to describe those that exist (Abell et al., 2007; Hedges et al., 2010; Hermoso et al., 2016). Statistically pooling fish abundance and biomass data from all lake-zones, from each replicate lake, allowed for an objective, and broad-scale, assessment into the effectiveness and utility of the Rideau Waterway FPAs. As this study is one of the first empirical evaluations of FPAs, understanding the broad scale influence of protection on fish community parameters is an essential first step in the investigation to better understand the variables that link conservation benefits to FPAs.

Largemouth bass remain one of the most highly sought-after sport fish in the Rideau Waterway system, and indeed much of North America, with catch rates of black bass (i.e., largemouth bass and smallmouth bass) rising from 2,084,586 in 2005 to 3,145,829 in 2010 within the Rideau Lakes Wildlife Management Unit alone (Hogg et al., 2010). As such, selection for FPAs by largemouth bass could be a response to growing angler pressure throughout the Rideau Waterway system, as fish inhabiting the non-protected lake areas are subject to open, and increasing, exploitation. As discussed above, other abiotic and biotic factors that are not accounted for include, but are not limited to, specific resource availability, micro-habitat features, state of shoreline development, and/or complex predator-prey interactions, all of which may have influenced these results. In particular, the methodology used in the current study only evaluated coarse scale habitat features (i.e., % vegetation coverage, substrate composition, and transect water depth) and, as such, it is possible that habitat variables that have not been accounted for (e.g., water chemistry parameters, specific macrophyte communities, etc.) could have played an influential role in determining space-use and residency behaviours of the various species of fishes inhabiting the study lakes. Furthermore, due to the finite observation period

applied in this study, the lack of physical barriers isolating FPAs from the non-protected lake areas, and the variability of largemouth bass home range size (<1.0 km² depending on habitat complexity) relative to the FPAs coverage areas (collective FPA coverage areas for each replicate lake: $OP \sim 1.0 \text{ km}^2$, $NB \sim 3.33 \text{ km}^2$, and $BR \sim 0.57 \text{ km}^2$) the results found from the present study may be exclusive/limited to the observation period applied. As such, it is possible that the largemouth bass populations may indeed be transient between the lake-zones, which further strengthens the need for telemetry-based research to more holistically evaluate long-term residency and movement patterns of fishes within the FPAs. It is also important to note that the variation in the FPAs sizes between the replicate study lakes may also be a factor influencing occupancy rates of certain non-target species with large home range sizes (e.g., northern pike); consequently, limiting the potential protective capacities of the FPAs to the broader fish community.

The results of this study support the initial mandate of the Rideau Waterway FPAs, which is to protect a subset of the largemouth bass population and to promote recruitment back into the main lake regions (Ontario Department of Game and Fisheries, 1946). Although these results suggest that not all Rideau Waterway FPAs are equal, with the Big Rideau Lake FPA providing the most detectable differences in measured community parameters, largemouth bass and shiner populations still benefitted from protection across all replicate lakes. As such, support for the continued management and use of the Rideau Waterway FPAs is merited. Although quantitative research pertaining to the effectiveness/utility of FPAs is scarce, examples are present in the literature to support the use of FPAs for conservation and fisheries benefits (Sztramko, 1985; Zuccarino-crowe *et al.*, 2016; Twardek *et al.*, 2017). Specifically, seasonal FPAs have been designed and successfully used to protect nesting smallmouth bass from angler exploitation during the spawning and brood care life-history stages, which has proven to increase population level reproductive success (Suski, Phelan, Kubacki, & Philipp, 2002) while increasing angler catch-per-unit-effort (Sztramko, 1985). Furthermore, the use of FPAs to protect and rehabilitate lake trout (*Salvelinus namaycush*, Walbaum, 1792) has proven successful within both Lake Huron (Reid *et al.*, 2001) and Lake Superior (Schram *et al.*, 1995; Zuccarino-crowe *et al.*, 2016), increasing both adult and juvenile abundance within both populations. The use of PAs has also positively benefitted European eels (*Anguilla anguilla*, Linnaeus, 1758) by increasing population size structure and migration rates in heavily fished waters (Cucherousset *et al.*, 2007).

2.5.3 Conclusion

The present study provides a unique opportunity to evaluate the effect of protection on fish community structure, through intra-lake evaluations of similar habitats that are managed under different fisheries management objectives (FPAs vs. fishable waters). The Rideau Waterway system allowed for comparative, unbiased, evaluations as each lake-zone analyzed consists of similar environmental and biological parameters. As such, accurate and reliable inferences regarding the effectiveness and utility of these intra-lake FPAs could be achieved, using comparative biological evaluations. Although fish community comparisons were not equal across all replicate FPAs, the effect of protection afforded by the Rideau Waterway FPAs was found to benefit both target (largemouth bass) and non-target (shiners) species through increased biomass and abundance. Current data regarding the effectiveness and utility of FPAs is lacking, and, given the current state of freshwater habitats and biodiversity, FPAs used in conjunction with other management tools could be an effective conservation strategy, as evidenced from the present study. As protection is more economically viable compared to restoration, the use of FPAs by resource managers could provide a cost effective means to promote freshwater conservation (Abell *et al.*, 2007, 2008). Beyond serving as a mechanism to maintain abundance, biomass and biodiversity, FPAs may also serve to protect fish populations from fisheries induced evolution (FIE; Kuparinen & Merilä, 2007; Twardek et al., 2017). FIE can occur as a result of intensive selection pressure on specific phenotype(s) (e.g., boldness) of a population (Heino and Dieckmann, 2009). As such, the Rideau Waterway FPAs may provide refuge for fish populations against FIE. Given that the Rideau Waterway FPAs were initiated in the 1940s, obvious questions arise about the time course for the conservation benefits of new FPA establishment to accrue. I encourage additional research on existing (especially long-standing) FPAs in different systems around the globe to learn more about their potential role in aquatic conservation.

Chapter 3: Space use and residency patterns of largemouth bass within a freshwater protected area

3.1 Abstract:

Understanding the movement dynamics of fishes within freshwater protected areas (FPAs) is essential to evaluate the effectiveness of reserve areas in providing conservation benefits. The Rideau Waterway system (Ontario, Canada) is home to some of the oldest single-resource FPAs in Ontario (> 70 years active). Initially, these FPAs were intended to provide holistic protection to the heavily exploited largemouth bass, but since their establishment, little is known regarding their protective capacity. Using a passive acoustic telemetry network, I measured how site fidelity varied with body size and across seasons in largemouth bass within one Rideau Waterway FPA. Collectively, 50 bass were tracked for an average of 227 days, with some individuals tracked upwards of 744 days. Tagged fish spent on average 55% of their time

at liberty within the FPA, with occupancy rates exceeding 85% for some individuals. Most of the tagged fish displayed cyclic and bi-directional movement behaviour between the FPA and non-protected areas, largely corresponding with known life-history stages. Largemouth bass occupancy was highest in the spring-summer seasons (i.e., reproductive period), with a sharp decline during the fall that sustained through the winter. FPA occupancy varied with body size, with large fish (>430 mm) using the FPA more extensively. Our findings show that this Rideau Waterway FPA provides temporal protection to a highly targeted sportfish, but highlights the importance of understanding habitat requirements of a species before a protected area is established, recognizing that space-use requirements are diverse and can vary with life-history stage.

3.2 Introduction:

Declines in freshwater biodiversity highlight the need for more effective conservation strategies to safeguard exploited species from overharvest as well as other adverse human-use impacts. Management actions in the form of freshwater protected areas (FPAs), which restrict/prohibit human-use activities within a designated area, have been garnering attention as a potential strategy to improve conservation outcomes. Similar to marine protected areas (MPAs), the objectives of FPAs are often to protect biodiversity within entire ecosystems; however, resource-based FPAs that target a single species for protection are common. Specifically, the establishment of FPAs to protect economically valuable species (e.g., largemouth bass, *Micropterus salmoides* [Lacépède, 1802]) are amongst the most common in North America. However, the effectiveness and utility of FPAs are still largely debated (Abell et al., 2007; Hedges et al., 2010). Unlike protected areas in the marine environment, FPAs are often small in size, seasonal, and/or obscurely placed within lakes and rivers (Hermoso et al., 2016), and can be installed without consideration of the movement behaviours of the target fish species to be protected. These factors have resulted in mixed resource management outcomes, and as a consequence, have created a paucity in the use of FPAs in resource regulation (Abell *et al.*, 2007; Acreman *et al.*, 2020).

Defining the movement behaviours of fish species to be protected with an FPA is paramount to guide design and management (e.g., FPA size, location, habitat coverage relative to individual movement patterns as in Schlosser 1991). For example, understanding the movement dynamics of a species can help evaluate whether an FPA is sufficiently large to encompass the entirety of an animal's home range, how the level of protection varies across seasons and in relation to life-history strategies of both target and non-target species, and whether reproduction occurs within the protected area boundaries. A useful and powerful technique to evaluate movement dynamics of fishes in, and around, protected areas can be achieved through the use of passive acoustic telemetry. Passive acoustic telemetry utilizes a network of submerged autonomous receivers that record the presence of animals fitted with an acoustic transmitter (Donaldson *et al.*, 2014). This fisheries-independent tracking technique functions continuously (i.e., 24 hr/day), providing fine-scale movement data that is generally unobtainable through traditional mark-recapture techniques and/or active tracking (Reyier et al., 2020). Telemetry techniques have been commonly used to investigate migration patterns and site fidelity of fishes within, and adjacent to, MPAs, which has provided vital information for guiding the development of certain MPAs to maximize conservations benefits (Knip et al., 2012; Lea et al., 2016; Revier et al., 2020). At present, similar information for FPAs is lacking (Loury et al., 2018).

Within Ontario there are over 600 designated FPAs, although only a few of these provide year-round protection (2020 Ontario Recreational Fishing Regulations). Some of these FPAs are created for holistic biodiversity protection purposes, but the majority are based on singleresource protection (i.e., designed for one species). The Rideau Waterway system (Ontario, Canada) is home to some of the oldest FPAs in Ontario. Established more than 70 years ago (circa 1940's), these year-round intra-lake FPAs were intended as a means to protect the viability of the largemouth bass fishery that was suffering from heavy exploitation through excessive recreational harvest (Ontario Department of Game and Fisheries Monthly Bulletin 1939). Remarkably, these FPAs were created prior to contemporary understanding of source-sink dynamics. In addition to the use of FPAs as a management strategy, the largemouth bass fishery in the Rideau Waterway system is managed through conventional harvest quotas and seasonal closure periods (i.e., the largemouth bass fishery is closed from December 15th until the 3rd Saturday in June within Rideau Waterway system). Recent research has shown that these FPAs have positively benefitted largemouth bass through supporting larger population densities within the protected area boundaries (Zolderdo et al., 2019). Furthermore, largemouth bass inside the FPAs are believed to exhibit basal phenotypes that have not been influenced by fisheries-induced selection pressure, such as high-performance metabolic phenotypes, increased reproductive effort, and reduced stress responsiveness (Cooke et al. 2017; Twardek et al. 2017; Zolderdo et al. Unpublished). Collectively, these results indicate some degree of protective capacity enabling FPA populations to maintain a more natural state relative to unprotected individuals outside of the FPA that have been influenced by humans through harvest and exploitation (Hessenauer et al., 2015; Louison et al., 2017). Thus, intra-lake FPAs may provide a refuge to protect against

fisheries-induced selection. However, the level of protective capacity across seasons and lifehistory stages has not been quantified.

Using passive acoustic telemetry, I quantified the seasonal and annual movement dynamics of adult and sub-adult largemouth bass within, and adjacent to, the Big Rideau Lake (BRL) FPA for the first time since its establishment in the 1940s. Specifically, the objectives of this study were to define how site fidelity within the FPA varied in relation to body size, as well as to evaluate the protective capacity of the FPA through quantifying how often, and when, fish tagged within the FPA stayed within its boundaries. Resolving largemouth bass movement dynamics across seasons and life stages will help to assist in the design and management needs of future FPAs intended to protect this heavily targeted sportfish.

3.3 Methods:

3.3.1 Study area

All fish tagging was conducted within the Ministry of Natural Resources and Forestry (MNRF) designated FPA on Big Rideau Lake (44.728977° N, 76.177343° W). The FPA serves as a strict fisheries exclusion zone and is regularly patrolled and respected by anglers. Relative to Big Rideau Lake, which has a surface area of 45.36 km², the FPA covers a surface area of 0.57 km² (1.26 % of the total surface area). The FPA is relatively shallow, with depths ranging from 0.5 m – 2.5m. The FPA has known spawning and nursery habitat for largemouth bass (Zolderdo, *unpublished*), and a single, narrow entrance/exit canal approximately 40 m at its narrowest constriction point through which all fish must pass if they enter or exit the FPA (Figure 3.1). There is little, to no, boat traffic that occurs within the FPA boundaries due to it being a fisheries exclusion zone, coupled with the shallow habitat conditions that are not conducive to recreational
boating. Furthermore, there is limited shoreline development with only two seasonal residences constructed within the protected area boundaries.

3.3.2 Fish tagging

Fifty largemouth bass comprising both adults and subadults (size range from 130-475mm) were collected from inside of the FPA boundaries, and implanted with one of three sizes of acoustic transmitters (Lotek Wireless Inc., ON., CA.; Table 3.1). All fish were captured within the Big Rideau Lake FPA during the summer of 2015 (Jun-Sept) using rod-and-reel angling (n = 33) or electrofishing (n = 17). Upon capture, fish were subjected to an initial assessment including a total length measurement and an inspection of any external indications of injury or disease. If fish looked unhealthy and/or showed signs of injury, they were immediately released. Following initial assessments, fish were placed onto a foam lined surgery table aboard the research vessel. The surgery tables were equipped with an independent water pump and water reservoir, which enabled a continuous flow of fresh oxygenated water to be passed over the gills during the surgical procedure, minimizing air-exposure and 'out-of-water' handling time. Fish were held in place on the surgery table using a pair of DC-electrified fish handling gloves with a standard voltage output of ~32 V and 5 current settings (4, 6.3, 10, 16, and 25 mA; Smith-Root Inc., Washington, USA; 2016). Current settings were established by beginning at the lowest setting and then incrementally increasing the current strength until tetany was observed and then returning to one setting lower, which induced a safe electroanesthesia (i.e., muscle relaxation, normal ventilation, loss of equilibrium, and reduced reactivity; see Abrams et al. 2018 for more detail). Once fish were safely immobilized, a ~25 mm longitudinal incision was made on the ventral side of the fish between the pectoral fins and the cloaca. A sterilized (betadine) acoustic transmitter was inserted into the coelom through the incision, which was then closed using a 3-0

monofilament suture (PDS II polydioxanone suture; violet monofilament, 3-0). Surgical tools were sterilised in a diluted solution of betadine between each surgery. A new pair of nitrile gloves were used for each surgery. Surgery times ranged between 3 - 6 min, with the same surgeon conducting all surgeries. Following tag implantation, fish were allowed to recover in coolers filled with fresh lake water. After a brief recovery period (recovery time not recorded), fish were released near their site of capture. All tag types emitted a coded signal frequency of 416.7 kHz, with a pulse repetition interval of 1 s minimum with 1 s increments, with a signal strength between 156 - 158 dB (re: uPA at 1 m). All experiments were conducted in accordance with the standards set by the Canadian Council of Animal Care (CCAC) under permit number BT-026 administered through the Carleton University Animal Care Committee.

3.3.3 Telemetry array setup and monitoring schedule

Six Lotek acoustic telemetry receivers (WHS 4250 4-Battery Delrin, Lotek Wireless Inc. ON., CA) were set up in an array to detect residency and movement patterns of largemouth bass within the FPA area (inside and directly outside of the Big Rideau Lake FPA; see Figure 3.1). Three of the five receivers were aligned at, or near, the entrance to the FPA to provide directionality of movement (i.e., site was gated). Furthermore, two receivers were placed at the two narrow channels leading outward into the main lake basin, which were ~40 m and ~60 m wide at each constricting point (Figure 3.1). Thus, if fish exited the FPA I would be able to detect their movement(s) beyond the transition area, which separated the FPA from the main lake basin (see Zolderdo et al. 2019 for more detail). One receiver was placed deep within the FPA in a back-bay area, previously identified as a key spawning and brood rearing habitat (Figure 3.1). Each receiver was powered by four Delrin batteries (Lotek Wireless Inc. ON., CA.), and

provided a run time of approximately 150 d. As such, receivers were regularly visited to replace spent batteries and download detection data.

3.3.4 Data Analysis

All statistical analyses were conducted using R (R Core Team, 2018) via RStudio (RStudio Team, 2016). Prior to analyses, data were first screened to remove erroneous detections that did not correspond to transmitter identification codes deployed in the study. This initial screening process was conducted using the Lotek software program (WHS Host x64 Build, v1.5.2870.1, Lotek Wireless Inc. 2012). Largemouth bass detections were then filtered to remove any false detections prior to analysis (Simpfendorfer et al. 2015) including those that occurred prior to tag deployment, repeated detections that occurred within less than the minimum tag transmission delay, and single detections that occurred within a 1-hour time period at a given receiver (i.e., minimum lag filter). Detections were then visually examined to assess whether any mortalities or tag shedding occurred, which results in repeated detections of an individual tag at an individual receiver over extended periods of time, without any subsequent detections at other receivers (Matley et al. 2020). No transmitters appeared to exhibit this pattern. However, prior to assessing and modeling fish movements in relation to the FPA, the dataset was further filtered to include the time period where there was sufficient receiver coverage in the region, and ≥ 8 individuals were present in the tracking system (Table 3.1, Figure 3.2; Appendix C). Further, individuals were only included in the dataset if they had tracking periods ≥ 30 days and ≥ 10 detections.

The filtered dataset was used to assign fish locations (i.e., inside, outside the FPA) using a modified version of the last-observation-carried-forward (LOCF) method (Shao and Zhong 2003). The LOCF method is often used to assess general animal locations using passive acoustic telemetry arrays, where individuals are assumed to be located in the discrete ecosystem segment where they were last detected until they are subsequently detected in another segment (e.g., Struthers et al. 2017; Kessel et al. 2018; Colborne et al. 2020). In this case, a modified set of decision rules were used (Figure 3.2) because an acoustic receiver was located at the entrance of the FPA (Figure 3.1). With this modified criterion, periods during and subsequent to detections at the entrance were considered either inside or outside the FPA depending on the location of the previous and subsequent detections. Using this criterion, positions for each fish were assigned (inside or outside the FPA) for every day from the tagging date to the date of the last detection. In some cases, individual fish were assigned as both inside and outside the FPA on a given day due to intraday movements.

