Physiological and Behavioural Responses of Lake Trout to Catch-And-Release Angling

by

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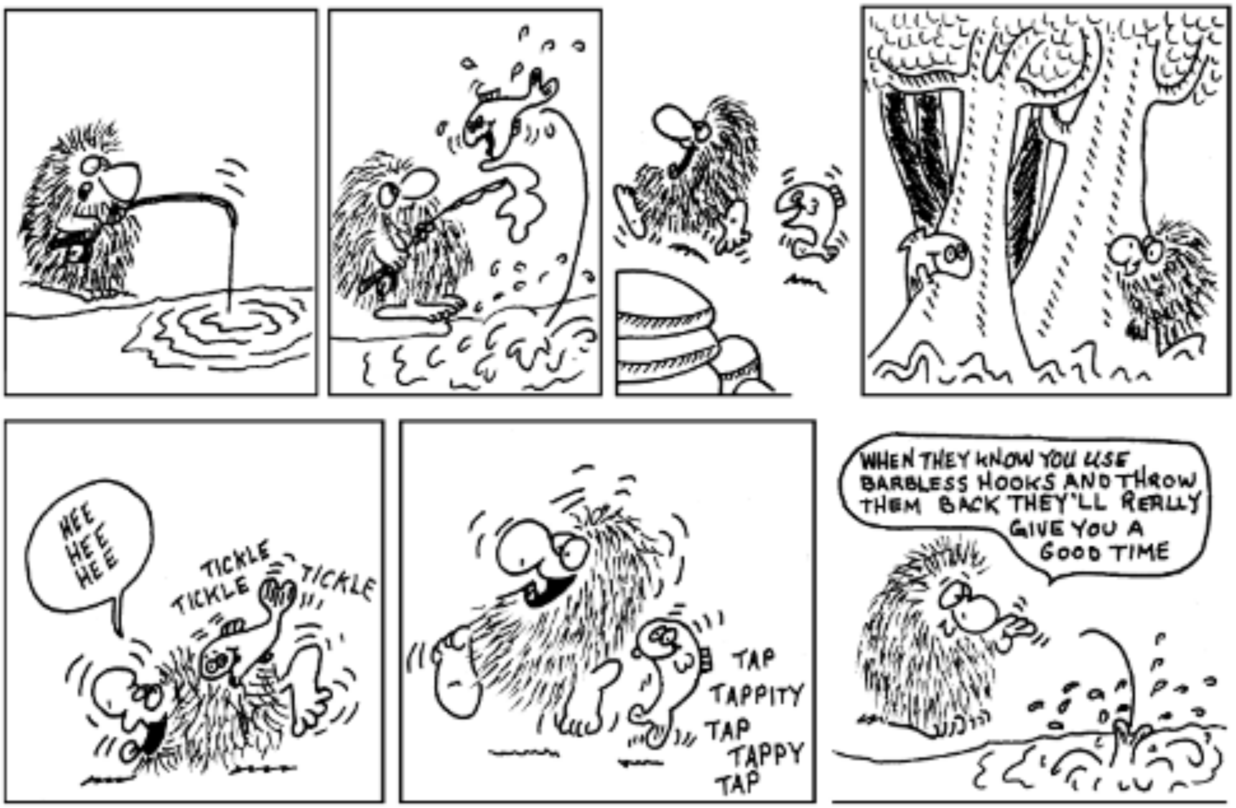
Abstract

Lake trout (*Salvelinus namaycush*), like many other native fishes in North America are a popular species typically targeted for recreational angling. Catch-and-release angling (C&R) relies on the assumption of high fish survival following release and is considered an effective way to preserve wild stocks of fish. Salmonids and other related species are susceptible to recreational angling, which can induce stress during different parts of the process (e.g., line fighting and air exposure). Other factors can impact fish health (e.g., water temperature and hooking location) and potentially lead to delayed mortality. In this thesis, I present empirical research where I used reflex impairment, physiology, and overall activity to assess the robustness of lake trout to C&R across seasons and time scales. During ice angling, lake trout experienced signs of reflex and physiological impairment up to 6 h and a high mortality rate. A key finding was that lake trout may exhibit pressure-related injuries in cooler water temperatures despite being physostomous. During open water angling, lake trout experienced barotrauma, reflex impairment, and physiological impairment immediately upon capture and 0.5 h post-angling. The addition of post-release activity monitoring via tri-axial accelerometry showed that lake trout rapidly swim to depth and exhibit reduced activity for the first 14 min after release. Collectively, I demonstrate that using multiple metrics of assessing angling-related impairment (i.e., both external and internal metrics) is necessary and future studies should not rely on one or few indices. The work presented here provides new information regarding context-specific aspects of C&R and is useful for recreational fisheries management.

Dedication

To Great-Grandma Irene, Grandma Brooks, and Grandma Howell. Each of you instilled in me a love for the natural world, one which I carry with me every day and share as often as I can.



Adapted from Falk et al. (1974)

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I have had the privilege of working with a diverse team of scientists, government collaborators, and resource users through the entirety of this project. Each one of you has shaped my understanding of what it means to be kind, understanding, and above all, a team-player. It has been a gift to work under the supervision Dr. Caleb Hasler, whom I have come to call a friend. I am inspired by his commitment to supportive mentorship, involvement in the scientific community, and vigour as an individual researcher. Personal and professional growth were abundant under his guidance. My advisory committee (Drs. Steven Cooke, Kenneth Jeffries, and Craig Willis) instilled confidence from the very beginning of this work, and I am encouraged by their insights. Partnership with Manitoba Fisheries ensured that my experience was well-rounded, and I was given opportunities outside of my research that greatly improved my success during remote field work. Derek Kroeker and Eric Mullen spent a substantial amount of time in the early stages of this project familiarizing me with Manitoba and the beauty of its fisheries. Ian Kitch, Cole Phillips, and Ethan Dobbs were incredibly generous with their time and resources during challenging field seasons. I was invited to participate in many notable initiatives led by Manitoba Fisheries, including stocking programs, lake sturgeon monitoring, and Clearwater Lake spawn camp. My two years in Manitoba were enriched by my research partner Giulio Navarroli, the other half of the lake trout team. The extent of his contributions to this work cannot be properly expressed here, so I will simply state that in no way would I have succeeded without him present through everything. Collectively, the team that surrounded me are what I would consider some of the greats.