To quantify the drivers of fish residency in relation to the FPA, daily fish positions assigned using LOCF were modelled using random forest (RF) algorithms (Breiman 2001). RF uses classification or regression trees to repeatedly create binary partitions in the data based on the predictors to optimize prediction of the response (Breiman et al. 1984; De'Ath and Fabricius 2000). RF fits numerous trees using random subsets of data and predictors each time to minimize overfitting to training data and improve prediction accuracy (Breiman 2001; Cutler et al. 2007). The RF model was fit as a classification problem with daily fish location as a binary response (either inside or outside the FPA), and predictors included individual fish (FishID), fish total length (TLmm), and Julian day (dayJ). RF were fit with 1000 trees, and the dataset was split into 10 folds, using a single fold at a time (repeated 10 times) to train the model, and the remaining 90% of the data used to assess model fit. Model performance was assessed based on prediction accuracy (MDA) and

interaction importance using Friedman's H-statistic. Because the latter is scaled from 0 to 1, MDA was also transformed to the same scale by dividing MDA scores for each predictor by the total MDA score for all predictors in the model. Predictors and interactions were considered important when confidence intervals of MDA generated from 10-fold cross validation did not overlap zero. Relationships between the predictors and the response, including predictor interactions, were assessed based on the marginal effects (\hat{y} ; average relationship between the predictor and the response holding other predictors at their mean) using partial dependencies. Random forests were fit with the 'randomForest' package (Liaw & Wiener 2002), crossvalidated model accuracy was assessed using the 'caret' package (Kuhn 2019), predictor interaction importance was calculated with the 'iml' package (Molnar et al. 2018), and partial dependencies were calculated using the 'pdp' package (Greenwell 2017).

3.4 Results

After applying false detection filters, the final acoustic telemetry dataset consisted of 19,177 detections of 48 of 50 total tagged individual largemouth bass from 2016-08-17 to 2018-09-27 (Table 3.1; Figure 3.1; Appendix B). Tracking durations were variable amongst individuals (227 ± 226 days; mean \pm standard deviation; 1.3-744 day range). Of these individuals, 38 were detected for extended periods (\geq 30 days and \geq 10 detections). All of these 38 individuals except for one were detected both inside and outside the FPA (Figure 3.3), spending variable periods of time within the FPA ($55 \pm 32\%$ of time; mean \pm standard deviation; 1-100% range; Appendix B; Table 3.1). Most fish exhibited repeated movements in and out of the FPA (see Appendix B; Figure 3.3). Over time, the highest proportion of individuals were detected in the spring and summer seasons, with a sharp decline in occupancy (i.e., number of days inside the FPA boundaries) during the fall that remained low through the winter (Figure 3.4). After the

tagging period in the summer and fall seasons of 2016, the majority of individuals that were still being tracked in the system (see Appendix B) returned to the FPA in the late winter and early spring of 2017 (Figure 3.4). FPA Residency remained high with some decline through the summer of 2017. This inter-annual occupancy pattern was repeatable between 2016 and 2017. However, in the latter part of the study the number of fishes being tracked was steadily declining, likely biasing the proportion of individuals using the FPA upward.

Examining the drivers of largemouth bass space use in relation to the FPA, RF models were able to predict fish location (inside | outside the FPA) with 88% accuracy in non-training data, and 88% accuracy balance between the two response categories using individual fish, fish length, and Julian day as predictors. All predictors were important and there were also important interactions between individual fish and Julian day, and fish length and Julian day (Figure 3.5 A). Marginal effects show clear patterns of occupancy amongst Julian day, with a rapid increase in FPA occupancy from days 60-100 (March-early April), sustained high occupancy through summer months and a decline in the fall (Figure 3.5 B). The effect of fish length was more moderate, but with a clear pattern of increased occupancy for the largest individuals. Specifically, individuals greater than >430 mm total length had the longest continuous occupancy within the protected area boundary (Figure 3.5 C). There was also an important effect of individual and an interaction between individual and Julian day (Figure 3.5 D, F). Across fish sizes, the majority of fish tended to occupy the FPA in the spring, summer, and fall months; however, the largest fish had a tendency to occupy the FPA for the most continual number of days in the spring months (Figure 3.5 E).

Table 3.1: Acoustic transmitter information implanted into 55 largemouth bass inhabiting the Big Rideau Lake protected area. Expected life of transmitters may vary by \pm 5%, depending on environmental conditions.

Size range [mm],	Transmitter weight	Transmitter model	Expected life (d)
(sample size)	(g)		
320-475 (25)	3.5	L-AMT 8.2	1522
240-449 (10)	1.1	L-AMT 5.2	568
130-449 (15)	0.28	L-AMT 1.416	131



Figure 3.1: Map of the study region with the freshwater protected area outlined in yellow and locations of acoustic receivers for tracking largemouth bass marked as red circles in Big Rideau Lake.



Figure 3.2: Criteria used for a modified last-observation-carry-forward (LOCF) assignment of fish locations (inside | outside the freshwater protected area in Big Rideau Lake) based on detections at stationary acoustic receiver locations.



Figure 3.3: Maps of detection and movement patterns of individual largemouth bass tracked with acoustic telemetry in Big Rideau Lake across the entire duration of the monitoring period. The number of detections at each station are indicated by the size of the circle and movements are connected by lines. Receiver locations are indicated by open red circles.



Figure 3.4: Temporal patterns of occupancy of the Big Rideau Lake freshwater protected area by largemouth bass expressed as a proportion of tracked individuals (green area) from 2016-08-03 to 2017-12-31 when at least 8 individuals were actively tracked in the system. Individuals were considered as being tracked in the period from the tagging date to the last detection. The dashed areas indicate open fishing seasons for largemouth bass in this system.



Figure 3.5: Random forest model outputs predicting largemouth bass location (inside | outside Big Rideau freshwater protected area), A) predictor (feature) importance scores $\pm 95\%$ confidence interval, marginal effects (\hat{y}) of predictors B) Julian day C) fish total length, D) individual fish, E) interaction between Julian day and fish total length (TLmm), F) interaction between Julian day and individual fish (FishID). Errors were generated by 10 fold cross validation.

3.5 Discussion:

Our findings show that largemouth bass captured in the FPA remained inside the protected area boundaries during a significant proportion of the open-access fishing season(s), suggesting that the spatial protection provided by the BRL FPA is of value from a fisheries management perspective. However, all fish (with the exception of one individual) spent time both inside and outside of the FPA within a given year. Largemouth bass, like many potadromous species, are known to undergo seasonal movements at various temporal and spatial scales to access favourable habitat for feeding, reproduction, and refuge (Fish and Savitz, 1983b; Waters and Noble, 2004; Hanson et al., 2008). The BRL FPA is a shallow, heavily vegetated, littoral area, ideal for largemouth bass during the reproductive period as well as the growing season (Kramer and Smith 1962; Brown et al. 2009; Cooke, pers obs). In spring, the early and accelerated macrophyte growth within shallow littoral habitats attracts various prey resources, which, in turn, attracts largemouth bass due to increased foraging opportunities (Massicotte et al., 2015). Furthermore, shallow vegetated habitat provides ideal conditions to support offspring development and growth (Kramer and Smith, 1962; Jennings, 1997). In the BRL FPA, dense macrophyte growth continues into the summer and early fall, creating highly complex habitat structure (Zolderdo et al., 2019), which is a key factor known to reduce home-range size in largemouth bass (Fish and Savitz, 1983b; Ahrenstorff et al., 2009). As water temperatures cool, largemouth bass transition to overwintering habitat, which generally comprises offshore, deepwater (<10 m in depth) structure (Hanson et al., 2008; Hasler et al., 2009). Previous research has shown that largemouth bass populations consolidate within select overwintering areas, and can travel significant distances to occupy these locations (Carlson, 1992; Raibley et al., 1997; Hasler et al., 2007). As the BRL FPA does not contain water depths greater then 2.5 m in depth,

remaining inside the FPA overwinter may be impossible due to the potential of certain areas freezing solid. As such, it is not surprising that largemouth bass moved outward from the protected area boundary during the cold-water period. Together, the BR FPA provides critical habitat for largemouth bass of all sizes to survive during the open warm water months, while also providing many months of protection from anglers by being a no-fishing zone.

Inter-annual variability in FPA occupancy between 2016 and 2017 may be linked to differences in environmental conditions between years. More specifically, record high water levels occurred throughout the Rideau Waterway system during the 2017 spring-summer season as a result of heavy snow melt coupled with extreme spring precipitation events (Zolderdo, pers obs). The increased water level within the BRL FPA during 2017 may have increased habitat availability, which, in turn, may have increased largemouth bass residency time within the FPA. Higher water levels not only provide access to new habitat (i.e., flooded shoreline), but can also buffer water temperature fluctuations during dynamic weather conditions (Meals and Miranda, 1991). Previous telemetry-based research has identified a negative correlation between habitat residency rates of largemouth bass and both water temperature and littoral zone water depth (Roy et al. 2018). Diurnal movement patterns have also been observed in largemouth bass, where telemetered fish have been observed to occupy deeper littoral habitats during daylight hours, and move into shallower areas during low light conditions (Demers et al., 1996; Hanson et al., 2007). Thus, the increased water depth throughout the FPA area during 2017 may have resulted in higher residency through increased habitat volume. Furthermore, differences in residency rates between years may also be related to fish growth. As occupancy was positively correlated with larger body sizes, it may be that juvenile tagged individuals grew large enough between seasons to reach sexual maturity (i.e., reproduce) and/or successfully compete for home range territories.

Population density is known to be higher with the FPA, with density-dependent spillover occurring across the protected area boundary (Zolderdo *et al.*, 2019). Natural population structuring relies on the senescence of older individuals to create niche space for younger, more fit, individuals (Metcalfe, 2006). Thus, it may be possible that the increased occupancy within the FPA for the 2017 year may, in part, be the result of natural population restructuring processes occurring with the FPA population.

Body size was observed to be an important factor influencing occupancy within the BRL FPA, with fish >430mm having the highest total number of days spent within the protected area boundaries (Figure 3.5 C) compared to smaller individuals. This increased occupancy amongst the largest telemetered fish could be related to condition factor following the overwintering period. More specifically, a larger body size enables a higher storage capacity for endogenous energy reserves (i.e., lipids; Cargnelli and Gross 1997) coupled with a lower size-specific metabolic rate (Norin and Clark, 2015). This would enable larger fish to exit the overwintering period in better condition and make seasonal movements into the shallow littoral FPA habitat sooner relative to smaller individuals (Hanson et al., 2008; Midwood et al., 2017). Furthermore, the residency-body size relationship may also be related to the reproductive life-history of largemouth bass. As a result of exiting the overwintering period in better physiological condition, larger fish require less nutritional intake prior to spawning. This enables larger individuals to initiate spawning earlier in the season relative to smaller individuals (Iguchi et al., 2004). Furthermore, larger fish are able to engage in reproductive activities (i.e., parental care behaviours) longer due to their increased energy reserve capacity (Cooke et al., 2006; Suski and Ridgway, 2007). Based on these factors, larger reproductively active individuals would remain within the spawning areas for longer durations of time relative to smaller fish, which may, in

part, be responsible for the increased occupancy amongst larger individuals observed within the FPA, especially during the spring-summer period (Figure 3.5 E). As such, our findings show that the protective capacity of the BRL FPA was greater for larger individuals, which may provide ecological benefits at the population level (i.e., increased reproductive output and recruitment).

Despite the small size of the BRL FPA (i.e., 0.57 km², 1.2 % of lake surface area), it was sufficient in protecting tagged largemouth bass for 55 ± 32 % of the year. However, fish did leave the protected area during portions of both the closed and open access fishing seasons. By this metric alone, the current FPA design does not provide holistic protection as initially intended (Ontario Department of Game and Fisheries Monthly Bulletin 1939). However, the lowest occupancy period (i.e., < 25% of tagged fish present inside the FPA) occurred between January – March, 2017, which overlapped with the closed fishing season for largemouth bass in the region (2017 Ontario Recreational Fishing Regulations Summary). As such, even if fish exited the boundaries of the FPA, an alternative form of protection from harvest/anglers was still in place, and the mandated closed fishing season indirectly extended the protective capacity of the BRL FPA. However, low occupancy still occurred during portions of the open access fishing season (i.e., $\sim 40-75\%$), largely during the fall transition months of October – December. During this time period, FPA largemouth bass may have been vulnerable to angler capture, but angling for largemouth bass is greatly reduced, and may not be occurring at all, during the October -December time period (Sheridan & Krishka 1994; Hogg et al. 2010). Thus, capture of FPA largemouth bass during the fall transition period may be minimal as a result of reduced fisheries pressure associated with changes in angler behviour. It is important to note, however, that these excursions outside of the FPA were most likely due to the lack of deep-water habitat within the BRL FPA, and occurred largely during the fall transition and overwintering periods. This

behaviour closely corresponds to previously identified seasonal movement patterns in largemouth bass (Carlson, 1992; Hanson *et al.*, 2008). The protective capacity of a FPA is a function of its size, as well as the habitat needs of the exploited species that occupy it (as reviewed in Acreman et al. 2020). Thus, to achieve a higher protective capacity for largemouth bass, FPAs will need to incorporate deep-water (overwintering) habitat.

Despite providing incomplete coverage of largemouth bass home ranges, the BRL FPA must still provide some degree of population level protection, as previous research has observed greater abundance and biomass of largemouth bass within the FPA borders (Zolderdo et al., 2019). Differences in key physiological markers, which are indicative of fisheries-induced selection (i.e., high-vulnerability phenotypes; Philipp et al. 2015), have also been observed between the FPA and main-lake largemouth bass populations. For example, largemouth bass occupying the BRL FPA have been observed to have lower stress responsiveness to an angling and air exposure challenge, coupled with greater metabolic capacity, compared to largemouth bass from adjacent main-lake areas (Zolderdo et al. In Prep). As such, these population-level differences may be the result of increased protection specifically during the reproductive lifehistory stage. Despite the fact that a closed fishing season for largemouth bass occurs during the reproductive life-history period across all of the Rideau Waterway lakes (i.e., December 15th -3rd Saturday in June), pre-season angling still occurs and has been increasing in prevalence since the 1990's (Philipp et al. In Prep). Although it is illegal to target largemouth bass during the reproductive period, Philipp et al. (In Prep) observed hook wounding rates as high as 61% on nest guarding largemouth bass in two inter-connected lakes within the Rideau Waterway system. This increased hook wounding is the direct result of pre-season angling, and resulted in significant reproductive failure (Suski et al., 2002). Angling-induced reproductive failure can

reduce year class recruitment, and lead to evolutionary change at a population level (Philipp *et al.*, 1997, 2015). As observed in the current study, high occupancy within the FPA boundaries occurred during the critical reproductive life-stage of largemouth bass. Thus, the protection afforded by the BRL FPA during the reproductive period may not only provide conservation benefits through protecting/promoting recruitment, but may also serve as an evolutionary enlightened management strategy to mitigate human-induced selection pressures on this heavily exploited sportfish population.

In conclusion, the current study highlights the importance of understanding the seasonal movements and habitat requirements of a fish species before a protected area is established, recognizing that space-use requirements are diverse and can vary temporally and with lifehistory stage (Acreman et al., 2020; Reyier et al., 2020). The BRL FPA essentially provided three season protection for largemouth bass, which was repeated across years, and protection was improved for large fish relative to small fish. However, largemouth bass have diverse seasonal habitat requirements, and individuals moved out of the FPA during the fall, with low occupancy over winter, reducing the protective capacity of the BRL FPA. Therefore, managers need to ensure that the goals of a protected area not only match the life history of a fish, but also must consider protection across ontogenetic changes to ensure protection at all life stages. To ensure a higher protective capacity for largemouth bass, as with any species to be protected, a more thorough quantification of home range size across seasons is needed, which requires a larger tracking array(s) then was established in the current study. Fortunately, advances in electronic fisheries tracking and monitoring technologies make it possible to evaluate the optimal location and coverage area(s) of future FPAs before they are established. However, largemouth bass have consistent summer habitat requirements, and protection for certain critical life-history periods

(i.e., reproductive and active growing periods) can be achieved by setting aside ~1 % of a lake area, which has resulted in significant population and community level benefits. For example, the small-scale spatial protection provided by the Rideau Waterway FPAs, has amounted to physiological benefits in largemouth bass through the protection of high-performance metabolic and stress-resilient phenotypes (Zolderdo et al., *In Prep*). Moreover, community level benefits including increased population densities of both largemouth bass and other non-target fish species have also been observed (Zolderdo *et al.*, 2019). Collectively, these results suggest that the current level of spatial protection provided by the Rideau Waterway FPAs is of value from a fisheries management perspective. However, additional research on the spatial ecology of other aquatic species is needed to understand how FPAs benefit aquatic biodiversity more broadly. Given that freshwater ecosystems are amongst the most threatened in the world (Reid *et al.*, 2019), there is urgent need to adopt evidence-based actions that will enable protection and restoration of freshwater biodiversity (Tickner *et al.*, 2020).

Chapter 4: Freshwater protected areas can increase angler catch rates and preserve highperformance phenotypes in a popular sportfish

4.1 Abstract:

Recreational angling has the potential to cause evolutionary change in fish populations; a phenomenon referred to as fisheries-induced evolution (FIE). However, detecting and quantifying the magnitude of FIE in the wild is inherently difficult, largely owing to the challenges associated with differing environmental factors and, in most cases, a lack of pre-selection/baseline-data for which comparisons can be made. However, exploration of FIE in wild populations may be possible in systems where fisheries exclusion zones exist. Lakes that possess

intra-lake freshwater protected areas (FPAs) can provide investigative opportunities to evaluate the evolutionary impact(s) of differing fisheries management strategies within the same waterbody. To address this, we comparatively evaluated how two physiological characteristics (metabolic phenotype and stress responsiveness) as well as a proxy for angling vulnerability, catch-per-unit-effort (CPUE), differed between populations of largemouth bass inhabiting longstanding (>70 years active) intra-lake FPAs and adjacent open access main-lake areas. FPA populations had significantly higher aerobic scope (AS) capacity (13%) and CPUE rates, as compared to fish inhabiting the adjacent main-lake areas. These findings are consistent with research and theory linking exploitation with reduced metabolic performance, supporting the hypothesis that recreational angling may be altering the metabolic phenotype of wild fish populations. Reductions in AS are concerning as this suggests a reduced scope for activity available to carryout essential life-history activities, which may result in fitness level implications. Furthermore, these results highlight the potential for unexploited FPA populations to serve as benchmarks to further investigate the evolutionary trajectory imposed by recreational angling on wild fish.

4.2 Introduction

Recreational angling is an important sport and leisure activity practiced globally in both freshwater and marine environments, and accounts for an estimated 12% of annual global fish harvest (Cooke and Cowx, 2004). However, as of late, there has been concern regarding the potential evolutionary consequences imposed by recreational angling on wild fish populations. Similar to commercial fishing, recreational angling has the selective potential to alter the phenotypes of highly pressured populations, a phenomena referred to as fisheries-induced evolution (FIE; Heino and Dieckmann, 2009). FIE occurs as a result of intensive selection pressures on specific phenotypes of a population (Kuparinen and Merilä, 2007; Heino and Dieckmann, 2008). Selection in this context arises through selective harvesting of individuals using fishing gear and tactics that target fish of a particular size class, sex, life-history stage, and/or behaviour (reviewed in Pauli and Sih, 2016; Wang et al., 2016). As such, FIE can induce evolutionary changes that directly oppose natural selection processes, resulting in the proliferation of suboptimal phenotypes (Sih *et al.*, 2004; Nussle *et al.*, 2016; Hollins *et al.*, 2018). Furthermore, the altered fish population(s) may be less desirable for recreational angling due to increased timidity, which impacts catch-per-unit-effort (CPUE) (Alós *et al.*, 2012; Philipp *et al.*, 2015).

Two key physiological traits that may be altered by fisheries practises include metabolism and the responsiveness of the stress axis (i.e., stress responsiveness). Specifically, fish with greater metabolic demands have a higher propensity to forage/feed due to increased nutritional requirements, which may increase their chances of interacting with fishing lures (Redpath *et al.*, 2010; Hessenauer *et al.*, 2015; Killen *et al.*, 2015a). Furthermore, fish that are less sensitive to external stimuli and/or stressors (e.g., fishing gear), may indirectly increase their exposure to angling capture through a reduced fear or caution towards fishing lures (Louison *et al.*, 2017; Hollins *et al.*, 2018). Collectively, pace-of-life syndrome (POLS) links both metabolic output and stress responsiveness (i.e., hypothalamic-pituitary-interrenal-axis [HPI] reactivity) to a suite of highly correlated life-history traits (e.g., growth rates, age at maturity, reproductive investment; Réale *et al.*, 2010). These traits are largely influenced through genetic correlation, whereby selection pressure on a specific trait has the potential to indirectly alter interconnected traits along the fast-slow pace of life spectrum (Réale *et al.*, 2010; Polverino *et al.*, 2018; Wright *et al.*, 2019). As a result, selective angling practises on a particular life-history traits(s) can impart various phenotypic changes at the population level (Heino and Dieckmann, 2008; Diaz Pauli and Sih, 2017; Hollins *et al.*, 2018). For example, Philipp et al. 2009 showed that vulnerability to angling capture (measured via catch per unit effort) is indeed a heritable trait ($h^2 = 0.146$) in largemouth bass (*Micropterus salmoides*, Lacépède, 1802), and that vulnerability to angling is correlated with a suite of physiological and behavioural phenotypes (e.g., increased metabolism and parental aggression; reviewed in Philipp *et al.*, 2015). Consequently, selection pressure resulting in changes to the HPI-reactivity and/or metabolism, may also indirectly select for phenotypic changes in essential life-history traits (e.g., reproductive investment) through pace of life mechanisms, resulting in fitness level impacts at the population level (Réale *et al.*, 2010).

To date, FIE research related to recreational angling has largely been laboratory based, evaluating captive/hatchery bred animals under highly controlled experimental conditions (Hessenauer et al., 2015; Louison et al., 2017; Philipp et al., 2015). Although, these experimental studies have been fundamental in advancing the mechanistic understanding regarding the selective potential associated with hook-and-line angling practises, how this selective potential translates to wild populations, under natural condition, is not well understood. Comparative studies evaluating FIE in wild fish populations are inherently challenging to conduct given the various abiotic (e.g., habitat loss) and biotic (e.g., density-dependent resource balancing) factors that may influence the magnitude and extent of a selective force (Stokes *et al.*, 1993; Law, 2000). It is also important to note that most systems lack pre-selection/base-line data for which to make comparisons may not exist, creating an inability to accurately measure or detect the true extent of a particular selective force over time (Law, 2000; Kuparinen and Merilä, 2007). Furthermore, making selection inferences between populations originating from different lake systems and exposed to differing fisheries practises can provide unreliable results given the potential differences in environmental factors between lakes (Stokes *et al.*, 1993). All of these factors can create challenges for the accurate assessment of FIE in the wild, thus constraining the ability to define the true extent that fisheries practises may be having from an evolutionary perspective (Reznick *et al.*, 1990; Kuparinen and Merilä, 2007; Stepien *et al.*, 2017).

Despite these challenges, exploration of FIE in wild populations may be possible in systems where fisheries exclusion zones (e.g., FPAs) exist. Lakes that possess intra-lake FPAs can provide investigative opportunities to evaluate the impact(s) of differing fisheries management strategies (e.g., FPAs vs. open exploitation areas) within the same waterbody, thus providing a whole-lake experimental arena governed by similar ecosystem processes (Suski and Cooke, 2007; Dunlop *et al.*, 2009; Twardek *et al.*, 2017). FPAs that exclude fisheries practises may provide a natural refuge to protect against FIE, enabling a proportion of a targeted population to re-establish a natural state (Bergseth *et al.*, 2016), while the remaining proportion of the population inhabiting the non-protected lake area(s) may still be subjected to fisheries pressure, potentially creating a directional shift in targeted phenotypes over time (Puali, Beatriz Diaz & Sih 2017; Hollins et al. 2018). Therefore, lakes with FPAs may be able to provide a holistic study system to investigate FIE in the wild, while controlling for potential differences in ecosystem factors.

There were two objectives for the current study. The first objective was to determine if there are differences in physiological traits of wild largemouth bass inside and outside of FPAs. The second objective was to determine if the presence of an FPA influences catch per unit effort (CPUE, capture rate) of largemouth bass residing inside and outside of FPAs. Using a series of lakes that contain long-established intra-lake FPAs (>70 years), we addressed the first objective by evaluating the metabolic phenotype, HPI-reactivity (measured via stress responsiveness), and glucose responsiveness of largemouth bass residing inside and outside of 3 different FPAs. Vulnerability to angling has been linked to a suite of correlated physiological traits associated with fast-POLS characteristics, including high activity phenotypes (i.e., high metabolic performance and low- HPI-reactivity; Philipp et al. 2009; Alós et al. 2012; Louison et al. 2017). Based on the evidence provided from the experimental literature on FIE, we predicted that largemouth bass inhabiting FPAs would have greater metabolic scope, as well as lower HPIreactivity, to an angling capture and air exposure stressor. To address the second objective, we quantified the rate at which largemouth bass were captured inside of an FPA relative to capture rates outside of the FPA, using a common team of anglers. Base on a number of factors including angling experience, learning, social learning and potential differences in physiological properties, we predicted that rates of fish capture would be higher inside the FPA relative to angling sessions outside the FPA. Together, this is one of the first studies to quantify how spatial protection in the form of FPAs can provide evolutionary-enlightened benefits. Results from this study will help to define the impacts that recreational angling may be having on the evolutionary trajectory of wild fish populations, and the potential role of non-fished individuals to act as benchmarks for angling selection research.

4.3 Methods

4.3.1 Study site

All work was conducted on three inter-connected lakes within the Rideau Waterway system (Ontario, Canada) including Opinicon Lake (OP), Newboro Lake (NB), and Big Rideau Lake (BR). Each of the three lakes have self-sustaining largemouth bass populations and are well known by local and non-resident anglers for their quality angling potential (Hogg *et al.*, 2010). Furthermore, Big Rideau Lake supports the greatest angling pressure (as measured by angling effort/day) of all lakes in Eastern Ontario (Hogg *et al.*, 2010). More importantly, these lakes also house long-standing FPAs that were established in the 1930's and 1940's by the Ontario Ministry of Natural Resources and Forestry (OMNRF, formerly Lands and Forests; Ontario Department of Game and Fisheries, 1946). These protected areas prohibit all forms of recreational angling year-round within the FPA borders, whereas the remaining areas of the lake have been open-access to recreational angling and some small scale commercial harvest operations through time (Larocque *et al.*, 2012). The FPAs within each lake vary considerably in size relative to the total surface area of each lake. Specifically, the surface area of Opincion Lake is 8.66 km² with a cumulative FPA coverage area of approximately 1.0 km² (~11 % FPA coverage area of Big Rideau Lake is 45.36 km² with an FPA coverage area of 0.57 km² (~1 % FPA coverage) and the surface area of Newboro Lake is 17.01 km² with a cumulative FPA coverage area of Newboro Lake is 17.01 km² with a cumulative FPA coverage).

4.3.2 Stress responsiveness experiment

Largemouth bass used in the stress responsiveness experiment were captured by rod-and-reel angling using a range of different soft-plastic lures typical of bass angling (i.e., worms, creature baits, and frogs) in an effort to maximize the variation in fish behaviour (Wilson et al., 2015). Due to the possibility of largemouth bass moving into/out of the FPA and being captured and misidentified, sampling within the FPAs was conducted at the furthest possible point of access from FPA boundary lines, and angling outside of the FPA was conducted far from the FPA (see Zolderdo et al., 2019). Once hooked, all fish were fought for a standardized 20 s, hoisted from the water using a rubber-meshed landing net to reduce potential tissue damage and placed in a foam lined trough devoid of water. A blood sample (approximately 1 ml) was taken from the caudal vasculature using a 21- gauge needle and a 3 ml vacutainer syringe containing lithium

heparin (B.D. Vacutainer, Franklin Lakes, NJ) within the first 60 s of being in the trough to provide a baseline value for plasma glucose and cortisol. Largemouth bass were then subjected to a 3-min air exposure (a period of time that is sufficient in elevating plasma cortisol levels; Lawrence et al., 2018). During this time, fish were measured (total length (TL) to the nearest mm), weighed (to the nearest g) and transferred to cylindrical bags with two permeable mesh endcaps submerged alongside the research boat for 27 minutes. Following the 27-minute holding period (i.e., a period determined to achieve maximal GC response in bass; McConnachie et al. 2012), largemouth bass were removed from the recovery bags and subject to a second blood sample following the procedure outlined above. This procedure allowed us to quantify the magnitude of the stress response for each individual (McConnachie et al. 2012; Louison et al. 2017). After the second blood sample fish were released.

All blood samples were processed directly aboard the research boat. Blood glucose levels for both the initial and post-holding period were measured using a handheld point-of-care blood glucose meter (Accucheck Compact Plus, Roche, Basel, Switzerland), a technique that has been validated for fish (Stoot et al., 2014). The remaining whole blood was centrifuged at 2500 rpm, and plasma and red cells were transferred into two separate aliquots and flash frozen in liquid nitrogen for future cortisol analyses. Plasma cortisol concentrations were analyzed using a commercial radioimminoassay kit (MP Biomedicals, Orange-burg, NY) following the methodology of O'Connor et al. 2009. Fish used in this experiment did not differ in size (mm) across lakes, or between sample locations (Table 4.1).

4.3.3 Metabolic phenotype experiment

All fish used in the metabolic phenotype experiment were captured between July 18 – Aug 31, 2018, in the same manner and locations as fish used in the stress responsiveness

experiment above. For this study, however, all captured largemouth bass were transported by boat to QUBS in coolers (dissolved oxygen saturation never dropped below 70% during transport; Handy Polaris, OxyGuard, Farum, Denmark). At QUBS, largemouth bass were held overnight in 200 L flow-through holding tanks supplied with ambient Opinicon Lake water at a rate of approximately 18 L/min where they were allowed to recover from handling and hauling stressors (McConnachie *et al.*, 2012). Due to the possibility of transient largemouth bass, collections from within the FPAs were conducted at the furthest possible point of access from FPA boundary lines (see Zolderdo et al., 2019). Fish used in this experiment did not differ in size (g) between sample locations within a lake. However, fish were approximately 15 % larger in BR, regardless of capture location, as compared to fish sampled from OP and NB Lakes (see Appendix C for details). Similarity, Fulton's condition factor did not differ between sample locations, but fish from BR scored greater condition factor on average when compared to fish from OP and NB lakes regardless of location (Table 4.1).

All metabolic assessments were performed using static, intermittent-flow respirometry (Loligo Systems[™], Tjele, Denmark) following methods outlined by Redpath et al. (2010), with a few modifications. Briefly, after the overnight acclimation period (approximately 7:00-8:00 am), each fish was removed from the holding tanks and placed into a 100 L circular tank, where it was exercised to exhaustion via manual chasing and tail pinches (Louison et al., 2017). Largemouth bass were deemed to be exhausted when they stopped responding to the stimulus. Fish were then removed from the exercise tank and held in a rubberized net for a 1 min air exposure post-exercise, before being placed into one of four 11.78 L respirometry chambers submerged within one of two ~200 L tanks equipped with multiple air stones to ensure oxygen saturation remained at 100% throughout the entire testing period. The measurement cycles used following exercise

were a 10 min 'flush' period, 3 min 'wait' period, and a 10 'min' measurement phase, which allowed r^2 values for each data point to be > 0.9 (Svendsen *et al.*, 2016). Measurements of oxygen saturation in each chamber were taken every 5 s during the measurement phase by a fiber-optic probe that allowed for the calculation of oxygen consumption (M_{O2}, in mg O₂ consumed kg⁻¹ fish h⁻¹). The highest individual M₀₂ value obtained from the measurement cycles was taken as the fish's maximum metabolic rate (MMR). Largemouth bass were left undisturbed within chambers overnight to collect standard metabolic rate data (SMR), calculated as the mean of the five lowest M₀₂ values (Nelson and Chabot, 2011; Louison et al. 2017). Aerobic scope (AS) was calculated as the difference between MMR and SMR (Redpath et al., 2010; Chabot et al., 2016; Louison et al., 2017). Fish were promptly removed from the respiormetry chambers in the morning (between 7:00-8:00am), and released, and this process started again with 4 new fish. During respirometry work, largemouth bass from different lakes, as well as FPA and main-lake fish, were run concurrently when possible, and the order that fish were processed was randomized. All equipment (chambers, pumps and tubing) was sterilized regularly with a 10 % bleach solution, and background respiration was evaluated periodically within each of the respirometry chambers and found to be negligible (Chabot et al., 2016). Each of the tanks were equipped with water heaters to ensure water temperatures remained between 22-25 °C during the duration of this study period.

4.3.4 Catch per unit effort

Catch per unit effort (CPUE) was calculated separately for FPA and main-lake based on the number of largemouth bass ≥ 200 mm caught per hour angling for all fish sampled during the stress responsiveness experiment. Approximately 55 hrs of angling time occurred (17:46:30 within the FPAs, and 36:50:16 within the main-lake areas) to capture the 193 largemouth bass used in this study (n=98 for FPAs, and n=95 for main-lake; see Appendix C for details). As multiple areas were fished within each lake during data collection, CPUE data were calculated as individual blocks of time only when angling occurred; angling start time was noted once angling began, and stopped once the last fish was captured, for each area fished. Calculating CPUE in this manner enabled data to be standardized through the removal of biases including, but not limited to, travel time between areas and initial equipment set up time upon arrival in new fishing areas. However, the start time for 6 of the 21 fishing sessions (n=1 FPA, and n=5 main-lake) were not precisely recorded, as such, the time at first fish capture was recorded as the start time for those fishing sessions. Furthermore, angling was conducted from one boat using the same 4 anglers, and tactics, for each angling session across each location fished.

4.3.5 Data analysis

Differences in physiological parameters were quantified in two different ways using R version 3.6.3 (R Core Team 2020). First, physiological parameters, as well as CPUE data, were compared for fish captured inside FPAs against those captured in the main-lake using a linear mixed-model approach (Bolker 2008; Bolker 2015). We used a mixed modeling approach to compare fish from the FPA and main-lake as it allowed us to treat lake as a random effect. Treating lake as a random effect allowed us to consider the lakes we used as random samples drawn from a larger 'population' of lakes (Bolker 2015), thereby allowing us to combine information across lakes and expand the scope of inference from our analyses beyond our 3 sites (Bolker et al. 2009; Bolker 2015). Given that nested factors are typically conceptually random factors (Quinn and Keough, 2002), we chose not to nest our main effect (lake location) within our random lake variable as to avoid violating model criteria (Schielzeth and Nakagawa, 2013). Mixed models were analyzed using the 'lme4' package (version 1.1-21) (Bates et al. 2015), and

the 'ImerTest' package (version 3.1-1) (Kuznetsova et al. 2017). If a significant difference was detected in a mixed model, Tukey multiple comparison tests were performed with estimated marginal means (least-squares means) using the 'emmeans' package (Version 1.4.4) (Searle et al. 1980; Lenth 2016). Marginal and conditional r² values were generated using the 'MuMIn' package (version 1.43.15) (Barton 2019).

In cases where grouping variables have fewer than five levels (as we have for our lake variable), uncertainty exists as to whether that variable should be treated as a fixed or random effect (Bolker et al. 2009; Bolker 2015). As such, in an effort to acknowledge this uncertainty, we supplemented our mixed models with a two-way analysis of variance (ANOVA) that did not use random effects. For these two-way ANOVAs, the main effects in the models were lake (Opinicon, Newboro and Big Rideau), location (fish captured inside the FPA and those caught in the main-lake) and their interaction. If a significant fixed effect was detected in the ANOVA model, Tukey multiple comparison tests were again performed using 'emmeans' (Searle et al. 1980; Lenth 2016).

All models were validated using standard techniques that included generating quantilequantile plots to quantify normality, fitting residuals versus fitted values to verify homogeneity, and examining residuals versus each explanatory variable to check for independence (Zuur et al. 2009). The presence of potential influential data points was also assessed (Zuur et al. 2009). In the event that normality or variance assumptions were not met, data were rank transformed, models were re-run, and assumptions were confirmed (Conover and Iman 1981; Iman et al. 1984; Potvin and Roff 1993). All data are presented as means \pm standard error (SE) where appropriate, and differences were considered significant if α was < 0.05.