Many others graciously volunteered their time during the fieldwork of this project, despite the demanding Manitoba winters and difficulty of angling for trophy-sized lake trout. A

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Preface

All research presented in this thesis was conducted in accordance with animal care protocols approved by the animal care committee of The University of Winnipeg (Animal Use Protocol #AE10491), following guidance set by the Canadian Council on Animal Care. All procedures outlined were also approved under a Provincial Scientific Collection (General) Permit (#22758865). We respectfully acknowledge that the work and learning were completed on the traditional territory of the Anishinaabe (Treaty 1), Muskegon Cree (Treaty 1), Ojibwa (Treaty 5), and Swampy Cree peoples (Treaty 5). We offer gratitude to the First Nations for their ongoing stewardship of this land.

Thesis format

This thesis is written in a manuscript-based format. Acknowledgements from each manuscript are combined at the start of the thesis and references are compiled at the end of the thesis. While the methods I used are similar between the two data chapters (manuscripts), they were separated because the time course and environmental conditions were very different between seasons. It will become clear why this separation was necessary from the explanations in the first and last chapters of this thesis.

Co-authorship

While this work is my own, I was fortunate to collaborate with a supportive team of co-authors. These individuals played a significant role in shaping the research and provided guidance during its production. I have listed below the manuscripts used as thesis chapters and the contributions of each co-author.

Chapter 2: Lake trout reflex impairment and physiological status following ice-angling

Howell, B.E., Navarroli, G., Mullen, E.J., Cooke, S.J., and Hasler, C.T.

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Bradley E. Howell: Conceptualization, Formal Analysis, Funding Acquisition, Investigation, Methodology, Project Administration, Visualization, Writing – Original Draft, Writing – Review & Editing. Giulio Navarroli: Investigation, Writing – Review & Editing. Eric J. Mullen: Conceptualization, Investigation, Methodology, Project Administration, Writing – Review & Editing. Steven J. Cooke: Conceptualization, Funding Acquisition, Resources, Writing – Review & Editing. Caleb T. Hasler: Conceptualization, Funding Acquisition, Methodology, Resources, Supervision, Writing – Original Draft, Writing – Review & Editing.

Chapter 3: Short-term impairment and post-release behaviour of angled lake trout

Howell, B.E., Navarroli, G., DePasquale, S.W., Cooke, S.J., and Hasler, C.T.

Prepared for *Conservation Physiology*.

Bradley E. Howell: Conceptualization, Formal Analysis, Funding Acquisition, Investigation, Methodology, Project Administration, Visualization, Writing – Original Draft, Writing – Review & Editing. Giulio Navarroli: Investigation, Writing – Review & Editing. Simon W. DePasquale: Investigation, Writing – Review & Editing. Steven J. Cooke: Conceptualization, Funding Acquisition, Resources, Writing – Review & Editing. Caleb T. Hasler: Conceptualization, Funding Acquisition, Methodology, Resources, Supervision, Writing – Original Draft, Writing – Review & Editing.

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Chapter 1. General Introduction

1.1 Freshwater recreational fisheries

Recreational fishing is defined as the capture of fish which do not constitute the dominant source of protein for an individual and which are not sold, bartered, or traded (Food and Agriculture Organization 2012). This form of fishing can be both simple and complex, consisting of wild, supplemented, cultured, or combinations of these types in both fresh and saltwater (Cowx 2002). Internationally, these fisheries provide leisure, food, and employment opportunities, and are expected to expand (Bower et al. 2020). A global average of 6.7% of populations engage in this activity, which is > 174.5 million people between North & South America, China, Europe, Oceania, and the Russian Federation (Funge-Smith 2011). This amounts to > $56 billion CAD in direct costs and > $128 billion CAD in indirect costs annually (Funge-Smith 2011). In Canada, recreational angling generates $8.8 billion CAD annually (Brownscombe et al. 2014a), with Canadian resident anglers contributing $2.5 billion CAD on direct expenditures in 2015 (Fisheries and Oceans Canada 2019). In 2010, the total number of licensed anglers in Canada was reported to be 3.6 million (Brownscombe et al. 2014). Recreational fishing may in fact overshadow inland capture production in multiple countries within North America, Europe, and Oceania (Arlinghaus et al. 2013).

In addition to economic growth, recreational angling offers both catch and noncatch related benefits. Of the noncatch benefits (e.g., social interaction or personal challenge) the most important benefit to anglers is relaxation and the nature experience (Freudenberg & Arlinghaus 2009). In other words, the sense of escape and freedom associated with recreational fishing can be as much of a draw as catching the fish. Fishing for food is another motive (Cooke et al. 2018), along with the psychological, social, educational, and economic benefits to individuals and their communities (Arlinghaus et al. 2019). Despite benefits, recreational fishery practices including over-harvest, habitat destruction, release mortality, and stocking and dispersal of non-native fish have been associated with negative effects on populations and ecosystems (Cooke et al. 2015).

1.2 Catch-and-release angling

When recreational angling is used as a pastime, fish are often released immediately without any apparent harm. This form of fishing termed catch-and-release angling (C&R) involves the capture of fish using rod and reels with subsequent release and assumed survival (Arlinghaus et al. 2007). While it remains a quintessential fishery management strategy, C&R science (i.e., the effective and accurate procedures for measuring and understanding the effects of C&R) is a growing field that must continue to develop and incorporate sublethal assessments (Cooke & Schramm 2007; Brownscombe et al. 2017; Sass and Shaw 2020). C&R literature documents the behavioural and physiological responses of fish to angling practices, offering insight to fishery managers and biologists on mortality measures or how to best protect and enhance their respective fisheries. C&R has been shown to be a valuable conservation tool if anglers practice behaviours which minimize impacts on fish (Danylchuk et al. 2018).

Many families of freshwater fish have presently been studied in the context of C&R such as centrarchids (Elliott et al. 2021; LaRochelle et al. 2021), esocids (Flink et al. 2021; Somers et al. 2021), percids (Twardek et al. 2018b; Logan et al. 2019), and salmonids (Thorstad et al. 2019; Joubert et al. 2020; Chhor et al. 2021). More uncommon families such as acipenserids (Mullen et al. 2020) and sciaenids (Card and Hasler 2021) are also being studied, yet the volume of research is still emerging. Research that formed the basis of our current understanding (i.e., research conducted prior to 1975) focused almost exclusively on freshwater fish, with prominent interest in salmonids and centrarchids (Arlinghaus et al. 2007). In addition to varying families of fish, methods of C&R angling have also been examined. Gear such as hook type (Cooke and Suski 2004; Trahan et al. 2021), nets (Barthel et al. 2003; Colotelo and Cooke 2011), and hook removal gear (Cooke et al. 2022) have been implicated with physical injury. Since the comprehensive review by Arlinghaus et al. (2007) there have been major innovations in the C&R research sector.