4.4 Results

4.4.1 Stress responsiveness experiment

When examined across study lakes, there were no differences in baseline cortisol, maximum cortisol, or cortisol responsiveness between fish captured within the FPAs and fish captured from the main-lake; results were consistent both for mixed model analyses (Table 3.1) as well as two-way ANOVA models (Figure 4.1 a-f, Table 4.2). When examined within lakes, largemouth bass captured from the FPA in BR had a cortisol scope that was almost half that of fish captured from the main-lake (Figure 4.1 e; Table 4.2). No differences were observed in the glucose parameters evaluated between locations, or across lakes (Table 4.1, 4.2, and 4.3).

4.4.2 Metabolic phenotype experiment

When all study lakes are considered together, there were no differences in SMR between fish captured within the FPA relative to individuals captured from the main-lake (Figure 4.3 a and b; Table 4.1). However, when examined across lakes, largemouth bass from Newboro Lake showed SMR values that were approximately 16 % greater than both Opinicon and Big Rideau Lakes (Figure 4.3 a; Table 4.3). Similarly, there were no differences in MMR across lakes or between FPA and main-lake regions (Figure 4.3 c and d; Tables 4.1 and 4.2). When examined across locations, fish residing inside FPAs showed AS values that were approximately 13 % greater than fish captured in the main-lake (Figures 4.3 e and f; Tables 4.1 and 4.2). *CPUE*

4.4.3 Catch per unit effort experiment

Angler catch per hour of fishing effort (CPUE) was significantly higher inside of FPAs relative to the main-lake areas, with catch rates approximately 1.5× higher inside both the Big

Rideau Lake and Newboro Lake FPAs, whereas catch rates were approximately 2.5× higher

inside the Opinicon Lake FPAs (Figure 4.2; Table 4.1, 4.2; also see Appendix C for details).

Table 4.1: Results of linear mixed effects models examining the factors influencing various physiological characteristics, as well as catch per unit angling effort (CPUE), of largemouth bass residing inside and outside of freshwater protected areas (FPAs), across three study lakes (Opinicon Lake, Newboro Lake, and Big Rideau Lake). Fixed effects for the models included 'location' (FPA and main-lake areas). Models included 'Lake' as a random effect. R^2_m refers to r^2 values for models without random effects, while R^2_c refers to conditional r2 values, which include random effects in the model.

	Estimate	SEM	df	t	р	$\mathbf{R}^{2}_{\mathbf{m}}$	R ² c
Baseline Cortisol							
Intercept	3.42	0.62	2.24	5.48	0.024	< 0.00	0.24
Location	-0.08	0.32	122.0	-0.25	0.80		
Maximum Cortisol							
Intercept	70.90	11.35	2.56	6.24	0.013	< 0.00	0.11
Location	2.97	8.46	122.0	-0.35	0.73		
Cortisol Scope							
Intercept	67.26	7.66	2.72	8.39	0.005	< 0.00	0.08
Location	1.17	6.36	122.0	0.184	0.85		
Baseline Glucose							
Intercept	2.71	0.07	3.26	38.70	<0.001	0.001	0.05
Location	-0.03	0.07	149.0	-0.44	0.66		
Maximum Glucose							
Intercept	6.08	0.30	3.61	20.51	<0.001	< 0.00	0.03
Location	-0.15	0.32	149.0	-0.46	0.64		
Glucose Scope							
Intercept	3.37	0.26	4.33	13.11	<0.001	< 0.00	0.01
Location	-0.121	0.32	149.0	-0.38	0.71		
Standard Metabolic Rate							
Intercept	27.0	5.3	2.8	5.1	0.18	0.04	0.22
Location	-7.3	4.2	57.3	-1.7	0.09		
Maximum Metabolic Rate							
Intercept	33.58	3.35	5.94	10.04	<0.001	0.02	0.04
Location	5.56	4.57	58.10	1.22	0.23		
Aerobic Scope							
Intercept	36.340	3.00	59.0	12.11	<0.001	0.073	0.07
Location	11.20	4.41	58.30	2.55	0.0134		
CPUE							
Intercept	8.23	2.66	2.27	3.10	0.08	0.259	0.689

Location	6.86	1.69	17.1	4.06	<0.001		
Bold italicized values indicated statistical significance at $\alpha < 0.05$							

Bold, italicized, values indicated statistical significance at $\alpha \le 0.05$

Table 4.2: Results of analysis of variance (ANOVA) models examining the factors influencing various physiological characteristics, and catch per unit angling effort (CPUE), of largemouth bass residing inside and outside of freshwater protected areas (FPAs) across three study lakes including Opinicon Lake, Newboro Lake, and Big Rideau Lake. Fixed effects for the models included 'Lake' and 'location', as well as the interaction between lake and location.

	DF	Sum	Mean Sq	F	р
Standard Metabolic Rate					-
Lake	2	311	1555	5.842	0.005
Location	1	798	797.7	2.996	0.089
Lake:Location	2	358	178.8	0.672	0.515
Maximum Metabolic Rate					
Lake	2	3010	1505	0.912	0.408
Location	1	2791	2791	1.691	0.199
Lake:Location	2	4068	2043	1.238	0.298
Aerobic Scope					
Lake	2	79.8	39.90	13.266	<0.001
Location	1	6856	6856	5.877	0.018
Lake:Location	2	5262	2631	2.255	0.114
Baseline Cortisol					
Lake	2	79.80	39.90	13.226	<0.001
Location	1	0.20	0.20	0.068	0.795
Lake:Location	2	25.20	12.580	4.171	0.017
Maximum Cortisol					
Lake	2	25183	12591	6.017	0.003
Location	1	277	277	0.132	0.716
Lake:Location	2	23720	11860	5.668	0.004
Cortisol Scope					
Lake	2	22432	11216	5.342	0.006
Location	1	292	292	0.139	0.709
Lake:Location	2	25112	12556	5.980	0.003
Baseline Glucose					
Lake	2	1.240	0.620	3.869	0.023
Location	1	0.027	0.027	0.170	0.681
Lake:Location	2	0.164	0.082	0.512	0.60
Maximum Glucose					
Lake	2	19.0	9.504	2.398	0.094
Location	1	0.8	0.773	0.195	0.659
Lake:Location	2	5.0	2.510	0.633	0.532
Glucose Scope					
Lake	2	13.0	6.479	1.649	0.196

Location	1	0.50	0.510	0.130	0.719
Lake:Location	2	3.70	1.874	0.477	0.622
CPUE					
Lake	2	328.8	164.39	11.47	<0.001
Location	1	216.4	216.39	15.01	0.001
Lake:Location	2	9.9	4.93	0.34	0.71

Bold, italicized, values indicated statistical significance at $\alpha \le 0.05$

Table 4.3: Data values for blood glucose responsiveness between largemouth bass populations residing inside fresh water protected areas (FPA) and within the main-lake areas across each of the study lakes including Opinicon Lake (OP), Big Rideau Lake (BR), and Newboro Lake (NB). See Results for details.

		FPA			Main-	
					Lake	
Physiological variable	OP	BR	NB	OP	BR	NB
Baseline Glucose (mmol 1 ⁻¹)						
N (fish)	20	23	32	22	26	30
Mean	2.6	2.7	2.9	2.7	2.7	2.8
Standard Error	0.08	0.08	0.08	0.08	0.07	0.08
Maximum Glucose (mmol l ⁻¹)						
N (fish)	20	23	32	23	26	30
Mean	1.8	6.5	6.6	5.8	6.1	6.3
Standard Error	0.41	0.44	0.28	0.42	0.46	0.38
Glucose Responsiveness (mmol 1 ⁻¹)						
N (fish)	20	23	32	22	26	30
Mean	2.8	3.8	3.7	3.2	3.5	3.5
Standard Error	0.40	0.45	0.29	0.41	0.45	0.4



Figure 4.1: Comparison of stress response variables of largemouth bass from inside and outside of freshwater protected areas (FPA) across study lakes. Panel (a) represents comparisons of baseline cortisol concentrations between study lakes, (c) represents comparisons of maximum cortisol concentrations between study lakes, and (e) represents comparisons of cortisol scope between study lakes. Whereas, panels (b), (d), and (f) represent that same corresponding comparisons but at a location level only. Different lowercase letters and asterisks in (a) denote a significant difference at a level of \propto =0.05 among treatment groups. Asterisk in (b) and (f) represent a significant difference at a level of \propto =0.05 between freshwater protected area (FPA) and Main-lake populations. See Results for details.



Figure 4.2: Catch-per-unit-effort (CPUE) data for largemouth bass captured via angling techniques inside (n= 98) and outside (n=95) of freshwater protected areas (FPAs) across each of the study lakes, including Opinicon Lake (OP), Big Rideau Lake (BR), and Newboro Lake (NB). An asterisk represente differences in catch rates between FPA and main-lake areas at a given lake, while dissimilar letters show differences in catch rates across lakes.


Figure 4.3: Comparison of metabolic variables of largemouth bass from inside and outside of freshwater protected areas (FPA) across three study lakes. Panel (a) represents comparisons of standard metabolic rate (SMR) between study lakes, (c) represents comparisons of maximum metabolic rates (MMR), and (e) represents comparisons of aerobic scope (AS). Panels (b), (d), and (f) represent that same corresponding comparisons but at a location level only. Different lowercase letters and asterisks in (a) denote a significant differences among treatment groups. Asterisk in (b) and (f) represent a significant difference between freshwater protected area (FPA) and Main-lake populations.

4.5 Discussion

Largemouth bass populations inhabiting FPAs had greater AS compared to individuals captured from adjoining main-lake areas across 3 replicate lakes. This finding supports the hypothesis that angling may be impairing the physiological phenotypes in wild fish populations (Hollins et al., 2018; Duncan et al., 2019). AS is defined as the ratio of the maximum sustainable rate of aerobic metabolism relative to the basal/standard metabolic rate, which sets the threshold for aerobic processes that can be performed simultaneously (Killen *et al.*, 2015b; Treberg *et al.*, 2016; Hollins et al., 2018). Reductions in AS at a population level can be highly concerning as this suggests a reduced scope for activity available to carryout essential life-history activities, which, in turn, can restrict key physiological functions including the capacity to adapt to dynamic environmental conditions (i.e., climate change) and result in fitness level implications (Duncan et al., 2019). As such, the lower AS shown by largemouth bass in the main-lake suggests that these individuals may be experiencing constrained energy partitioning capabilities, potentially resulting in a reduced ability to perform energy intensive activities (e.g., parental care; Cooke et al. 2006; Sutter et al. 2012) relative to individuals residing in the FPA on that same lake. Recent telemetry work by Zolderdo et al. (unpublished) has shown that FPA largemouth bass have high site fidelity within the protected area boundaries, especially during the spring-summer seasons. As such, it is likely that FPA individuals, such as those captured in the current study, are naïve to angling. In contrast, largemouth bass from the main-lake would have been exposed to anglers, likely subjecting them to harvest, incidental mortality (i.e., deephooking, angling stress; Siepker et al. 2007), and/or angling-induced reproductive failure (Philipp *et al.*, 1997), which has the potential to selectively remove certain phenotypes from the population.

While metabolic parameters have not been shown to drive angling vulnerability in largemouth bass (Louison et al. 2017), exposure to angling-induced selection has been shown to have consequences for the metabolic properties of largemouth bass, with individuals captured from lakes with no angling pressure (Hessenauer et al., 2015), or those that had been shown to be highly vulnerable to angling in an experimental setting (Redpath et al., 2010) having increased metabolic performance, relative to fish that had been subjected to angling, similar to the current study. The maintenance of high-performance AS phenotypes as a result of protection from human disturbance is consistent with both theory and empirical studies linking exploitation with functional trait diversity (Mouillot et al., 2013; Diaz Pauli and Sih, 2017; Hollins et al., 2018). For examples, studies with red roman (*Chrysoblephus laticeps*), a commercially targeted marine fish, showed that protection from hook-and-line fisheries from a marine protected area resulted in increased AS capacity (Duncan et al. 2019). Therefore, through reduced exploitation, the highperformance AS phenotype observed in largemouth bass populations inhabiting FPAs may more closely represent the optimal threshold for aerobic performance in this species indicative of natural selection processes (Allendorf and Hard, 2009; Bull and Maron, 2016; Otto, 2018). Overall, largemouth bass residing inside of an FPA had higher AS capacity than individuals captured outside of the FPA within the same lake.

Catch-per-unit-effort was significantly higher inside of the FPAs relative to the adjacent main-lake areas across the 3 sites examined. For recreational fisheries, high CPUE is desirable and highly sought after by the angling community and resource managers alike, and a number of conditions can interact to influence capture rates. For example, the interaction between habitat and prey availability can be a key component influencing CPUE rates, as habitat availability/quality can support a higher density and diversity of food resources, which has been

correlated to capture likelihood in largemouth bass. Specifically, Keiling et al. (2020), observed higher capture rates of largemouth bass in systems with lower prey resource availability. In the current series of lakes, not only is habitat similar between FPA and the main-lake areas sampled, but prey resources are greater inside of the FPAs relative to the main lake areas (Zolderdo et al., 2019). Thus, it likely that the higher CPUE in the FPA populations are not related to habitat, or differences in prey availability. However, increased capture rates could be due to a reduced experience with fishing lures as fish residing in the FPA likely have not experienced a fishing lure in almost a century (Louison et al., 2019). Higher population densities of largemouth bass inside the FPAs may have also influenced CPUE rates (Zolderdo et al., 2019). However, CPUE may not accurately reflect population density as capture rates can remain high even in systems with low population densities due to habitat aggregation processes (Dassow *et al.*, 2020). It is also important to note that some angling trips were short due to high catch rates thereby limiting the number of replicates of fishing excursions, and also that variance in CPUE was high within some sites. Despite these caveats, however, the difference in CPUE observed between FPAs and main-lake areas are quite pronounced suggesting an accurate representation of the CPUE metrics occurring between the FPAs and adjacent main-lake areas. Regardless of the mechanism, angler catch rates were almost twice as high inside the FPAs when compared to outside main-lake areas despite standardizing the anglers and tackle engaged in fish capture.

No differences were detected in baseline cortisol, cortisol responsiveness, or cortisol scope when all FPA and main-lake populations are considered together. Cortisol responsiveness has previously been identified as the strongest driver of angling vulnerability in largemouth bass (relative to behavioral metrics such as boldness or exploration), with individuals expressing lower rises in plasma cortisol following a stressor being more likely to be captured via angling (Louison et al. 2107). Furthermore, HPI-axis sensitivity is known to be heritable, and correlated to certain behavioural traits linked to angling vulnerability including bolder personality types (Øverli et al. 2002; Oswald et al. 2012, Wilson et al. 2015; Lennox et al. 2017; Koeck et al. 2019). These bold behavioural types have also been correlated to high AS phenotypes (Killen et al., 2014; Binder et al., 2016). Despite a lack of detectable differences across all lakes combined, differences in cortisol values were observed for Big Rideau Lake when examined individually, with individuals residing in the FPA having a lower cortisol responsiveness than those from the main-lake. This finding supports current research and theory linking angling vulnerability with fast-POLS phenotypes. For instance, individuals aligning under the fast-POLS profile express bolder behaviours coupled with a reduced HPI-axis responsivity (Réale et al., 2010). This profile fits with the high-performance AS phenotypes observed inside the FPAs, as well as recent work showing increased parental aggression of FPA largemouth bass (Twardek et al., 2017). It is unclear why this finding was isolated to only Big Rideau lake, but it may be possible that undetected/unmeasured differences in FPA parameters (e.g., coverage area of FPA) exist between replicate lakes. For example, the FPA on Big Rideau lake has the most restrictive entrance boundary of all replicate FPAs (Zolderdo et al., 2019), which may increase the protective capacity, or alternatively, reduced fish migration in/out of the FPA over time relative to the other FPAs, potentially making this FPA population more isolated relative to the other locations examined. However, as cortisol responsiveness is directly correlated to capture likelihood in largemouth bass, the establishment of FPAs have the potential to protect pro-active stress coping phenotypes, which, in turn, may increase capture potential.

Although, fisheries-induced selection remains the most parsimonious explanation for the observed trends in both metabolic parameters and cortisol, aspects of phenotypic plasticity and/or environmental differences may also have been partially responsible for the trends observed. For example, Zolderdo et al. (2019), observed higher densities and biomass of shiner species within the Rideau Lake FPAs as compared to the adjacent main-lake areas. Food availability has been linked to aerobic metabolism, where abundant access to food can lead to increased SMR and AS in certain fish species (Burton *et al.*, 2011; Auer *et al.*, 2015a), and the increased aerobic metabolism of FPA populations may have been influenced by food availability. However, it is important to note that no differences were detected in largemouth bass condition factor across populations in the current study, suggesting that food is not a limiting factor within main-lake areas.

Alternatively, it is possible that unmeasured variances in environmental factors (e.g., water chemistry; Pickering and Pottinger 1987) may have influenced the physiological differences observed. However, all fish were collected from similar habitats within both FPA and main-lake areas to reduce any potential biases associated with environment. Previous research evaluating the Rideau Waterway FPAs have also noted a high degree of habitat similarity to adjacent main-lakes areas (Twardek *et al.*, 2017; Zolderdo *et al.*, 2019; Moynes *et al.*, 2020). As such, intra-lake habitat differences between sampling locations are likely negligible, if present at all, and thus may not have contributed to the physiological differences observed. In fact, differences in AS were seen across the three replicate lakes despite this potential for inter-site variation. It is also important to note that the use of angling as the only method to collect fish may have created a sampling bias within the dataset. Angling can target specific personality types (Wilson *et al.*, 2015; Arlinghaus *et al.*, 2017), which has been linked to metabolic

performance in certain species, including largemouth bass (Redpath et al., 2010; Hollins et al., 2018). For example, parental care capacity in male largemouth bass is positively correlated to aerobic metabolism, and also to angling vulnerability (Sutter et al., 2012). However, all sampling for the current study was conducted outside of the parental care period, when boldness and aggression are known not to be drivers of angling vulnerability in largemouth bass (Louison et al., 2017; Keiling et al., 2020), and, while not quantified, it is likely that female fish were captured in addition to males. Yet, angling vulnerability outside of the parental care period in largemouth bass is negatively correlated to food availability as well as prior angling experience (Hessenauer et al., 2015; Louison et al., 2019; Keiling et al., 2020). As such, a sampling bias for naïve, and hungry, individuals may have occurred across locations. Thus, angling may have potentially reduced the variance in phenotypes sampled, and future work should use multiple sampling gears (i.e., trap netting) when collecting fish to avoid possible sampling biases. Although, this study has not specifically tested fisheries-induced evolution (i.e., comparisons across generations), it has shown evidence that differing fisheries management strategies applied within the same lake systems can alter the distribution of AS phenotypes in wild fish populations.

Freshwater habitats and the biodiversity they support are among the most imperiled worldwide (Dudgeon *et al.*, 2006a; Abell *et al.*, 2007; Reid *et al.*, 2019), and the main threats facing freshwater ecosystems stem from anthropogenic resource uses (e.g., exploitive fisheries; Arthington et al. 2016). The use of protected areas has been a cornerstone conservation strategy in terrestrial (Watson *et al.*, 2014; Chu *et al.*, 2018), and now more recently, marine environments (Agardy, 1994; Halpern and Warner, 2002; Edgar *et al.*, 2014). Despite the host of benefits associated with the establishment of protected areas, their application within freshwater systems has been limited, and consequently research into their effectiveness/utility is lacking (Suski and Cooke, 2007; Hermoso *et al.*, 2016; Acreman *et al.*, 2020). Previous studies have shown a number of conservation benefits from the presence of FPAs, including improved biodiversity, increased species abundance, and greater reproductive output (Suski *et al.*, 2002; Hedges *et al.*, 2010b; Zolderdo *et al.*, 2019).

The current study provides 4 additional benefits that can be realized from FPAs that limit angling pressure that should help protect biodiversity and promote their use in the future. First, the current study is the first to show population level physiological benefits from establishing a FPA through increased AS. A greater AS capacity can increase the scope of activity for an animal to perform work, ultimately reducing potential energy budgeting issues (e.g., growth and/or reproduction), which can result in fitness level benefits (Priede, 1985, Evans, 1990; Claireaux and Lefrançois, 2007). For example, reproductive fitness is positively correlated to AS capacity in largemouth bass, where parental males with greater aerobic performance achieve higher reproductive success (Redpath et al., 2010; Sutter et al., 2012). Second, while not pronounced across all sites, data from 1 site suggest that the presence of a FPA can reduce cortisol responsiveness, which can increase the likelihood of capture for largemouth bass. Beyond increased capture likelihood, a reduced cortisol responsiveness to challenges may improve adaptability to dynamic environmental conditions (e.g., climate change), as negative health consequences can arise through sustained, over-activation, of the HPI-axis (Koolhaas et al., 1999; Barton, 2002; Romero, 2012). Third, the presence of the FPA provides a physiological 'baseline' against which the impacts of angling, and other anthropogenic stressors, could be quantified. Fourth, spatial protection was found to significantly improve CPUE. Not only are high CPUE metrics sought after by resource managers and anglers alike, but are also potential

markers of FIE. Together, these 4 benefits, when coupled with previous work on protected areas for largemouth bass and aquatic communities, should encourage managers and practitioners to think about implementing protected areas to enhance fisheries, particularly for a fish species subjected to intensive recreational fisheries practices. It is important to note that these benefits were achieved, not through closure of an entire lake system, but rather through the establishment of intra-lake exclusions zones, ranging from 1-20% of lake area. However, the importance of certain physical characteristics of the FPAs examined (e.g., coverage area, water depth, spawning habitat), which contributed to the successful protection of the high-performance AS phenotypes, is unknown. These FPAs have been in place for almost a century, so it is not known how long it would have taken for differences to arise. As such, I urge future research to focus efforts into identifying which habitat factors contribute most significantly to protective capacity, along with potential temporal effects, in an effort to maximize conservation gains. Together, the results from this study illustrate the benefits of how spatial protection can be utilized as a conservation tool impacting multiple levels of organization.

In conclusion, the current study provides evidence that FPAs can provide benefits at a number of levels, including protecting high-performance AS phenotypes from angling selection and enhancing angler catch rates. The high degree of similarity in phenotypic traits observed in all three wild populations strongly supports the hypothesis that recreational angling may indeed be a critical mechanism altering the functional trait diversity in wild fish populations. The findings presented here support the use of FPAs as a conservation strategy to counteract the selective potential associated with recreational fisheries practices along with the potential for unexploited FPA populations to serve as benchmarks to further investigate the evolutionary trajectory imposed by recreational angling on wild fish. Furthermore, the current study highlights

the effectiveness of exclusion zones to protect exploited fish in a more natural physiological state, which suggests the potential for lakes that house intra-lake FPAs to serve as holistic study systems to investigate other factors associated with human-use activities through comparative evaluations using unexploited FPA populations as a natural reference. With evidence highlighting physiological differences associated with spatial protection, further research should employ 'common garden' based approaches to more holistically evaluate physiological, behavioural, and genetic differences under controlled experimental conditions. Indeed, the results of the current study provide evidence linking metabolic performance with differing fisheries management strategies, likely as a result of FIE processes, which should encourage resource managers to consider utilizing protected areas as an evolutionary-enlightened management tool, especially for a fish species subjected to intensive recreational fisheries practices.

Chapter 5: General conclusions and future directions

The research presented in this dissertation describes how spatial protection, in the form of FPAs, can provide multiple conservation benefits to freshwater fish communities, and supports the use of FPAs as an effective resource management strategy to enhance the conservation of freshwater fish populations. Through intra-lake evaluations of similar habitats that are managed under different fisheries management objectives (FPAs vs. fishable waters), the Rideau Waterway system allowed for comparative, unbiased, evaluations as each lake-area (i.e., FPA, transition zones, and main-lake areas) analyzed consist of similar environmental and biological parameters. As such, accurate and reliable inferences regarding the effectiveness and utility of these intra-lake FPAs, using a series of comparative biological and ecological evaluations, could be achieved. In this thesis, I demonstrate that the protection provided by the Rideau Waterway

FPAs strongly benefitted largemouth bass, a heavily exploited sportfish and focal species for which these FPAs were created, through increased population densities within the protected area boundaries (Chapter 2, 3). Furthermore, the protection provided by these FPAs also indirectly benefitted several non-target fish species by supporting increased population densities and species richness (Chapter 2). Beyond serving as a mechanism to improve fish community ecology dynamics, FPAs were also found to protect key phenotypes linked to angling vulnerability in largemouth bass, suggesting that this form of spatial protection may provide evolutionary-enlightened benefits (Chapter 4). Collectively, I found remarkable consistency in results across all replicate lakes examined, suggesting that the conservation benefits achieved from the establishment of the Rideau Waterway FPAs may be highly transferable to other freshwater systems. Thus, FPAs used in conjunction with other management tools could be an effective strategy to promote freshwater fish conservation as evidenced from the data presented in this dissertation. Below, I summarize the salient findings and general conclusions of each chapter:

In Chapter 2, I demonstrate that the protection provided by FPAs yielded benefits across the fish community, yet, the most pronounced benefits (in terms of abundance and biomass) were observed in largemouth bass as well as various shiner species. Although not statistically significant across all FPAs examined, gradient effects (i.e., spillover) were observed where fish abundance, biomass, and species richness (in certain FPAs) decreased with increasing distance from the FPA boundaries. Spillover, which generally occurs through density-dependent processes, is an important biological metric used to infer the health and status of the fish communities inhabiting PAs. These findings outline the conservation potential of FPAs to enhance fish community structuring both inside and outside of protected area boundaries, highlighting the value of spatial protection to advance fisheries management practices in freshwater systems. Despite the benefit of protection on fish community dynamics, increases in fish species richness (a proxy for biodiversity) was not consistently correlated with protection. However, improving biodiversity was not an initial objective of the FPAs evaluated, thus was not a consideration during their establishment. As such, the increased species richness observed within certain FPAs represents an unintentional and indirect benefit of spatial protection, highlighting the potential of FPAs to bolster biodiversity irrespective of intent, which is an avenue I would like to investigate further (see Future Directions).

After establishing that the spatial protection provided by the Rideau Waterway FPAs uniformly benefitted largemouth bass through increased population densities, I selected one representative FPA (the BRL FPA) to further investigate the seasonal space-use dynamics of adult and sub-adult largemouth bass (Chapter 3). Here, I observed that occupancy was highest in the spring-summer seasons, declining in the fall and remaining low over the winter period. Furthermore, this occupancy pattern was repeatable between years, indicating a high seasonal site fidelity within the FPA borders. Occupancy within the FPA was also positively correlated to body size, with larger individuals utilizing the protected area for longer durations of time relative to smaller individuals. These space-use patterns strongly correlate to the known habitat preferences that support two critical life-history periods of largemouth bass, including the reproductive and active growing periods (i.e., spring-summer seasons). However, it is unknown why occupancy declined during the fall-winter periods, but is likely related to a lack of deepwater habitat available to support overwintering within the FPA boundaries. From the data presented, it is clear that the BRL FPA does not provide holistic protection as initially intended, and questions remain to where FPA largemouth bass go during the overwinter period (see Future Directions). However, despite the potential for largemouth bass to emigrate outside of the protective boundaries, the consistent differences observed in the community ecology (Zolderdo *et al.*, 2019), behaviour (Cooke *et al.*, 2017; Twardek *et al.*, 2017), and physiology (see Chapter 4) between FPA and main-lake largemouth bass suggests that the current level of protection provided can elicit conservation benefits at both a population and community level. This data indicates that even partial protection from fisheries exploitation, particularity during critical life-history periods, can provide value to fisheries management practices.

Lastly, I demonstrated that FPAs can protect against the selective potential of recreational fisheries (Chapter 4). As predicted, FPA sourced largemouth bass had greater metabolic capacity (i.e., greater AS) relative to individuals collected from the main-lake areas. A greater AS can increase the scope of activity for an animal to perform work, which can ultimately result in fitness level benefits (i.e., increased capacity to perform reproductive activities; Sutter et al., 2012). Furthermore, CPUE (a proxy for capture vulnerability) for largemouth bass was observed to be significantly higher inside the FPAs. These physiological and capture vulnerability differences between populations of largemouth bass residing inside and outside of FPAs supports the hypothesis that recreational angling may indeed be a critical mechanism altering the functional trait diversity in wild fish populations (Philipp et al., 2015). This is the first research to document intra-lake differences in metabolic phenotype, as a result of fisheries exploitation, in a wild freshwater fish species. Moreover, these results suggest that fish populations inhabiting FPAs may provide a physiological 'baseline' against which the selective impacts of angling may be quantified. This research is also among the first to support the use of FPAs as a means to provide evolutionary-enlightened benefits by protecting phenotypes linked to angling vulnerability in wild fish populations.

A recent systematic review by Acreman et al. (2020) outlines the current scientific understanding of FPAs and their resource management value. However, a deficiency in research pertaining to the effectiveness of FPAs is highlighted as a key knowledge gap, which has led to debate amongst stakeholders regarding the efficiency, utility, and general need for FPAs as a conservation tool. As such, the research carried out in this dissertation sought to address this knowledge deficiency by conducting a series of empirical-based studies to evaluate the effectiveness and utility of multiple long-standing intra-lake FPAs in eastern Ontario. The results obtained from this research showcases a host of biological benefits associated with spatial protection that were remarkably consistent across all FPAs evaluated, indicating an effective and transferable resource management strategy that may help to enhance freshwater fish conservation across multiple levels of biological organization. It is also important to note that these biological benefits were achieved from isolating relatively small areas (i.e., 0.5% - 18% of lake area coverage by the FPAs evaluated), indicating high conservation gains at relatively small spatial scales. The results presented in this thesis outline a conservation success story, as well as an optimistic perspective that these FPAs may provide additional, yet to be realized, benefits that may very well extend beyond fish to include other vertebrate and invertebrate taxa. As threats to freshwater habitats and the biodiversity they support continue to mount, the need for rigorous and effective management strategies are at an all-time high. As such, the research presented in this thesis is timely, as it identifies several conservation benefits associated with spatial protection in freshwater systems, and provides overwhelming support for the continued use of the Rideau Waterway FPAs as a valuable, and effective, fisheries management tool.

Future directions

To date, the use of protected areas within freshwater environments has been limited, largely due to inconsistencies in conservation outcomes stemming from a lack of evidence-based research on the species and/or community to be protected. This is particularly true for the Rideau Waterway FPAs, with some of the first evaluations of these FPAs, and the fish communities that inhabit them, presented in this thesis. As such, the avenues for future work are far reaching. However, to keep within the context of this dissertation, I will present future research avenues in a focused perspective that directly relates to the experiments conducted in this body of work.

Consistent biological and ecological benefits were observed across all FPAs evaluated, However, given the operational age of the Rideau Waterway FPAs (established in the 1940's), a logical question arises regarding the time it will take for conservation benefits, such as spillover, to manifest in a newly established FPA. As such, future work could employ an experimental approach utilizing a series of regulated FPAs to be monitored at various temporal scales (i.e., across seasons and years) in an effort to quantify the timescale needed to provide meaningful resource management benefits. Furthermore, as certain FPAs were better at supporting species richness, another research avenue worth pursing is how FPAs protect and promote biodiversity. Given the similarities in design and objective, future work should investigate the factors and mechanisms which may be driving the differences in species richness observed between the FPAs evaluated. A starting point may be to conduct a fine-scale comparison across all Rideau Waterway FPAs to investigate potential differences in habitat variables, that were unmeasured in this thesis, including, but not limited to, water chemistry (e.g., dissolved oxygen), toxicants (e.g., mercury, DDT, fluorene), and/or microhabitat complexities (e.g., finite differences in macrophyte communities). Results obtained from this type of investigation may help to identify

key factors that may influence space-use dynamics in certain fish species, which may, in part, explain the inter-specific differences in species richness observed between certain FPAs. Collectively, this course of future work would help to explain potential mechanisms underpinning the community ecology benefits associated with the Rideau Waterway FPAs, and may provide transferable knowledge to better aid resource managers in the design and application of future FPAs.

In Chapter 3, largemouth bass were observed to have cyclic movement behaviours, exiting the BRL FPA during the fall-winter months, and returning in early spring. However, from the data collected, it is unclear where the tagged FPA largemouth bass transition to during the cold weather seasons as these movements exceeded the detection capabilities of the acoustic telemetry array that was established. As such, future work should seek to identify where FPA largemouth bass transition to during the cold weather months. To achieve this, a subset of largemouth bass sourced from the FPA could be outfitted with radio telemetry equipment, which would enable the collection of real-time movement information needed to identify overwintering locations. Identifying overwintering areas could then guide the design of a larger, more inclusive, acoustic telemetry array to more holistically investigate the movement dynamics of FPA largemouth bass. By extension, conducting additional research on the spatial ecology of other aquatic species would be of value to better understand how FPAs benefit aquatic biodiversity more broadly.

Although AS capacity was consistently higher in FPA largemouth bass, it is unknown to what extent phenotypic plasticity and/or environmental factors may be influencing these population-level differences. Furthermore, I also recognize the inherent confounds in only comparing fish populations in lakes that contain FPAs. From an analytical perspective, including fish populations from lakes without FPAs would help to evaluate the extent to which FPAs may, or may not, be benefitting main-lake populations. Thus, including lakes without FPAs may act as a functional 'control' group in future experimental designs, and should be considered as such. Therefore, future work should employ a common garden-based experiment to re-evaluate both physiological traits (i.e., metabolic phenotype and stress responsiveness) as well as capture efficiency across multiple generations of FPA and main-lake largemouth bass as well as largemouth bass sourced from lakes without FPAs. This type of experimental approach would allow for strict control over environmental variables (e.g., prey availability, populations density, social learning) that are otherwise impossible to control under natural conditions, while providing a control group to better evaluate the extent to which FPAs may influence main-lake populations. This is a logical next step that would be able to test for, and quantify, evolutionary change through multi-generational assessments. Establishing whether the phenotypic differences observed between FPA and main-lake largemouth bass are genetically based would then enable further investigation into how spillover may facilitate the dispersal of high-performance phenotypes into the main-lake populations.

Appendix A: Equation to calculate fish biomass

Table A.1: Biomass (g) data was calculated for all fish species analyzed using the length (L) - weight (W) equation below:

$$Log_{10} W = a + b \cdot (log_{10} L)$$

When Log W is graphed against Log L, a straight line is formed with the slope of b and a Y-axis (log W) intercept of log a (Schneider *et al.*, 2000). If the length of the fish(es) are known, then the above equation can use the species-specific length-weight parameters to solve for weight (g).

Length-weight equation parameters for the select species analyzed:

Species*	Slope (b)*	Intercept (a)*
Pumpkinseed	3.21060	-5.11138
Bluegill	3.17266	-5.10377
Yellow perch	3.17285	-5.33475
Largemouth bass	3.12735	-5.16885
Shiner**	3.32000	-5.61240

* All species-specific parameters related to length-weight data listed above were sourced from Schneider *et al.* 2000. **The length-weight parameters for common shiner was used as a proxy to provide a biomass index for the grouped shiner species.