1.3 Innovations in catch-and-release

The growth of C&R science over the past half century has led to extensive literature, with management-focused reviews (Cooke & Schramm 2007; Cooke et al. 2012; Elmer et al. 2017), new technologies (Cooke et al. 2021), and social movements (Danylchuk et al. 2018) still emerging. Improvements to hook technology, lure and bait technology, and fishing rod, reel, and line technology have made anglers more effective. These innovations coincide with other advancements such as underwater cameras, remotely operated underwater vehicles, boat-based electronics, fish attractants, and social media and online forums (Cooke et al. 2021). All these innovations aim to provide anglers with more information about fish and their behaviour, increase capture rates, and disseminate regional information. While positively impacting angling experiences, these additions to the recreational angling repertoire also have the potential to amplify pre-existing challenges with fish welfare and management. Some of the major difficulties in fisheries management is the uncertainty of scientific, technical, economic, and political information upon which anglers and managers base decisions (Hewison 1996). A lack of research into new technologies leave fish populations exposed, as appropriate management has yet to be developed. For example, recent and potential changes to hook technology are skewed towards increasing capture rate and minimizing losses of hooked fish (Cooke et al.

2021). The capture of fish while using J-hooks has been associated with a post-release decrease in growth (Jenkins Jr 2003) and mortality (Weltersbatch et al. 2018).

Movements such as #KeepEmWet (now a non-profit known as Keep Fish Wet) have greatly increased public outreach and promotion of fishing best practices (Keep Fish Wet 2022). While these practices can be derived from findings in scientific research, fisheries managers require mixed outreach approaches to communicate and engage all anglers in responsible fishing (Nguyen et al. 2012). The ability of social media to facilitate information sharing has greatly improved upon previous government and NGO programs, which may not always be accurate or up to date (Sims and Danylchuk 2017). Participation in sharing fish size, time of year, and location information has also impacted the way that fishers distribute their effort. Fishing locations that are perceived to produce a higher number of larger, more diverse species are likely to receive more shares on social media. In the case of bull trout, their popularity as a sportfish has greatly increased due to media outlets. Magazine and internet articles which focus attention on their species-at-risk status as well as their size and uniqueness, have resulted in more prospective fishers (Joubert et al. 2020). With anglers becoming more effective, the implications of fish recovery become clear.

1.4 Effects on Fish

While C&R is promoted as a tool to improve recreational fisheries through greater fish abundance, angler catch rates, and trophy growth potential, it may also induce stress and mortality (Sass and Shaw 2020). The process of angling involves many stressors which, when combined, induce a generalized stress response which can be measured through changes in behaviour, physiology, or activity (Arlinghaus et al. 2007). Fish may experience stress associated with angling multiple times in their lifetime, for example, 29% of rainbow trout (*Oncorhynchus mykiss*) caught in Alaska display signs of previous capture (Meka 2003). Behavioural impairments are the most recognizable signs of stress associated with angling and normal swimming behaviors are critical to fish recovery (Davis et al. 2010). Impairments that inhibit fish from returning to depth can accelerate mortality (Gravel and Cooke 2008; Drumhiller et al. 2014) and expose fish to predation (Jarvis and Lowe 2008; Raby et al. 2014; Ferter et al. 2015). Barotrauma occurs when fish are brought rapidly from depth to the surface of the water, which results in major changes in external pressure (Carlson 2012). When the swim bladder becomes hyperinflated due this pressure change, injuries such as displaced organs, internal bleeding, and tissue damage can occur (Rummer and Bennett 2005; Hannah et al. 2008; Pribyl et al. 2011). The use of behavioural assessments such as reflex action mortality predictors (RAMP) and barotrauma indicators are simple and inexpensive field-based assessment techniques (Davis 2010; Althoff et al. 2021) that measure fish vitality by examining multiple behavioural reflexes that have been shown to effectively predict future survival of caught fish prior to their release (Raby et al. 2012; Schreer et al. 2009).

Coupling physiological methods of measuring stress responses with reflex assessments provide additional information that allow robust estimates of recovery. Typically, researchers use non-lethal blood sampling to provide information on changes in hormones, metabolites, or acid-base status (Wendelaar Bonga 1997; Lawrence et al. 2020). Collectively, these metrics shed light on internal coordination to increase the availability of oxygen and energy (Rodnick and Planas 2016; Schreck and Tort 2016) and illustrate correlates of mortality after release (Skomal et al. 2007). Plasma cortisol is of particular interest since it is the primary stress hormone and prolonged exposure to elevated levels may have impacts on fish growth, reproduction, and immune function (Wendelaar-Bonga 1997). Lactate is predictive of mortality as a by-product of glucose metabolism (Wood 1991) and may play a role in mitigating pathological effects of exhaustion (Wang et al. 1994; Holder et al. 2022).

Biotelemetry has become more prevalent in C&R research in recent years (Donaldson et al. 2008) and is a powerful tool for understanding post-release recovery. Tri-axial accelerometry can measure fish energy expenditure in three spatial dimensions and has been used to explore fine-scale movement, kinematics, and metabolism (Halsey et al. 2009; Gleiss et al. 2010; Brown et al. 2013; Brownscombe et al. 2014a; Metcalfe et al. 2015; Bouyoucos et al. 2017). Swimming behaviours are indicators of survival (Beitinger 1990) and can provide long-term information about recovery once a fish has been released. By incorporating information regarding behaviour (Brownscombe et al. 2022), physiology (Wedemeyer and Wydoski 2008; Donaldson et al. 2014), and measures of locomotor activity (Lennox et al. 2019), biologists and managers have become more effective in identifying cause-and-effect relationships (Cooke et al. 2013a). Studies that incorporate both external and internal cues for monitoring stress in fish are therefore useful, not only for fishery managers but also to individual resource users who wish to reduce their impact on the population. This holistic understanding fosters further advancements in the field of C&R, building upon previous knowledge from fundamental works (e.g., Muoneke and Childress 1994).

In addition to stress, C&R events can inflict physical damage. DuBois and Dubielzig (2004) found that 10% of stream salmonids experienced eye damage associated with hooks. Other research has proposed varying explanations for observed mortality in angled lake trout (*Salvelinus namaycush*). Variables such as hook placement and bleeding (Falk et al. 1974; Persons and Hirsch 1994), fish size (Loftus et al. 1988), and hook type (Dextrase & Ball 1991) have been examined in different seasons. Comparing these studies, winter angling superficially appears to be associated with higher mortalities, with total mortality rates of 10% (Dextrase and Ball 1991) and 24% (Persons and Hirsch 1994) opposed to 6.98% (Falk 1974) and 14.9% (Loftus 1988) in the summer. However, conclusions are based on observed mortality without taking into consideration the possibility for delayed mortality via behavioural impairment and physiological disturbances. Angling mortality in salmonids has been suggested to be a two-stage process in which injury location is affected by hook and barb type, and then mortality is affected by injury location and species (Gjernes et al. 1992). Angler-induced mortality is in direct conflict of recreational fisheries management aims.