Appendix B: Data summary statistics for acoustic telemetry analyses

Table B.1: Summary statistics of tracking metrics for individual largemouth bass in Big Rideau

 Lake

FishI D	TLm m	tag_date	dets	statio ns	first_det	last_det	trackleng th	insi de	outsid e	prop_i n	enter	depa rt	inclu de
1	427	2016-08- 03	115 8	6	2016-09- 16	2017-05- 20	290.3	127	164	0.44	1	1	у
11	354	2016-08- 03	410	6	2016-09- 07	2017-12- 23	507.5	238	270	0.47	4	4	у

12	386	2016-09- 13	15	3	2016-09- 24	2016-10- 15	32.3	32	1	0.97	1	1	У
13	475	2016-09- 13	47	5	2016-09- 22	2016-10- 21	38.3	34	7	0.83	3	2	у
14	352	2016-09- 13	90	4	2016-09- 15	2017-06- 10	270	63	207	0.23	1	1	У
15	423	2016-09- 13	442	5	2016-10- 08	2016-11- 19	67.1	36	34	0.51	3	3	У
16	384	2016-09- 13	118	6	2016-09- 15	2017-04- 14	213.3	37	178	0.17	2	3	У
17	372	2016-09- 13	138	6	2016-09- 14	2018-09- 23	740.2	374	367	0.50	6	6	у
18	320	2016-09- 13	29	3	2016-09- 14	2017-04- 09	208.8	2	207	0.01	1	1	у
19	200	2016-09- 13	74	5	2016-09- 18	2016-10- 27	44.4	21	25	0.46	1	2	у
2	462	2016-08- 03	36	3	2016-08- 17	2016-11- 03	92.9	68	25	0.73	0	1	у
20	445	2016-09- 13	90	3	2016-09- 18	2018-09- 27	744.7	741	5	0.99	3	3	У
21	447	2016-09- 13	215	6	2016-10- 06	2018-07- 19	674.5	508	168	0.75	6	5	у
22	430	2016-09- 13	56	5	2016-10- 07	2017-04- 10	209.7	56	155	0.27	2	2	У
23	283	2016-09- 13	171 9	5	2016-09- 28	2017-06- 22	282.3	277	7	0.98	3	3	У
24	380	2016-09- 13	180 0	6	2016-09- 14	2018-07- 16	671.2	586	87	0.87	3	3	у
26	346	2016-09- 13	294	6	2016-09- 15	2017-04- 12	211.5	53	160	0.25	2	1	у
27	354	2016-09- 13	200	2	2016-09- 14	2016-12- 30	108.5	2	107	0.02	0	1	У

29	130	2016-09- 13	927	3	2016-09- 16	2016-10- 13	30.7	25	6	0.81	2	1	у
30	449	2016-09- 14	693	3	2016-09- 20	2016-11- 17	64.3	26	40	0.39	1	2	у
31	450	2016-09- 14	97	5	2016-11- 02	2017-12- 31	473.5	460	14	0.97	2	1	у
32	460	2016-09- 14	199 4	6	2016-09- 16	2018-06- 13	637.7	419	219	0.66	2	2	у
33	390	2016-09- 14	726	6	2016-09- 15	2017-05- 22	250.9	69	183	0.27	3	3	у
34	345	2016-09- 14	758	6	2016-09- 14	2017-05- 08	236.6	61	176	0.26	1	1	у
35	249	2016-09- 14	376	6	2016-10- 03	2017-04- 10	209	98	113	0.46	3	3	у
36	449	2016-09- 14	199 6	6	2016-09- 22	2017-05- 29	257.2	251	7	0.97	2	2	у
37	273	2016-09- 14	792	6	2016-09- 16	2017-06- 18	277.1	73	207	0.26	3	3	у
38	167	2016-09- 14	374	4	2016-09- 17	2016-10- 27	43.6	38	8	0.83	3	3	у
4	380	2016-08- 03	226	6	2016-10- 20	2018-04- 08	613.1	86	528	0.14	2	2	у
40	413	2016-09- 16	481	5	2016-09- 17	2016-11- 18	63	62	3	0.95	2	3	у
41	407	2016-09- 16	37	3	2016-09- 24	2016-12- 12	87.7	8	80	0.09	1	1	у
44	224	2016-09- 16	343	2	2016-09- 26	2016-10- 20	34.6	11	24	0.31	0	1	у
45	205	2016-09- 16	39	3	2016-10- 22	2016-10- 24	38.7	37	3	0.92	1	1	у
48	223	2016-10- 21	387	4	2016-10- 21	2016-12- 28	68.6	69	0	1.00	1	0	У

49	209	2016-10- 21	144 9	5	2016-10- 22	2017-02- 26	128.4	94	36	0.72	1	2	У
50	189	2016-10- 21	20	2	2016-10- 21	2016-12- 11	51.6	2	50	0.04	2	1	У
6	405	2016-08- 03	366	6	2016-08- 18	2018-02- 28	574.7	406	173	0.70	7	7	У
7	378	2016-08- 03	48	4	2016-09- 02	2017-12- 10	494.1	294	201	0.59	1	1	У
10	350	2016-08- 03	6	2	2017-01- 21	2017-07- 29	360.4	315	46	0.87	1	2	n
25	360	2016-09- 13	31	1	2016-09- 30	2016-10- 10	27.7	17	11	0.61	0	1	n
28	333	2016-09- 13	5	1	2016-09- 28	2016-09- 28	15.6	15	1	0.94	1	1	n
39	390	2016-09- 16	2	1	2016-09- 19	2016-09- 19	3.3	4	0	1.00	0	0	n
42	385	2016-09- 16	22	2	2016-09- 17	2016-09- 29	13.3	9	6	0.60	3	2	n
43	437	2016-09- 16	8	1	2016-10- 04	2016-10- 28	42.8	43	0	1.00	0	0	n
46	260	2016-10- 21	25	3	2016-10- 21	2016-10- 22	1.3	2	1	0.67	1	0	n
47	245	2016-10- 21	10	2	2016-10- 22	2016-11- 17	27.9	26	2	0.93	0	1	n
8	362	2016-08- 03	4	2	2016-08- 23	2017-06- 14	315.6	316	0	1.00	0	0	n
9	347	2016-08- 03	4	1	2016-09- 24	2016-09- 24	52	52	0	1.00	0	0	n



Figure B.1: Abacus plot showing detections of individual largemouth bass at each acoustic receiver station (unique colors) over time, and tagging date (black circles), and tag battery expiration date (black crosses).



Figure B.2: Receiver deployment periods (top left), receiver locations (top right), the number of largemouth bass being tracked over time (bottom left) and detection periods (black) with tagging dates in red (bottom right)



Figure B.3: Latitudinal movement patterns of individual Largemouth bass over time as inferred from acoustic telemetry detections. The dashed red line indicates the location of the freshwater protected area in Big Rideau Lake

Appendix C: Data summary statistics for physiological and CPUE experiments

Table C.1: Data for sample size, weight (g), condition factor (Fulton's K), and catch per unit angling effort (CPUE) for largemouth bass used in the different experiments in this study. Largemouth bass were captured from either inside freshwater protected areas (FPA) or from the main-lake areas across each of three study lakes: Opinicon Lake (OP), Big Rideau Lake (BR), and Newboro Lake (NB).

	FPA						
				Lake			
Fish parameter data	OP	BR	NB	OP	BR	NB	
Metabolic Phenotype							
Experiment							
N (fish)	7	13	12	9	11	9	
Mean Weight (g)	726	889	746	672	994	882	
Standard Error	60	69	61	43	103	72	
Mean Fulton's K	195	231	203	186	252	225	
Standard Error	9.85	13.06	12.18	8.13	18.02	12.45	
Stress Responsiveness							
Experiment							
N (fish)	19	17	26	19	17	28	
Mean Total Length (mm)	354	337	348	356	361	336	
Standard Error	11	15	9	15	12	12	
Glucose Responsiveness							
Experiment							
N (fish)	20	23	32	22	26	30	
Mean Total Length (mm)	356	338	350	351	358	334	
Standard Error	11	11	7	14	9	11	
CPUE							
N (fish)	33	32	33	33	31	31	
Mean Total Length (mm)	348	351	350.01	347.62	363.26	330.63	
Standard Error	7	1	0.2	1	0.2	1	
Mean fish caught per hour	13.45	4.63	5.55	4.69	1.89	3.00	

References:

- Abell R, Allan JD, Lehner B. 2007. Unlocking the potential of protected areas for freshwaters. *Biological Conservation* **134**: 48–63.
- Abell R, Thieme ML, Revenga C, Bryer M, Kottelat M, Bogutskaya N, Coad B, Mandrak N,
 Balderas SC, Bussing W, et al. 2008. Freshwater Ecoregions of the World: A New Map of
 Biogeographic Units for Freshwater Biodiversity Conservation. *BioScience* 58: 403–414.
- Abesamis RA, Russ GR, Alcala AC. 2006. Gradients of abundance of fish across no-take marine reserve boundaries : evidence from Philippine coral reefs. **371**: 349–371.
- Abrams AEI, Rous AM, Brooks JL, Lawrence MJ, Midwood JD, Doka SE, Cooke SJ. 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.
- Acreman M, Dueñas M, Hughes KA, Arthington AH, Tickner D. 2020. Protected areas and freshwater biodiversity : a novel systematic review distils eight lessons for effective conservation. *Conservation Letters*: 1–14.
- Agardy MT. 1994. Advances in marine conservation: the role of marine protected areas. *Trends in ecology & evolution* **9**: 267–70.
- Ahrenstorff TD, Sass GG, Helmus MR. 2009. The influence of littoral zone coarse woody habitat on home range size, spatial distribution, and feeding ecology of largemouth bass (Micropterus salmoides). *Hydrobiologia* 623: 223–233.
- Allendorf FW, Hard JJ. 2009. Human-induced evolution caused by unnatural selection through harvest of wild animals. *In the Light of Evolution* **3**: 129–147.
- Alós J, Palmer M, Arlinghaus R. 2012. Consistent Selection towards Low Activity Phenotypes
 When Catchability Depends on Encounters among Human Predators and Fish. *PLoS ONE* 7: 22–24.
- Arlinghaus R, Klefoth T, Kobler A, Cooke SJ. 2008. Size Selectivity, Injury, Handling Time, and Determinants of Initial Hooking Mortality in Recreational Angling for Northern Pike:

The Influence of Type and Size of Bait. *North American Journal of Fisheries Management* **28**: 123–134.

- Arlinghaus R, Laskowski KL, Alós J, Klefoth T, Monk CT, Nakayama S, Schröder A. 2017. Passive gear-induced timidity syndrome in wild fish populations and its potential ecological and managerial implications. *Fish and Fisheries* 18: 360–373.
- Arthington AH, Dulvy NK, Gladstone W, Winfield IJ. 2016a. Fish conservation in freshwater and marine realms: status, threats and management. *Aquatic Conservation: Marine and Freshwater Ecosystems* 26: 838–857.
- Arthington AH, Dulvy NK, Gladstone W, Winfield IJ. 2016b. Fish conservation in freshwater and marine realms: status, threats and management. *Aquatic Conservation: Marine and Freshwater Ecosystems* 26: 838–857.
- Ashley M, Willson MF, Pergams ORW, Dowd DJO, Gende SM, Brown JS. 2003. Evolutionarily enlightened management. *Biological Conservation* **111**: 115–123.
- Ashworth JS, Ormond RFG. 2005. Effects of fishing pressure and trophic group on abundance and spillover across boundaries of a no-take zone. *Biological Conservation* **121**: 333–344.
- Auer SK, Salin K, Anderson GJ, Metcalfe NB. 2015a. Aerobic scope explains individual variation in feeding capacity. *Biology Letters* **11**: 10–12.
- Auer SK, Salin K, Rudolf AM, Anderson GJ, Metcalfe NB. 2015b. The optimal combination of standard metabolic rate and aerobic scope for somatic growth depends on food availability. *Functional Ecology* 29: 479–486.
- Auer SK, Dick CA, Metcalfe NB, Reznick DN. 2018. Metabolic rate evolves rapidly and in parallel with the pace of life history. *Nature Communications* **9**: 8–13.
- Barton B. 2002. Stress in fishes: a diversity of responses with particular reference to changes in circulating corticosteroids. *Integrative and comparative biology* **42**: 517–525.
- Barton K. 2019. MuMIn: Multi-Model Inference. R package version 1.43.15. https://CRAN.Rproject.org/package=MuMIn
- Bates B, Maechler M, Bolker B, Walker S. 2015. Fitting Linear Mixed-Effects Models Using

lme4. Journal of Statistical Software, 67(1), 1-48.

- Bergseth BJ, Williamson DH, Frisch AJ, Russ GR. 2016. Protected areas preserve natural behaviour of a targeted fish species on coral reefs. *Biological Conservation* **198**: 202–209.
- Binder TR, Wilson ADM, Wilson SM, Suski CD, Godin JGJ, Cooke SJ. 2016. Is there a pace-oflife syndrome linking boldness and metabolic capacity for locomotion in bluegill sunfish? *Animal Behaviour* 121: 175–183.
- Biro PA, Garland T, Beckmann C, Ujvari B, Thomas F, Post JR. 2018. Metabolic scope as a proximate constraint on individual behavioral variation: Effects on personality, plasticity, and predictability. *American Naturalist* **192**: 142–154.
- Bolker, B.M., 2008. Ecological models and data in R. Princeton University Press.
- Bolker, B.M., 2015. Linear and generalized linear mixed models. Ecological Statistics: Contemporary theory and application, pp.309-333 in: Fox, G.A., Negrete-Yankelevich, S. and
- Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution* 24: 127–135.
- Bouchet P, Falkner G, Seddon MB. 1999. Lists of protected land and freshwater molluscs in the Bern Convention and European Habitats Directive: Are they relevant to conservation? *Biological Conservation* **90**: 21–31.
- Brodie ED. 1992. Correlational selection for color pattern and antipredator behavior in the garter snake Thamnophis ordinoides. *Evolution* **46**: 1284–1298.
- Brown TG, Runciman B, Pollard S, Grant ADA. 2009. Biological Synopsis of Largemouth Bass (Micropterus salmoides). *Canadian Manuscript Report of Fisheries and Aquatic Sciences* 2884: 1–27.
- Bryan MD, Scarnecchia DL. 1992. Species richness, composition, and abundance of fish larvae and juveniles inhabiting natural and developed shorelines of a glacial Iowa lake. *Environmental Biology of Fishes* 35: 329–341.

- Bull JW, Maron M. 2016. How humans drive speciation as well as extinction. *Proceedings of the Royal Society B* **283**: 1–10.
- Burton T, Killen SS, Armstrong JD, Metcalfe NB. 2011. What causes intraspecific variation in resting metabolic rate and what are its ecological consequences? *Proceedings of the Royal Society B: Biological Sciences* 278: 3465–3473.
- Cargnelli LM, Gross MR. 1997. Fish Energetics: Larger Individuals Emerge from Winter in Better Condition. *Transactions of the American Fisheries Society* **126**: 153–156.
- Carlson DM. 1992. Importance of wintering refugia to the Largemouth bass fishery in the Hudson River Estuary. *Journal of Freshwater Ecology* 7: 173–180.
- Chabot D, Steffensen JF, Farrell AP. 2016. The determination of standard metabolic rate in fishes. *Journal of Fish Biology* **88**: 81–121.
- Chu C, Ellis L, de Kerckhove DT. 2018. Effectiveness of terrestrial protected areas for conservation of lake fish communities. *Conservation Biology* **32**: 607–618.
- Claireaux G, Lefrançois C. 2007. Linking environmental variability and fish performance: integration through the concept of scope for activity. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* **362**: 2031–2041.
- Conover DO, Munch SB. 2002. Sustaining fisheries yields over evolutionary time scales. *Science* **297**: 94–96.
- Conover DO, Munch SB, Arnott SA. 2009. Reversal of evolutionary downsizing caused by selective harvest of large fish. *Proceedings of the Royal Society B: Biological Sciences* 276(1664): 2015-2020.
- Conover WJ, Iman RL. 1981. Rank transformations as a bridge between parametric and nonparametric statistics. *American Statistician* **35**: 124–129.
- Cooke ELL, Wilson ADM, Elvidge CK, Cooke SJ. 2017. Does capture method or the presence of aquatic protected areas influence the selective harvest of behavioural types in largemouth bass? *Canadian Journal of Fisheries and Aquatic Sciences* **74**: 1151–1157.
- Cooke SJ, Cowx IG. 2004. The role of recreational fishing in global fish crises. Bioscience 54:

857-859.

- Cooke SJ, Steinmetz J, Degner JF, Grant EC, Philipp DP. 2003a. Metabolic fright responses of different-sized largemouth bass (Micropterus salmoides) to two avian predators show variations in nonlethal energetic costs. *Canadian Journal of Zoology* 81: 699–709.
- Cooke SJ, Suski CD, Siepker MJ, Ostrand KG. 2003b. Injury rates, hooking efficiency and mortality potential of largemouth bass (Micropterus salmoides) captured on circle hooks and octopus hooks. *Fisheries Research* **61**: 135–144.
- Cooke SJ, Philipp DP, Wahl DH, Weatherhead PJ. 2006. Energetics of parental care in six syntopic centrarchid fishes. *Oecologia* **148**: 235–249.
- Cooke SJ, Midwood JD, Thiem JD, Klimley P, Lucas MC, Thorstad EB, Eiler J, Holbrook C, Ebner BC. 2013. Tracking animals in freshwater with electronic tags: Past, present and future. *Animal Biotelemetry* **1**: 1–19.
- Côté IM, Mosqueira I, Reynolds JD. 2001. Effects of marine reserve characteristics on the protection of fish populations: A meta-analysis. *Journal of Fish Biology* **59**: 178–189.
- Cucherousset J, Paillisson JM, Carpentier A, Thoby V, Damien JP, Eybert MC, Feunteun E,
 Robinet T. 2007. Freshwater protected areas: An effective measure to reconcile
 conservation and exploitation of the threatened European eels (Anguilla anguilla)? *Ecology* of Freshwater Fish 16: 528–538.
- Dassow CJ, Ross AJ, Jensen OP, Sass GG, Poorten BT Van, Solomon CT, Jones SE. 2020. Experimental demonstration of catch hyperstability from habitat aggregation not effort sorting in a recreational fishery. *Canadian Journal of Fisheries and Aquatic Science* 769: 762–769.
- Demers E, York B, Mckinley RS, Weatherley AH, Mcqueen DJ. 1996. Activity Patterns of Largemouth and Smallmouth Bass Determined with Electromyogram Biotelemetry. *Transactions of the American Fisheries Society* 125: 434–439.
- Demille MJ. 2010. The behaviour of largemouth bass in Lake Opincion, Ontario: A Biological Perspective for the evaluation of Muphy Bay fish sanctuary. *Unpublished Thesis*.