The effects of C&R are largely dependent on environmental factors. Recovery can vary with season (Weber and Weber 2021) since environmental factors can impact physiology and behaviour (McLean et al. 2020). In cases where fish are protected by voluntary or regulatory C&R, instant or delayed mortality can still occur. Behavioural and physiological disturbances (Twardek et al. 2018a; Pinder et al. 2019; McLean et al. 2020) can compound with environmental conditions such as water temperature and air exposure (Joubert et al. 2020; Van Leeuwen et al. 2020; Card and Hasler 2021; Larochelle et al. 2021) to induce mortality, resulting in sublethal effects on reproduction and growth (Watson et al. 2020; Papatheodoulou et al. 2022). Thus, conclusions drawn from C&R research continues to be context-specific and further work needs to expand current knowledge regarding long-term post-release recovery over multiple temperature regimes (Somers et al. 2021; Keefe et al. 2022).

1.5 Human dimensions

Understanding the socioecological nature of C&R fisheries is vital when creating effective waterbody restrictions (Post et al. 2008; Hunt et al. 2011). For example, the way fishing effort is distributed across space and time can influence fish population distribution, and vice versa (Pitman et al. 2019). The scale and intensity of recreational fishing effort can fluctuate due to changes in stock abundance (Hunt et al. 2011) and socioeconomic conditions (Arlinghaus et al. 2015). Strategies employed to harvest trout populations should therefore consider whether exploitation influences the growth of trout and if it depends on how the biomass and production are distributed in that population (Healey 1978). There is potential instability with angler-fish interactions; resulting from angler and fish behaviour, management responses to depleted populations, and ecological responses to food web disruption (Post et al. 2002). Dynamics between different resource users can be an important factor when managing stock populations. Lake trout recreational catch in Lake Michigan declined by an estimated 50% between 1978–1981 and was attributed to the commercial fishery of the same population (Clark Jr and Huang 1985). Model testing suggested that egg production of the population would be unable to increase without imposing catch restrictions on both groups. This demonstrates that legislation must be dispersed among resource users, limitations put on only one group would prove to be ineffective. In addition to changes in population numbers, high and selective exploitation may lead to evolutionary changes if some phenotypes experience higher mortality (Arlinghaus and Cooke 2009). The notion of fishing-induced selective evolution is growing (Cooke et al. 2007; Jørgensen et al. 2007).

Resource users may react to management decisions differently, on both a temporal and spatial scale. Despite social and economic importance, recreational fisheries are often managed locally or regionally and lack comprehensive policy and development frameworks (Arlinghaus et al. 2012). Initiatives such as the Global Code of Practice for Recreational Fisheries attempt to unite sustainable and ethically appropriate fishing regulations (Arlinghaus et al. 2010). However, the integration of such a wide framework would require changes in popular practices to increase pro-environmental behaviours (Arlinghaus et al. 2012). Governance may influence the emergence and resolution of conflicts and thus, may be criticized for being political rather than based on the sustainability of the resource (Bower et al. 2014). Angler perspectives are important to consider in this regard. For example, certain anglers may perceive themselves as having no direct effect on ecosystems through their angling behaviour (Gray and Jordan 2010). Regulations limiting the use of certain bait would likely seem unnecessary to those groups, introducing the potential for conflict. Certain initiatives attempt to reduce this conflict by introducing opportunities for anglers to self-regulate. Catch and release may be both voluntary and obligatory depending on species, location, and time of year. The use of voluntary sanctuaries, informally enforced seasonal closures, personal daily bag limits, self-imposed constraints on gear, development of entirely live-release fisheries, and adoption of conservation-oriented gears and practices are alternatives to traditional regulatory options (Cooke et al. 2013b). Unfortunately, these actions also have the potential to generate conflict (Arlinghaus 2007), as both biophysical and social settings influence compliance to voluntary C&R (Stensland et al. 2013). Better communication and understanding of different perspectives among fisheries researchers, managers, and anglers are needed when addressing issues relating to the fishing sector (Hasler et al. 2011).

1.6 Fisheries Management

As mentioned previously, recreational angling can impact populations through selective pressure and mortality. In addition to exploitation-induced population bottlenecks, intensive stocking with foreign genotypes can contribute to irreversible loss of locally adapted populations (Arlinghaus et al. 2017). Physiological research is often disconnected from conservation practitioners and managers (Cooke and O'Connor 2010), but positive examples of using physiological knowledge to improve fisheries management are beginning to emerge (Cooke et al. 2012). Understanding socio-ecological dynamics has been suggested as an important part of ensuring sustainable recreational fisheries management (Post et al. 2008; Hunt et al. 2011). Partnerships between scientists and government bodies have great potential for advancing fishery protection and angler satisfaction. By implementing science-based management practices, unintended immediate and delayed mortality can likely be reduced. This form of "mandated science (i.e., science that responds to political and legal questions) is a key to determining which questions are important and what answers are relevant to various stakeholders (Wilson 1999). The concept of co-management is also relevant here, in which participation in the management process by those who are to be regulated will improve compliance to those regulations (Kaplan and McKay). Improving recreational fisheries management globally could result in substantial social benefits, which would be as impactful as reforming commercial fisheries (Abbott et al. 2018). Therefore, studies that examine economically and socially important fish while being inclusive of resource users, managers, and addressing gaps in literature are strong in their application.

While increased public interest in lake trout C&R necessitates management that effectively protects and enhances populations, the complexity of these fisheries make decision making difficult. Maximum size limits have been suggested to be the best management strategy for lakes when opting to preserve trout size over quantity (García-Asorey et al. 2011). Yet, management should be dynamic, with differences likely needing to occur on a population-by-population basis since there can be differences in behaviour, growth rate, recruitment, and sex and age class distribution (Marin et al. 2016; Pollack et al. 2021). Many lakes have the potential to produce large lake trout yet sustaining prey populations has historically been problematic due to the voraciousness of lake trout and their competitive advantage over other salmonid species (Pate et al. 2014). Many anglers prefer to catch large fish over smaller individuals (Connelly and Brown 2000; Johnston et al. 2013; Beardmore et al. 2015). For recreational fisheries that are managed according to length-based creel limits, there can be size-selective removal of the largest individuals (Arlinghaus 2005). This can result in length- and age-frequencies being forced towards smaller and younger fishes (Almodóvar and Nicola 2004). While mortality, growth and maturity may be used as indicators of fishery potential and development, they are not certain indicators in trout populations (Healey 1978).