- Diaz Pauli B, Sih A. 2017. Behavioural responses to human-induced change: Why fishing should not be ignored. *Evolutionary Applications* **10**: 231–240.
- Donaldson MR, Hinch SG, Suski CD, Fisk AT, Heupel MR, Cooke SJ. 2014. Making connections in aquatic ecosystems with acoustic telemetry monitoring. *Frontiers in Ecology* and the Environment 12: 565–573.
- Dudgeon D, Arthington AH, Gessner MO, Kawabata ZI, Knowler DJ, Lévêque C, Naiman RJ,
 Prieur-Richard AH, Soto D, Stiassny MLJ, et al. 2006b. Freshwater biodiversity:
 Importance, threats, status and conservation challenges. *Biological Reviews of the Cambridge Philosophical Society* 81: 163–182.
- Dulvy NK, Freckleton RP, Polunin NVC. 2004. Coral reef cascades and the indirect effects of predator removal by exploitation. *Ecology Letters* **7**: 410–416.
- Duncan MI, Bates AE, James NC, Potts WM. 2019. Exploitation may influence the climate resilience of fish populations through removing high performance metabolic phenotypes. *Scientific Reports* 9: 11437.
- Dunlop ES, Baskett ML, Heino M, Dieckmann U. 2009. Propensity of marine reserves to reduce the evolutionary effects of fishing in a migratory species. *Evolutionary Applications* 2: 371– 393.
- Edgar GJ, Stuart-Smith RD, Willis TJ, Kininmonth S, Baker SC, Banks S, Barrett NS, Becerro MA, Bernard ATF, Berkhout J, et al. 2014. Global conservation outcomes depend on marine protected areas with five key features. *Nature* **506**: 216–220.
- Eikeset AM, Dunlop ES, Heino M, Storvik G, Stenseth NC, Dieckmann U. 2016. Roles of density-dependent growth and life history evolution in accounting for fisheries-induced trait changes. *Proceedings of the National Academy of Sciences*: 1–6.
- Endler JA. 1980. Natural Selection on Color Patterns in Poecilia reticulata. *Evolution* 34: 76–91.
- Finlayson MC, Arthington AH, Pittock J. 2018. *Freshwater Ecosystems in Protected Areas* (MC Finlayson, AH Arthington, and J Pittock, Eds). Routledge: New York.
- Fish PA, Savitz J. 1983a. Variations in Home Ranges of Largemouth Bass, Yellow Perch,

Bluegills, and Pumpkinseeds in an Illinois Lake. *Transactions of the American Fisheries Society* **112**: 147–153.

- Fish PA, Savitz J. 1983b. Variations in Home Ranges of Largemouth Bass, Yellow Perch, Bluegills, and Pumpkinseeds in an Illinois Lake. *Transactions of the American Fisheries Society* 112: 147–153.
- Fleming C. 1947. When the fish are rising: tales of the Rideau lakes. Duell Sloan and Pearce Inc., 270 Madison Ave., New York 16, N.Y. pp 205.
- Foster JG, Algera DA, Brownscombe JW, Zolderdo AJ, Cooke SJ. 2016. Consequences of Different Types of Littoral Zone Light Pollution on the Parental Care Behaviour of a Freshwater Teleost Fish. *Water, Air, & Soil Pollution* 227: 404.
- Gall GAE. 1975. Genetics of Reproduction in Domesticated Rainbow Trout. *Journal of Animal Science*, **40**(1): 19–28.
- Gillis D. 2018. Testing for fine-scale genetic structure of largemouth bass (Micropterus salmoides) in Lake Opinicon. Queens University.
- Gobin J, Lester NP, Fox MG, Dunlop ES. 2018. Ecological change alters the evolutionary response to harvest in a freshwater fish. *Ecological Applications* **0**: 1–12.
- Goñi R, Hilborn R, Díaz D, Mallol S, Adlerstein S. 2010. Net contribution of spillover from a marine reserve to fishery catches. *Marine Ecology Progress Series* **400**: 233–243.
- De Haan H. 1993. Solar UV-light penetration and photodegradation of humic substances in peaty lake water. *Limnology and Oceanography* **38**: 1072–1076.
- Hall DJ, Werner EE. 1977. Seasonal distribution and abundance of fishes in the littoral zone of a Michigan lake. *Transactions of the American Fisheries Society* **106**: 545–555.
- Halpern BS, Warner RR. 2002. Marine reserves have rapid and long lasting effects. *Ecology Letters* **5**: 361–366.
- Halpern BS, Lester SE, Kellner JB. 2009. Spillover from marine reserves and the replenishment of fished stocks. *Environmental Conservation* **36**: 268–276.

- Hambright KD, Trebatoski RJ, Drenner RW, Kettle D. 1986. Experimental study of the impacts of bluegill (Lepomis macrochirus) and largemouth bass (Micropterus salmoides) on pond community structure. *Canadian Journal of Fisheries and Aquatic Science* 43: 1171–1176.
- Hammer Ø, Harper D, Ryan P. 2009. PAST-PAlaeontological STatistics, ver. 1.89. Palaeontologia Electronica 4: 1–31.
- Hansen SL, Hunt Von Herbing I. 2009. Aerobic scope for activity in age 0 year Atlantic cod Gadus morhua. *Journal of Fish Biology* 74: 1355–1370.
- Hanson KC, Cooke SJ, Suski CD, Niezgoda G, Phelan FJS, Tinline R, Philipp DP. 2007.
 Assessment of largemouth bass (Micropterus salmoides) behaviour and activity at multiple spatial and temporal scales utilizing a whole-lake telemetry array. *Hydrobiologia* 582: 243–256.
- Hanson KC, Hasler CT, Cooke SJ, Suski CD, Philipp DP. 2008. Intersexual variation in the seasonal behaviour and depth distribution of a freshwater temperate fish, the largemouth bass. *Canadian Journal of Zoology* 86: 801–811.
- Harmelin-Vivien M, Le Diréach L, Bayle-Sempere J, Charbonnel E, García-Charton JA, Ody D, Pérez-Ruzafa A, Reñones O, Sánchez-Jerez P, Valle C. 2008. Gradients of abundance and biomass across reserve boundaries in six Mediterranean marine protected areas: Evidence of fish spillover? *Biological Conservation* 141: 1829–1839.
- Harrison IJ, Green PA, Farrell TA, Juffe-bignoli D, Sáenz L, Vörösmarty CJ. 2016a. Protected areas and freshwater provisioning : a global assessment of freshwater provision , threats and management strategies to support human water security. *Aquatic Conservation: Marine and Freshwater Ecosystems* 26: 103–120.
- Harrison IJ, Green PA, Farrell TA, Juffe-Bignoli D, Sáenz L, Vörösmarty CJ. 2016b. Protected areas and freshwater provisioning: a global assessment of freshwater provision, threats and management strategies to support human water security. *Aquatic Conservation: Marine and Freshwater Ecosystems* 26: 103–120.
- Hasler CT, Hanson KC, Cooke SJ, Tinline R, Suski CD, Niezgoda G, Phelan FJS, Philipp DP. 2007. Frequency, composition and stability of associations among individual largemouth

bass (Micropterus salmoides) at diel, daily and seasonal scales. *Ecology of Freshwater Fish* **16**: 417–424.

- Hasler CT, Suski CD, Hanson KC, Cooke SJ, Tufts BL. 2009. The influence of dissolved oxygen on winter habitat selection by largemouth bass: An integration of field biotelemetry studies and laboratory experiments. *Physiological and Biochemical Zoology* 82: 143–152.
- Hedges KJ, Koops MA, Mandrak NE, Johannsson OE. 2010a. Use of aquatic protected areas in the management of large lakes. *Aquatic Ecosystem Health & Management* **13**: 135–142.
- Hedges KJ, Koops MA, Mandrak NE, Johannsson OE, Hedges KJ, Koops MA, Mandrak NE, Ora E, Hedges KJ, Koops MA, et al. 2010b. Use of aquatic protected areas in the management of large lakes. 13: 135–142.
- Heino M, Dieckmann U. 2008. Detecting fisheries-induced life-history evolution : an overview of the reaction-norm approach. *Bulletin of Marine Science* **83**: 69–93.
- Heino M, Dieckmann U. 2009. Fisheries-induced evolution. *Encyclopedia of Life Sciences* September: 1–7.
- Hermoso V, Abell R, Linke S, Boon P. 2016. The role of protected areas for freshwater biodiversity conservation: challenges and opportunities in a rapidly changing world. *Aquatic Conservation: Marine and Freshwater Ecosystems* 26: 3–11.
- Hessenauer JM, Vokoun JC, Suski CD, Davis J, Jacobs R, O'Donnell E. 2015. Differences in the metabolic rates of exploited and unexploited fish populations: A signature of recreational fisheries induced evolution? *PLoS ONE* 10: 1–12.
- Hogg SE, Lester NP, Ball H. 2010. 2005 Survey of recreational fishing in Canada: Results for Fisheries Management Zones of Ontario
- Hollins J, Thambithurai D, Koeck B, Crespel A, Bailey DM, Cooke SJ, Lindström J, Parsons KJ, Killen SS. 2018. A physiological perspective on fisheries-induced evolution. *Evolutionary Applications* 11: 561–576.
- Hoyle J. 1990. Northern pike-smallmouth bass-largemouth bass communi- ties and sport fisheries in Ontario inland lakes. Sharbot Lake, Ontario: Rideau Lakes Fisheries

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- Hudon C, Lalonde S, Gagnon P. 2000. Ranking the effects of site exposure, plant growth form, water depth, and transparency on aquatic plant biomass. *Canadian Journal of Fisheries and Aquatic Sciences* 57: 31–42.
- Iguchi K, Yodo T, Matsubara N. 2004. Spawning and brood defense of smallmouth bass under the process of invasion into a novel habitat. *Environmental Biology of Fishes* **70**: 219–225.
- Iman RL, Hora SC, Conover WJ. 1984. Comparison of asymptotically distribution-free procedures for the analysis of complete blocks. *Journal of the American Statistical Association*, **79**: 674–685.
- Jenkins M. 2003. Prospects for Biodiversity. Science 302: 1175–1177.
- Jennings MJ. 1997. Centrarchid Reproductive Behavior: Implications for Management. North American Journal of Fisheries Management: 493–495.
- Jennings S, Polunin NVC. 1995. Biased underwater visual census biomass estimates for targetspecies in tropical reef fisheries. *Journal of Fish Biology* **47**: 733–736.
- Keast A, Harker J. 1977. Fish distribution and benthic invertebrate biomass relative to depth in an Ontario lake. *Environmental Biology of Fishes* **2**: 235–240.
- Keast A, Harker J, Turnbull D. 1978. Nearshore fish habitat utilization and species associations in Lake Opinicon (Ontario, Canada). *Environmental Biology of Fishes* **3**: 173–184.
- Keiling TD, Louison MJ, Suski CD. 2020. Big, hungry fish get the lure: Size and food availability determine capture over boldness and exploratory behaviors. *Fisheries Research* 227: 105554.
- Killen SS, Mitchell MD, Rummer JL, Chivers DP, Ferrari MCO, Meekan MG, Mccormick MI. 2014. Aerobic scope predicts dominance during early life in a tropical damselfish. *Functional Ecology* 28: 1367–1376.

Killen SS, Nati JJH, Suski CD. 2015a. Vulnerability of individual fish to capture by trawling is

influenced by capacity for anaerobic metabolism. *Proceedings of the Royal Society B* **282**: 1–8.

- Killen SS, Reid D, Marras S, Domenici P. 2015b. The interplay between aerobic metabolism and antipredator performance: Vigilance is related to recovery rate after exercise. *Frontiers in Physiology* 6: 1–8.
- Kinghorn B. 1983. Genetic variation in food conversion efficiency and growth in rainbow trout. *Aquaculture* **32**: 141–155.
- Knip DM, Heupel MR, Simpfendorfer CA. 2012. Evaluating marine protected areas for the conservation of tropical coastal sharks. *Biological Conservation* **148**: 200–209.
- Koeck B, Závorka L, Aldvén D, Näslund J, Arlinghaus R, Thörnqvist PO, Winberg S, Björnsson BT, Johnsson JI. 2019. Angling selects against active and stress-resilient phenotypes in rainbow trout. *Canadian Journal of Fisheries and Aquatic Sciences* 76: 320–333.
- Koolhaas JM, Korte SM, De Boer SF, Van Der Vegt BJ, Van Reenen CG, Hopster H, De Jong IC, Ruis MAW, Blokhuis HJ. 1999. Coping styles in animals: Current status in behavior and stress-physiology. *Neuroscience and Biobehavioral Reviews* 23: 925–935.
- Kuznetsova A, Brockhoff PB, Christensen RHB. 2017. ImerTest Package: Tests in Linear Mixed Effects Models. *Journal of Statistical Software*, **82**(13): 1-26.
- Kramer RH, Smith LLJ. 1962. Formation of Year Classes in Largemouth Bass. *Transactions of the American Fisheries Society* **91**: 29–41.
- Kuparinen A, Merilä J. 2007. Detecting and managing fisheries-induced evolution. *Trends in Ecology and Evolution* **22**: 652–659.
- Lankford TE, Billerbeck JM, Conover DO. 2001. Evolution of intrinsic growth and energy acquisition rates. II. Trade-offs with vulnerability to predation in Menidia menidia. *Evolution* 55: 1873–1881.
- Larocque SM, Colotelo AH, Cooke SJ, Blouin-Demers G, Haxton T, Smokorowski KE. 2012. Seasonal patterns in bycatch composition and mortality associated with a freshwater hoop net fishery. *Animal Conservation* 15: 53–60.
- Law R. 2000. Fishing, selection, and phenotypic evolution. *ICES Journal of Marine Science* **57**: 659–668.
- Lawrence MJ, Godin JGJ, Cooke SJ. 2018a. Does experimental cortisol elevation mediate risktaking and antipredator behaviour in a wild teleost fish? *Comparative Biochemistry and Physiology -Part A : Molecular and Integrative Physiology* **226**: 75–82.
- Lawrence MJ, Jain-Schlaepfer S, Zolderdo AJ, Algera DA, Gilmour KM, Gallagher AJ, Cooke SJ. 2018b. Are 3-minutes good enough for obtaining baseline physiological samples from teleost fish? Running Title: Sampling times for baseline blood physiological values. *Canadian Journal of Zoology*: 1–35.
- Lea JSE, Humphries NE, Brandis RG Von, Clarke CR, Sims DW, Lea JSE. 2016. Acoustic telemetry and network analysis reveal the space use of multiple reef predators and enhance marine protected area design. *Proceedings of the Royal Society B* 283: 1–8.
- Lennox RJ, Alós J, Arlinghaus R, Horodysky A, Klefoth T, Monk CT, Cooke SJ. 2017. What makes fish vulnerable to capture by hooks? A conceptual framework and a review of key determinants. *Fish and Fisheries*: 986–1010.
- Lenth RV. 2016. Least-squares means: the R package lsmeans. *Journal of statistical software* **69**(1): 1-22.
- Lewis WM, Flickinger S. 1967. Home Range Tendency of the Largemouth Bass (Micropterus Salmoides). *Ecological Society of America* **48**: 1020–1023.
- Loreau M, Naeem S, Inchausti P, Grime JP, Hector A, Hooper DU, Huston MA, Raffaelli D, Schmid B, Tilman D, et al. 2001. Biodiversity and Ecosystem Functioning: Current Knowledge and Future Challenges. *Science* 294: 804–808.
- Di Lorenzo M, Claudet J, Guidetti P. 2016. Spillover from marine protected areas to adjacent fisheries has an ecological and a fishery component. *Journal for Nature Conservation* **32**: 62–66.
- Louison MJ, Adhikari S, Stein JA, Suski CD. 2017. Hormonal responsiveness to stress is negatively associated with vulnerability to angling capture in fish. *Journal of Experimental Biology* 220: 2529–2535.

- Louison MJ, Stein JA, Cory su. 2018. Metabolic phenotype is not associated with vulnerability to angling in bluegill sunfish. *Canadian Journal of Zoology* **96**: 1264–1271.
- Louison MJ, Hage VM, Stein JA, Suski CD. 2019. Quick learning, quick capture: largemouth bass that rapidly learn an association task are more likely to be captured by recreational anglers. *Behavioral Ecology and Sociobiology* **73**: 1–13.
- Loury EK, Ainsley SM, Bower SD, Chuenpagdee R, Farrell T, Guthrie AG, Heng S, Lunn Z, Mamun A Al, Oyanedel R, et al. 2018. Salty stories, fresh spaces: Lessons for aquatic protected areas from marine and freshwater experiences. *Aquatic Conservation: Marine and Freshwater Ecosystems* 28: 485–500.
- Macpherson E, Gordoa A, García-Rubies A. 2002. Biomass size spectra in littoral fishes in protected and unprotected areas in the NW Mediterranean. *Estuarine, Coastal and Shelf Science* 55: 777–788.
- Massicotte P, Bertolo A, Brodeur P, Hudon C, Mingelbier M, Magnan P. 2015. Influence of the aquatic vegetation landscape on larval fish abundance. *Journal of Great Lakes Research* 41: 873–880.
- McConnachie SH, O'Connor CM, Gilmour KM, Iwama GK, Cooke SJ. 2012. Supraphysiological Cortisol Elevation Alters the Response of Wild Bluegill Sunfish to Subsequent Stressors. *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology* **317**: 321–332.
- McLeod E, Salm R, Green A, Almany J. 2009. Designing marine protected area networks to address the impacts of climate change. *Frontiers in Ecology and the Environment* 7: 362– 370.
- Meals KO, Miranda LE. 1991. Variability in Abundance of Age-0 Centrarchids among Littoral Habitats of Flood Control Reservoirs in Mississippi. North American Journal of Fisheries Management 11: 298–304.
- Metcalfe JD. 2006. Fish population structuring in the North Sea: understanding processes and mechanisms from studies of the movements of adults. *Journal of Fish Biology* **69**: 48–65.

Metcalfe NB, Van Leeuwen TE, Killen SS. 2016. Does individual variation in metabolic

phenotype predict fish behaviour and performance? Journal of Fish Biology 88: 298-321.

- Midwood JD, Chapman JM, Cvetkovic M, King GD, Ward TD, Suski CD, Cooke SJ. 2016. Diel variability in fish assemblages in coastal wetlands and tributaries of the St. Lawrence River: a cautionary tale for fisheries monitoring. *Aquatic Sciences* 78: 267–277.
- Midwood JD, Peiman KS, Burt AJAEW, Sarker MY, Nannini MA, Wahl DH, Cooke SJ. 2017. Size-Dependent Consequences of Exogenous Cortisol Manipulation on Overwinter. *Journal of Experimental Zoology 327A*: 5–17.
- Mommsen TP, Vijayan MM, Moon TW. 1999. Cortisol in teleosts:dynamics, mechanisms of action, and metabolic regulation. *Reviews in Fish Biology and Fisheries* **9**: 211–268.
- Montiglio PO, Dammhahn M, Dubuc Messier G, Réale D. 2018. The pace-of-life syndrome revisited: the role of ecological conditions and natural history on the slow-fast continuum. *Behavioral Ecology and Sociobiology* **72**.
- Mouillot D, Graham NAJ, Villéger S, Mason NWH, Bellwood DR. 2013. A functional approach reveals community responses to disturbances. *Trends in Ecology and Evolution* 28: 167– 177.
- Moynes EN, Lawrence MJ, Zolderdo AJ, Prystay TS, Abrams AEI, Holder P, Cooke SJ. 2020. Comparative Behavior of Wild Bluegill Captured Inside and Outside of a Long-Standing Aquatic Protected Area. *Transactions of the American Fisheries Society* **149**: 174–183.
- Nelson JA, Chabot D. 2011. General energy metabolism. *Encyclopedia of Fish Physiology*, **1-3**: 1566-1572.
- Nilsson C, Reidy CA, Dynesius M, Revenga C. 2005. Fragmentation and Flow Regulation of the World 's Large River Systems. *Science* **308**: 405–408.
- Norin T, Clark TD. 2015. Measurement and relevance of maximum metabolic rate in fishes. *Journal of Fish Biology*: 1–30.
- Norin T, Malte H. 2012. Intraspecific variation in aerobic metabolic rate of fish: Relations with organ size and enzyme activity in brown trout. *Physiological and Biochemical Zoology* **85**: 645–656.