Lake trout are widely distributed across Canada, as their natural Canadian range spans from Nova Scotia to British Columbia (Scott and Crossman 1973). Within Manitoba, lake trout are valued sportfish that provide food and economic benefits to isolated communities. Tourism associated with catch-and-release (C&R) angling opportunities and the pristine aquatic environments lake trout inhabit have brought more attention to Manitoba's north, with places like The Pas (Figure 1.1) becoming famous due to the nearby trophy fishery at Clearwater Lake Provincial Park (Tuli 2018). The provincial Master Angler program (Travel Manitoba 2021) is one tool that is currently used to promote these fisheries, highlighting individual catches and their location. Through academic-governmental partnership, this thesis provides information which can be used to assess current management techniques aimed at protecting and enhancing lake trout populations.

1.7 Hypothesis and objectives

The objective of this thesis is to provide contemporary information regarding the susceptibility of lake trout populations to catch-and-release angling. To address the wide range of angling conditions fish experience, I examined lake trout responses across multiple seasons and time courses. Specifically, I aimed to: (1) quantify reflex impairment and recovery post-capture; (2) explore how plasma stress metrics differ with time post-capture; (3) examine interactions of blood metrics and reflex impairment responses to angling to predict mortality; (4) characterize factors that influence reflex impairment and physiology; and (5) determine how fish recover post-release. I hypothesized that angling would induce stress and cause impairment that would be observable through behaviour, physiology, and activity.

In Chapter 2, I angled lake trout during the winter and explore ice angling effects in extended and immediate recovery experiments. I use reflex, barotrauma, and blood metrics to assess stress and examine interactions that may lead to angling-induced mortality. My study is the first to report barotrauma during winter angling in a physostomous species and addresses multiple knowledge gaps that have been identified in ice fishing (Lawrence et al. 2022). In Chapter 3, I expand on the winter work, angling lake trout during both summer and fall and assessing short-term impacts of C&R. I use reflex, barotrauma, and blood metrics along with post-release activity to quantify how lake trout respond to capture. The addition of tri-axial accelerometry provides more insight into how fish behave once released as well as depth preferences, which may assist them in recovering from pressure-related impairment. My study builds on previous research assessing the effectiveness of quick-release external biologging (Chhor et al. 2022). Chapters 2 and 3 explore responses to C&R over varying time scales between seasons. Seasonality has major effects on physiology (Davis et al. 1984; Barton and Schreck 1987; Guderly 2004; Louison et al. 2017b), thus, experiments were broken into two separate manuscripts based on time of year rather than being combined. In Chapter 4, I synthesize the findings from the two data chapters and discuss future directions for C&R

research. This thesis in its entirety provides novel information regarding context-specific aspects of C&R fishing and will be useful for future management of recreational fisheries.

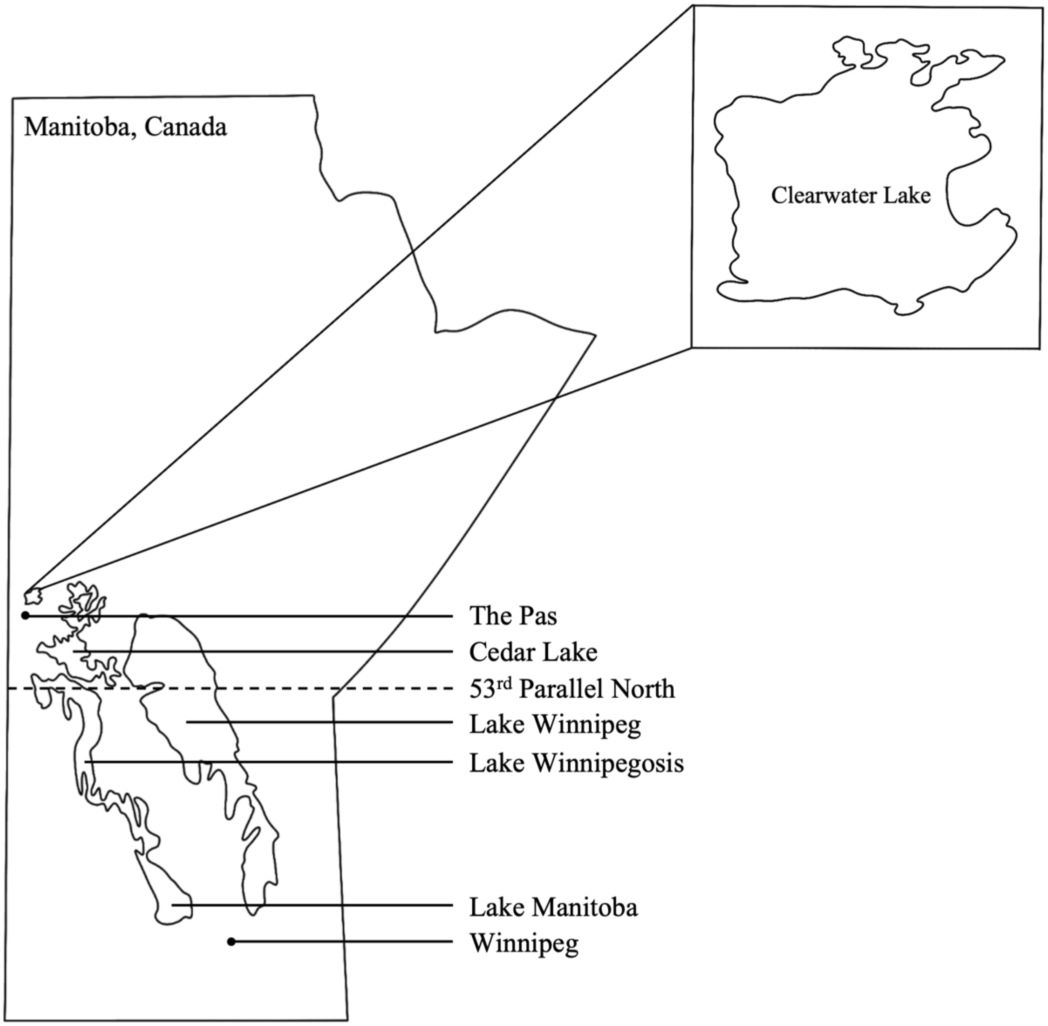

Figure 1.1 Map of Manitoba indicating Clearwater Lake, the study area where research occurred for this thesis (54.0570° N, 101.0564° W).