- Nussle S, Hendry AP, Carlson SM. 2016. When Should Harvest Evolution Matter to Population Dynamics? *Trends in Ecology and Evolution* **xx**: 1–3.
- O'Connor CM, Gilmour KM, Arlinghaus R, Van Der Kraak G, Cooke SJ. 2009. Stress and parental care in a wild Teleost fish: insights from exogenous supraphysiological cortisol implants. *Physiological and biochemical zoology* **82**: 709–719.
- Oksanen AJ, Blanchet FG, Friendly M, Kindt R, Legendre P, Mcglinn D, Minchin PR, Hara RBO, Simpson GL, Solymos P, et al. 2013. Vegan: community ecology package. R package version 2.0-10. : 0–291.
- Ontario Department of Game and Fisheries. 1946. Annual Report, 1935–1946. Game and Fisheries Department, Toronto, Ontario. Available from Ontario Government Archive at: https://archive.org/details/ annualreportofga193546ontauoft.
- Oswald ME, Drew RE, Racine M, Murdoch GK, Robison BD. 2012. Is Behavioral Variation along the Bold-Shy Continuum Associated with Variation in the Stress Axis in Zebrafish?*. *Physiological and Biochemical Zoology* 85: 718–728.
- Otto SP. 2018. Adaptation, speciation and extinction in the Anthropocene. *Proceedings of the Royal Society B* **285**: 1–9.
- Øverli Ø, Pottinger TG, Carrick TR, Øverli E, Winberg S. 2002. Differences in behaviour between rainbow trout selected for high- and low-stress responsiveness. *Journal of Experimental Biology* 205: 391–395.
- Øverli Ø, Winberg S, Pottinger TG. 2005. Behavioral and neuroendocrine correlates of selection for stress responsiveness in rainbow trout A review. *Integrative and Comparative Biology* 45: 463–474.
- Paavola J. 2004. Protected Areas Governance and Justice: Theory and the European Union's Habitats Directive. *Environmental Sciences* 1: 59–77.
- Paradis Y, Bertolo A, Mingelbier M, Brodeur P, Magnan P. 2014. What controls distribution of larval and juvenile yellow perch? The role of habitat characteristics and spatial processes in a large, shallow lake. *Journal of Great Lakes Research* 40: 172–178.

- Philipp DP, Toline CA, Kubacki MF, Philipp DBF, Phelan FJS. 1997. The Impact of Catch-and-Release Angling on the Reproductive Success of Smallmouth Bass and Largemouth Bass. North American Journal of Fisheries Management 17: 557–567.
- Philipp DP, Cooke SJ, Claussen JE, Koppelman JB, Suski CD, Burkett DP. 2009. Selection for Vulnerability to Angling in Largemouth Bass. *Transactions of the American Fisheries Society* 138: 189–199.
- Philipp DP, Claussen JE, Koppelman JB, Stein JA, Cooke SJ, Suski CD, Wahl DH, Sutter DAH, Arlinghaus R. 2015. Fisheries-induced evolution in Largemouth Bass: linking vulnerability to angling, parental care, and fitness. *American Fisheries Society Symposium* 82: 223–234.
- Pickering AD, Pottinger TG. 1987. Poor water quality suppresses the cortisol response of salmonid fish to handling and confinement. *Journal of Fish Biology* **30**: 363–374.
- Pittock J, Hansen LJ, Abell R. 2008. Running dry: Freshwater biodiversity, protected areas and climate change. *Biodiversity* **9**: 30–38.
- Policansky D. 1993. Fishing as a Cause of Evolution in Fishes. In: Stokes K., McGlade J.M., Law R. (eds) The Exploitation of Evolving Resources. Lecture Notes in Biomathematics, vol 99. Springer, Berlin, Heidelberg.
- Polverino G, Santostefano F, Díaz-Gil C, Mehner T. 2018. Ecological conditions drive pace-oflife syndromes by shaping relationships between life history, physiology and behaviour in two populations of Eastern mosquitofish. *Scientific Reports* 8: 1–10.
- Potvin C, Roff DA. 1993. Distribution-free and robust statistical methods: viable alternatives to parametric statistics? *Ecology* **74**: 1617–1628.
- Pusey BJ, Arthington AH. 2003. Importance of the riparian zone to the conservation and management of freshwater fish: a review. *Marine and Freshwater Research* **54**: 1–16.
- Quinn GP, Keough MJ. 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge.
- R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <u>https://www.R-project.org/</u>.

- Raibley PT, Irons KS, O'Hara TM, Blodgett KD, Sparks RE. 1997. Winter Habitats Used by Largemouth Bass in the Illinois River, a Large River-Floodplain Ecosystem. North American Journal of Fisheries Management 17: 401–412.
- Rakitin A, Kramer DL. 1996. Effect of a Marine Reserve On the Distribution of Coral Reef Fishes in Barbados. *Marine Ecology Progress Series* 131: 97–113.
- Randall RG, Minns CK, Cairns VW, Moore JE. 1996. The relationship between an index of fish production and submerged macrophytes and other habitat features at three littoral areas in the Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 53: 35–44.
- Réale D, Garant D, Humphries MM, Bergeron P, Careau V, Montiglio PO. 2010. Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365: 4051–4063.
- Redpath TD, Cooke SJ, Arlinghaus R, Wahl DH, Philipp DP. 2009. Life-history traits and energetic status in relation to vulnerability to angling in an experimentally selected teleost fish. *Evolutionary Applications* 2: 312–323.
- Redpath TD, Cooke SJ, Suski CD, Arlinghaus R, Couture P, Wahl DH, Philipp DP. 2010. The metabolic and biochemical basis of vulnerability to recreational angling after three generations of angling-induced selection in a teleost fish. *Canadian Journal of Fisheries* and Aquatic Sciences 67: 1983–1992.
- Reid AJ, Carlson AK, Creed IF, Eliason EJ, Gell PA, Johnson PTJ, Kidd KA, MacCormack TJ, Olden JD, Ormerod SJ, et al. 2019. Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biological Reviews* 94: 849–873.
- Reid DM, Anderson DM, Henderson BA. 2001. Restoration of Lake Trout in Parry Sound, Lake Huron. *North American Journal of Fisheries Management* **21**: 156–169.
- Reyier EA, Scheidt DM, Stolen ED, Lowers RH, Karen G, Ahr BJ. 2020. Residency and dispersal of three sportfish species from a coastal marine reserve: Insights from a regionalscale acoustic telemetry network. *Global Ecology and Conservation*: e01057.
- Reznick DA, Bryga H, Endler JA. 1990. Experimentally induced life-history evolution in a natural population. *Nature* **346**: 357–359.

- Ricciardi A, Rasmussen JB. 1999. Extinction rates of North American freshwater fauna. *Conservation Biology* **13**: 1220–1222.
- Rodrigues ASL, Andelman SJ, Bakarr MI, Boitani L, Brooks TM, Cowling RM, Fishpool LDC, da Fonseca GAB, Gaston KJ, Hoffman M, et al. 2004. Effectiveness of the global protected area network in representing species diversity. *Letters to Nature* **428**: 640–643.
- Romero LM. 2012. Using the reactive scope model to understand why stress physiology predicts survival during starvation in Galápagos marine iguanas. *General and comparative endocrinology* **176**: 296–9.
- Roy R, Tissot L, Argillier C. 2018. Environmental drivers of fish spatial distribution and activity in a reservoir with water level fluctuations. *Hydroecologie Appliquee*.
- Saunders DL, Meeuwig JJ, Vincent a CJ. 2002. Freshwater Protected Areas: Strategies for Conservation. *Conservation Biology* 16: 30–41.
- Savino JF, Stein RA. 1982. Predator-Prey Interaction between Largemouth Bass and Bluegills as Influenced by Simulated, Submersed Vegetation. *Transactions of the American Fisheries* Society 111: 255–266.
- Schielzeth H, Nakagawa S. 2013. Nested by design: Model fitting and interpretation in a mixed model era. *Methods in Ecology and Evolution* **4**: 14–24.
- Schlosser IJ. 1991. Stream Fish Ecology: A Landscape Perspective. 41: 704–712.
- Schneider JC. 2002. Fish as Indicators of Lake Habitat Quality and a Proposed Application and a Proposed Application
- Schneider JC, Laarman PW, Gowing H. 2000. Length-weight relationships. In *Manual of Fisheries Survey Methods II: with periodic updates* Ann Arbor; 17.1-17.16.
- Schram ST, Selgeby JH, Bronte CR, Swanson BL. 1995. Population Recovery and Natural Recruitment of Lake Trout at Gull Island Shoal, Lake Superior, 1964–1992. *Journal of Great Lakes Research* 21: 225–232.
- Schreck CB, Contreras-Sanchez W, Fitzpatrick MS. 2001. Effects of stress on fish reproduction, gamete quality, and progeny. *Aquaculture* **197**: 3–24.

- Scott MC. 2006. Winners and losers among stream fishes in relation to land use legacies and urban development in the southeastern US. *Biological Conservation* **127**: 301–309.
- Searle SR, Speed FM, Milliken GA. 1980. Population marginal means in the linear model: An alternative to least squares means. *American Statistician* **34**: 216–221.
- Seitz RD, Lipcius RN, Olmstead NH, Seebo MS, Lambert DM. 2006. Influence of shallow-water habitats and shoreline development on abundance, biomass, and diversity of benthic prey and predators in Chesapeake Bay. *Marine Ecology Progress Series* **326**: 11–27.
- Sheridan JE, Krishka BA. 1995. 1994 creel summaries for Opinicon and Sydenham Lakes. Sharbot Lake, Ontario: Ministry of Natural Resources, Rideau Lakes Fisheries Assessment Unit. File Report 1995-1.
- Siepker MJ, Ostrand KG, Cooke SJ, Philipp DP, Wahl DH. 2007. A review of the effects of catch-and-release angling on black bass, Micropterus spp.: Implications for conservation and management of populations. *Fisheries Management and Ecology* 14: 91–101.
- Sih A, Bell A, Johnson JC. 2004. Behavioral syndromes: An ecological and evolutionary overview. *Trends in Ecology and Evolution* **19**: 372–378.
- Sinervo B, Svensson E. 2002. Correlational selection and the evolution of genomic architecture. *Heredity* **89**: 329–338.
- Søgaard Jørgensen P, Folke C, Carroll SP. 2019. Evolution in the Anthropocene: Informing policy and governance. *Annual Review of Ecology, Evolution, and Systematics*: 1–20.
- Sosa VJ. eds., 2015. Ecological statistics: contemporary theory and application. Oxford University Press, USA. DOI:10.1093/acprof:oso/9780199672547.001.0001
- Stahr KJ, Shoup DE. 2016. The Effects of Macrophyte Stem Density and Structural Complexity on Foraging Return of Invertivorous Juvenile Largemouth Bass. North American Journal of Fisheries Management 36: 788–792.
- St John J, Russ G, Gladstone W. 1990. Accuracy and bias of visual estimates of numbers, size structure and biomass of a coral reef fish. *Marine Ecology Progress Series* **64**: 253–262.

Stepien CA, Karsiotis SI, Sullivan TJ, Klymus KE. 2017. Population genetic structure and

comparative diversity of smallmouth bass Micropterus dolomieu: congruent patterns from two genomes. *Journal of Fish Biology* **90**: 2125–2147.

- Stokes K, McGlade MJ, Law R. 1993. *The expolitation of evolving resources*. Springer-Verlag: Berlin, Heidelberg.
- Suski CD, Cooke SJ. 2007. Conservation of aquatic resources through the use of freshwater protected areas: Opportunities and challenges. *Biodiversity and Conservation* 16: 2015– 2029.
- Suski CD, Philipp DP. 2004. Factors Affecting the Vulnerability to Angling of Nesting Male Largemouth and Smallmouth Bass. *Transactions of the American Fisheries Society* 133: 1100–1106.
- Suski CD, Ridgway MS. 2007. Climate and body size influence nest survival in a fish with parental care. *Journal of Animal Ecology* **76**: 730–739.
- Suski CD, Phelan FJS, Kubacki MF, Philipp DP. 2002. The use of sanctuaries for protecting nesting black from angling. *American Fisheries Society Symposium* **31**: 371–378.
- Sutter D a H, Suski CD, Philipp DP, Klefoth T, Wahl DH, Kersten P, Cooke SJ, Arlinghaus R.
 2012. Recreational fishing selectively captures individuals with the highest fitness potential. *Proceedings of the National Academy of Sciences of the United States of America* 109: 20960–5.
- Svendsen MBS, Bushnell PG, Christensen EAF, Steffensen JF. 2016. Sources of variation in oxygen consumption of aquatic animals demonstrated by simulated constant oxygen consumption and respirometers of different sizes. *Journal of Fish Biology* 88: 51–64.
- Sztramko KL. 1985. Effects of a Sanctuary on the Smallmouth Bass Fishery of Long Point Bay, Lake Erie. North American Journal of Fisheries Management **5**: 233–241.
- Tickner D, Opperman JJ, Abell R, Acreman M, Arthington AH, Bunn SE, Cooke SJ, Dalton J, Darwall W, Edwards G, et al. 2020. Bending the Curve of Global Freshwater Biodiversity Loss: An Emergency Recovery Plan. *BioScience* 70: 330–342.

Treberg JR, Killen SS, MacCormack TJ, Lamarre S, Enders EC. 2016. Estimates of metabolic

rate and major constituents of metabolic demand in fishes under field conditions: Methods, proxies, and new perspectives. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*: 1–13.

- Tupper MH. 2007. Spillover of commercially valuable reef fishes from marine protected areas in Guam, Micronesia. *Fishery Bulletin* **105**: 527–537.
- Twardek WM, Shultz AD, Claussen JE, Cooke SJ, Stein JA, Koppelman JB, Phelan FJS, Philipp DP. 2016. Potential consequences of angling on nest-site fidelity in largemouth bass. *Environmental Biology of Fishes*.
- Twardek WM, Elvidge CK, Wilson ADM, Algera DA, Zolderdo AJ, Lougheed SC, Cooke SJ.
 2017. Do protected areas mitigate the effects of fisheries-induced evolution on parental care behaviour of a teleost fish? *Aquatic Conservation: Marine and Freshwater Ecosystems*: 1–8.
- VanLandeghem MM, Wagner CP, Wahl DH, Suski CD. 2013. Physiological Disturbances and Overwinter Mortality of Largemouth Bass from Different Latitudes. *Physiological and Biochemical Zoology* 86: 716–726.
- Wang H-Y, Chen Y-S, Hsu C-C, Shen S-F. 2016. Fishing-induced changes in adult length are mediated by skipped-spawning. *Ecological Applications* 27: 1–9.
- Waters DS, Noble RL. 2004. Spawning Season and Nest Fidelity of Largemouth Bass in a Tropical Reservoir. *North American Journal of Fisheries Management* **24**: 1240–1251.
- Watson JEM, Dudley N, Segan DB, Hockings M. 2014. The performance and potential of protected areas. *Nature* **515**: 67–73.
- Wenger S. 1999. A review of the scientific literature on riparian buffer width, extent and vegetation. *Office of Public Service & Outreach*: 1–59.
- Werner EE, Hall DJ, Laughlin DR, Wagner DJ, Wilsmann LA, Funk FC. 1977. Fish Communityr Habitat Partitioning in a Freshwater. *Journal of Fisheries Research Board of Canada* 34: 360–370.

Westera M, Lavery P, Hyndes G. 2003. Differences in recreationally targeted fishes between

protected and fished areas of a coral reef marine park. *Journal of Experimental Marine Biology and Ecology* **294**: 145–168.

- Wilson ADM, Brownscombe JW, Sullivan B, Jain-Schlaepfer S, Cooke SJ. 2015. Does angling technique selectively target fishes based on their behavioural type? *PLoS ONE* **10**: 1–14.
- Worm B, Barbier EB, Beaumont NJ, Duffy E, Folke C, Halpern BS, Jackson JBC, Lotze HK, Micheli F, Palumbi SR, et al. 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science* **314**: 787–90.
- Wright J, Bolstad GH, Araya-Ajoy YG, Dingemanse NJ. 2019. Life-history evolution under fluctuating density-dependent selection and the adaptive alignment of pace-of-life syndromes. *Biological Reviews* 94: 230–247.
- Zolderdo AJ, Algera DA, Lawrence MJ, Gilmour KM, Fast MD, Thuswaldner J, Willmore W, Cooke SJ. 2016. Stress, nutrition and parental care in a teleost fish: Exploring mechanisms with supplemental feeding and cortisol manipulation. *Journal of Experimental Biology*: 1237–1248.
- Zolderdo AJ, Abrams AEI, Reid CH, Suski CD, Midwood JD, Cooke SJ. 2019. Evidence of fish spillover from freshwater protected areas in lakes of eastern Ontario. *Aquatic Conservation: Marine and Freshwater Ecosystems*: 1–17.
- Zuccarino-crowe CM, Taylor WW, Hansen MJ, Seider MJ, Krueger CC. 2016. Effects of lake trout refuges on lake white fi sh and cisco in the Apostle Islands Region of Lake Superior. *Journal of Great Lakes Research* 42: 1092–1101.
- Zuckerman ZC, Suski CD. 2013. Predator burden and past investment affect brood abandonment decisions in a parental care-providing teleost. *Functional Ecology* **27**: 693–701.
- Zuckerman ZC, Philipp DP, Suski CD. 2014. The influence of brood loss on nest abandonment decisions in largemouth bass Micropterus salmoides. *Journal of Fish Biology* 84: 1863– 1875.
- Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM. 2009. Mixed effects models and extensions in ecology with R. *Springer Science & Business Media*.