Chapter 2. Lake trout reflex impairment and physiological status following ice-angling

2.1 Abstract

Catch-and-release is a common practice used to promote survival of angled fish but is understudied in the context of winter conditions. I examined extended impairment and physiological disturbance of lake trout (*Salvelinus namaycush*) following ice-angling. Fish were ice-angled and placed in a water-filled tub for 0.5, 4, and 6 h to recover (n = 19). Reflex impairment and physiological status (using blood-based indicators) were assessed repeatedly for every individual. Fight time was a predictor of physiological disturbance 0.5 h post-angling with longer fight times leading to higher lactate and glucose, and lower extracellular pH. Loss of orientation was the most common reflex impairment (84% of fish) 4h post-angling. Mortality (36.8%) was observed during the study; however, variation in handling, barotrauma, and issues with sampling may have confounded angling effects. To determine if barotrauma impacted impairment and mortality, lake trout at a later sampling date (n = 29) were exposed to air for either 60, 120, 180, 240, 300, or 420 s before assessment of reflex impairment (3.4% mortality). For fish air exposed for 300 s or more, 14% lost orientation during immediate assessment. Bloating occurred in 20% of fish air exposed for 60 s. An air exposure duration of 420 s significantly impaired reflexes. Recreationally caught lake trout show behavioural and physiological impairment with such impairments magnified by extended air exposure. My results support responsible catch-and-release practices with emphasis on reducing reflex impairment and mortality.

2.2 Introduction

Catch-and-release angling (C&R) relies on the assumption that fish survive and exhibit negligible long-term impairment (Wydoski 1977). If those assumptions are satisfied, C&R can be a valuable conservation tool and enable use of various harvest management regulations (Arlinghaus et al. 2007; Danylchuk et al. 2018). However, negative consequences for fish are observed following angling (e.g., Muoneke and Childress 1994; Bartholomew and Bohnsack 2005; Sass and Shaw 2020) and these consequences compound with water temperature and air exposure to induce mortality (Gingerich et al. 2007) or sublethal effects on reproduction and growth (Watson et al. 2020; Papatheodoulou et al. 2022). Additionally, fish released immediately upon capture may not necessarily exhibit external signs of harm and thus, cryptic impairment may lead to unobserved delayed mortality (Coggins Jr et al. 2007; Gilman et al. 2013). It is therefore imperative to incorporate behaviour, physiology, and mortality assessments into C&R science to fully assess angling impacts on fishes (e.g., Cooke and Schramm 2007; Brownscombe et al. 2022).

For fish, the process of angling involves fighting the line, air exposure, and being handled. These individual stressors can combine to induce a generalized stress response (Cooke and Suski 2005), which allows fish to regain homeostasis through coordinated physiological changes (Schreck and Tort 2016). Responses to stress in fish are tiered. The immediate response includes endocrine changes such as higher levels of catecholamines and corticosteroids (Wendelaar Bonga 1997). Endocrine changes then induce effects on cardiac output, oxygen uptake, and the mobilization of energy substrates (Wendelaar Bonga 1997). Should homeostasis not be regained, reduction in growth, poor disease resistance, or altered behaviour may affect long-term reproduction and survival (Barton 2002). The generalized stress response varies with environmental factors, for example, fish exhibit a more pronounced hormonal or metabolic response in warmer temperatures (Barton and Schreck 1987; Wilkie et al. 1996), compared to colder temperatures (Guderley 2004).

An understudied fish in the context of C&R science is the lake trout (*Salvelinus namaycush*), despite many jurisdictions across North America promoting all season angling opportunities. These fish exhibit slow growth, longevity, late maturation, low reproductive potential, and slow replacement of adults, making them vulnerable to fishing pressure (Shuter et al. 1998). Other closely related salmonid species, like brook trout (*Salvelinus fontinalis*), experience blood chemistry disturbances such as elevated blood glucose (Wedemeyer et al. 2008) and reflex impairment (Brownscombe et al. 2022) following angling. Lake trout are one of only a handful of species that have pre-existing research on the consequences of winter angling, leaving a gap in our understanding of related impairment or mortality (e.g., Dextrase and Ball 1991; Persons and Hirsch 1994). The scarcity of information regarding physiology, behaviour, and survival inhibits our ability to assess effects of unique environmental conditions and specialized fishing techniques associated with ice-angling (Lawrence et al. 2022). Despite our understanding of seasonal differences in growth, movement, and habitat use (Binder et al. 2017; Gallagher et al. 2018; Hébert and Dunlop 2020), we have yet to fully describe how winter angling directly impacts post-release behaviours and physiology of lake trout.

Lake trout share similar trophic ecologies and habitat use with other salmonids that inhabit deep and cold oligotrophic lakes (Ivanova et al. 2021; Nawrocki et al. 2022; Ridgway et al. 2022). These salmonids are adapted for rapid vertical movement, displaying diel vertical migration and air gulping from the surface to fill their swim bladders (Saunders 1953; Keyler et al. 2019; Macaulay et al. 2020; Pelster 2021; Larocque et al. 2022). Despite this, fish angled from depths > 30 m are sensitive to pressure and temperature changes (McLennan et al. 2014; Sitar et al. 2017) and may experience barotrauma regardless of season. Barotrauma occurs in fish that are rapidly brought towards the surface from depth due to the decompression of gases in the blood and organs (Carlson 2012). The change in gas pressure can result in a range of injuries such as displaced organs, internal bleeding, and tissue damage (Rummer and Bennett 2005; Hannah et al. 2008; Pribyl et al. 2011). Physostomous species, like lake trout, are vulnerable to barotrauma despite the ability to belch excess gas from the swim bladder through the esophagus *via* a pneumatic duct (Saunders 1953; St John 2003). This is becoming widely recognized as a conservation concern by anglers (Schreer et al. 2009; Elliot et al. 2021). Barotrauma symptoms have been more heavily explored during open water angling, but recent research has shown high post-release mortality from barotrauma in cold lakes where fish are angled from deep depths (Althoff et al. 2021).

Another important issue associated with lake trout and C&R science is that lake trout are often considered ‘trophy’ fish. Lake trout reach large sizes (> 1 m), and size is an important factor with regards to effects of angling on fish because larger fish often have longer fight times (Reeves and Staples 2011), experience higher levels of angling-induced stress (Wydoski et al. 1976; Meka and McCormick 2005) and mortality (Loftus et al. 1988; Nuhfer et al. 1992; Lee and Bergersen 1996). Therefore, trophy-sized lake trout fisheries may be at risk from angler-induced effects. Beyond size, mortality in angled lake trout can also be explained by hook placement and bleeding (Falk et al. 1974; Persons and Hirsch 1994) and hook type (Dextrase and Ball 1991).

In my study, I examined the physiological and behavioural responses of lake trout to C&R ice-angling in Clearwater Lake, Manitoba. The objectives of my study were to: (1) quantify reflex impairment and recovery post-capture; (2) explore how plasma stress metrics (i.e., cortisol, lactate, glucose, and pH) differ with time post-capture (samples taken at 0.5, 4, and 6 h); (3) examine interactions of blood metrics and reflex impairment responses to angling to predict mortality; (4) characterize factors that influence reflex impairment and physiology, including size, fight time, and length of air exposure; and, (5) determine if barotrauma might be occurring in lake trout angled during the winter. For the extended recovery sampling (objectives 1–4), I hypothesized that fish capture would induce stress and impair behaviour that would affect survivorship. Specifically, I expected that fish would have delayed recovery but low reflex impairment, stress metrics would increase with time, high behavioural and physiological responses would be predictive of mortality, and fish length would affect stress and impairment. For the immediate recovery sampling (objective 5), I hypothesized that fish capture would impair behaviour and lead to barotrauma. I expected that fish would display reflex impairment within the first several minutes following capture.

2.3 Methods

2.3.1 Study location

I angled lake trout from Clearwater Lake, Manitoba, Canada (54.0570° N, 101.0564° W) between January 10–16, 2022 and March 28–April 8, 2022. The surface area of the lake is 593 km^2 and its average depth is 13.1 m. In January, air temperatures fluctuated between -30 and -1.3 °C (mean = -16.50 °C) (Environment and Climate Change Canada 2022) and water temperatures 10 m below the lake surface were between -0.2 and 0 °C (mean = -0.05 °C) (Pro20 model, YSI Inc., Yellow Springs, OH, USA; range = -5 – 55 ºC, accuracy = ± 0.3 ºC). I angled for fish between 16 and 18.6 m (mean = 16.40 m) where dissolved oxygen levels were between 122.43 and 150.92% air saturation (mean = 126.09% air saturation) (17.36–21.4 mg/L, mean = 18.84

mg/L). In March, air temperatures were between -13 and 6.2 °C (mean = -1.60 °C) and water temperatures at 10 m below the lake surface were between 0.2 and 1 °C (mean = 0.53 °C). I angled for fish between 6.1 and 21.3 m (mean = 15.23 m) where dissolved oxygen levels were between 84.15 and 123.91% air saturation (mean = 100.28% air saturation) (11.73–17.42 mg/L, mean = 14.02 mg/L).

2.3.2 Fish capture and holding

I divided our study into two sampling periods. In January, after fish capture, I held fish in tubs for up to 6 h to monitor physiological recovery in blood parameters and reflex impairment (extended recovery). In March, after fish capture, I held fish for 420 s to quantify barotrauma and reflex impairment (immediate recovery).

During both sampling periods, I captured fish using 1.17 m extra-heavy-action fiberglass ice fishing rods (46XH Slugger, Fish Frostbite, CA) that were spooled with 13.61 kg braided line and a 1.22 m 5.44 kg fluorocarbon leader on a size 35 reel (Pflueger President XT, Pure Fishing, Columbia, SC, USA). I either held the rods or fitted them to a tip-up (I Fish Pro 2.0, Tactical Ice Gear, CA). For rods I held, I rigged them with spoons, plastic swimbaits, jigging tubes, or quick-strike rigs with size 1/0 treble hooks (Plate 2.1). For the tip-ups, I baited size 1/0 treble hooks with dead whole cisco (*Coregonus artedi*) (152–330 mm) and placed these within 50 m of anglers (12 experienced anglers). I angled fish from various locations on the lake and caught fish within and outside uninsulated heated ice fishing tents (Plate 2.2). Once an angler felt a strike or observed a tip-up flag, they quickly raised the rod to set the hook and lift the fish from the water. I recorded the time between hooking the fish and the fish clearing the ice hole (i.e., fight time). I then immediately unhooked the fish, noted the hooking location, and scored the level of bleeding using a three-point scale (adapted from Falk et al. 1974): 0 score, none, no external bleeding near the hook entry point; 1 score, slight, a small amount of bleeding localized near the hook entry point; and 2 score, flowing, blood surrounding and obscuring the hook entry point. Because anglers were spread out in a general area around our sampling tent, I transported fish within a tub filled with fresh lake water on a sleigh. The maximum distance I transported a fish was 400 m. For each fish captured, I recorded the duration of air exposure time during handling.

2.3.3 Extended Recovery Sampling

During the first sampling period, in January, upon entry into the sampling tent, I measured each fish (n = 19) for length and weight, and then transferred it to a tub of fresh surface water for reflex assessment (see below). Once I completed the reflex assessment, I moved fish to a covered 378 L stock tank filled with fresh surface water. I frequently changed the water in the tank and water temperature fluctuated between 0 and 0.1 °C (mean = 0.05 °C) with dissolved oxygen levels between 61.67 and 131.83 % air saturation (mean = 99.83% air saturation) (12.8–18.64 mg/L, mean = 14.12 mg/L). I left fish to recover in the tank for 0.5, 4, and 6 h. I never held more than four fish at a time in the stock tank and was cognisant of total fish size in the tank.

At each time point, I assessed fish for impairment using a reflex assessment and a blood sample (size dependent, see below). For the reflex assessment, I followed previously established methods (Davis 2007; Raby et al. 2012; McLean et al. 2016; Brownscombe et al. 2022) and conducted it in a tub (78.74 × 45.72 × 30.48 cm) that we filled with fresh lake water. The assessment included the following metrics: (1) tail grab, burst swimming response to caudal peduncle grab; (2) body flex, attempted escape when held out of the water by midsection; (3) head complex, opening of jaws in normal ventilation pattern when held out of water; (4)

vestibular-ocular response, tracking of eye to remain level when rotated horizontally and held out of water; (5) orientation, vertical alignment after being placed upside-down in holding bin. I scored failure to demonstrate a metric "1", and I calculated totaled reflex impairment score as the sum of each of the five impairments that were not present for all individuals at each time point. I conducted all reflex assessments to limit variation between samplers. The assessment took less than 60 s.

Following each of my reflex assessments, I sampled fish for blood using best practices described in Lawrence et al. (2020). Briefly, I held fish ventral-side up with their gills submerged in the water of the tub. I drew 1.5 mL of blood *via* caudle puncture with a 10 mL lithium heparin vacutainer and 21-G needle. I then immediately centrifuged the blood at 6000 g for 3 min to separate plasma from other blood components (red blood cells) and allocated the plasma into three 0.6 mL vials. I stored the plasma and other blood component samples in a vapour shipper that was charged with liquid nitrogen (Cryopro 3.6 L, VWR International, Radnor, PA, USA) until I could move them to a laboratory freezer (– 80 °C). Total blood sampling time varied between fish due to difficulties associated with outside temperatures, and I sampled fish > 1500g during each of the three time points. I could only sample fish < 1500g twice (i.e., a random two out of the three time points) to ensure less than 10% of total blood volume was removed (Lawrence et al. 2020). Following the end of sampling at the 6 h time point, I inserted a T-bar anchor tag on the left side of the dorsal fin of each released fish to ensure fish were not resampled. No fish were recaptured.

For each fish and time point, I quantified concentrations of plasma cortisol, lactate, and glucose and measured intracellular and extracellular pH. For plasma cortisol, I used a commercially available enzyme-linked immunosorbent assay (ELISA) kit (#402710, Neogen, Lexington, KY, USA) and a microplate spectrophotometer (SpectraMax i3, Molecular Devices, San Jose, CA, USA). The ELISA kit that I used was previously validated for analysis of salmonid plasma samples (Raby et al. 2015). I ran the assay in triplicate at a dilution factor of 200 after having completed a dilution series of 25, 50, 100, 200, and 400 to choose the appropriate dilution factor based on a standard curve. The intra-assay variation (% CV) for my plates was 7.48% and the inter-assay variation was 12.2%, which are acceptable ranges for plasma cortisol in salmonids (Barry et al. 1993). I determined concentrations of plasma lactate and glucose following the enzymatic methods of Lowry and Passonneau (1972). I did each sample in triplicate and used a dilution factor of 3.75 for plasma lactate. The intra-assay variation for plasma lactate was 5.08% and inter-assay variation was 15%. The intra-assay variation for plasma glucose was 4.22% and inter-assay variation was 12.9%. I measured extracellular pH from thawed plasma and intracellular pH from lysed red blood cells that went through five freeze-thaw cycles (e.g., Mullen et al. 2020) (HI98165 pH Meter, HANNA Instruments, Woonsocket, RI, USA).

2.3.4 Barotrauma and Immediate Recovery Sampling

In April, I sampled a second group of lake trout (n = 29). I angled these fish using the same methods described above. I monitored angler interaction with fish according to four time intervals defined by times T_0 to T_4 (adapted from Lyon et al. 2022). The first time interval (T_0–T_1) began when an angler set the hook (T_0) and ended when fish were out of the ice hole and exposed to the air (T_1). The second time interval (T_1–T_2) began when fish were exposed to the air (T_1) and ended after fish had been placed onto the ice surface and exposed to air for a randomly specified amount of time (60s, 120s, 180s, 240s, 300s, 420s) before I placed it into a tub filled with fresh water (T_2). Between T_1 and T_2, I recorded hooking location, level of bleeding, length, and weight in the same fashion as described above. I also attached to each fish a coloured T-bar anchor tag on the left side of the dorsal fin to ensure fish were not resampled. The third time interval (T_2–T_3) began once fish were placed into water inside the assessment tub (T_2) and ended once the reflex and barotrauma assessments (described below) had been completed and I returned the fish to the ice hole (T_3). The fourth time interval (T_3–T_4) began once I placed the fish into the ice hole and ended when the fish kicked-off (T_4). During this time, I retained a loose grip on the caudal peduncle in case I had to retrieve the fish due to it not having the ability to swim away. I scored the vigour of release using a three-point scale: 0 or poor, lethargic movement, and lack of consistent tail beats; 1 or good, regular movement and consistent tail beats; and 2 or excellent, energetic movement and fast-paced tail beats.

During the T_2 and T_3 time period, after fish were air exposed for one of the randomly selected time intervals, I completed two assessments of the captured fish. First, I did a reflex assessment, which was done in the same manner as the first sampling period. The second assessment was a barotrauma assessment (adapted from Althoff et al. [2021]; indicators are noted in several studies, e.g., Morrissey et al. [2005]; Gravel and Cooke [2008]; Schreer et al. [2009]; Eberts et al. [2018]), which I did in the same tub as the reflex assessment (Figure 2.1). For the barotrauma assessment, I scored the presence of the following metrics (“1” present, “0” not present): (1) oral organ eversion, gastric herniation into the buccal cavity; (2) exophthalmia, bulging eyes; (3) bloating, overinflation of the midsection; (4) anal organ eversion, prolapsed anus; and (5) hemorrhaging, redness in the mouth/gills/fins/anus. Similar to the reflex assessment, I did all barotrauma assessments. I calculated totaled barotrauma score as the sum of each of the five impairments that were not present for all individuals at each time point. It took less than 60 s to complete the assessment.

2.3.5 Data analysis and statistics

I used R version 4.1.2 (R Core Team 2021) and assessed significance at $\alpha \leq 0.05$, unless noted otherwise. For the first sampling period (i.e., extended recovery experiment), I tested whether blood plasma and pH parameters differed across recovery times using paired t-tests ("stats" package, R Core Team [2021]). I could not use repeated-measures ANOVA because not all fish were sampled at each time point. Prior to analysis, I tested for outliers using Grubbs' tests for outliers ("outliers" package, Komsta [2022]) and removed them from the analysis. Then, to ensure model assumptions were met, I tested homogeneity of variance using a Levene's test ("cars" package, Fox and Weisberg [2019]) and normality using a Shapiro-Wilk test ("stats" package, R Core Team [2021]). When the model assumption tests failed for the blood parameters, I used a square root transformation prior to the paired t-test. For significant comparisons, I calculated effect size using Cohen's D test ("effsize" package, Torchiano [2020]). When individuals were missing a blood parameter value at a particular recovery time, I removed it from the dataset for comparisons using that recovery time and blood parameter. Because I did multiple statistical analyses using the blood, I used a Bonferroni correction to offset the likelihood of a type-I error, thus for the tests involving the blood metrics, I used a significance level of $\alpha = 0.01$. To relate mortality with the blood parameters I used binary logistic regression models ("stats" package, R Core Team [2021]). I regressed mortality against each blood parameter at each recovery time (0.5 h, 4.0 h, 6.0 h) to address whether the blood parameters predicted death. Again, I used a Bonferroni correction to account for multiple statistical tests being performed and thus, I used $\alpha = 0.01$ to determine significance of the blood parameter versus mortality models. The next analysis I did was to determine at each recovery time point the effects of total length, fight time, air exposure, and reflex impairment on each of the blood parameters. To do this, I created 17 candidate linear models based on various combinations of the independent variables and used an information theoretic approach (second-order Akaike's Information Criterion; "AICcmodavg" package , Mazerolle [2020]; and, "lme4" package, Bates et al. [2015]). Likewise to above, outliers were removed, model assumptions were validated, and data was transformed as needed. The last statistical analysis I did for the first sampling period was to analyze whether reflex impairment could be predicted by any of the independent variables, including recovery time, total length, fight time, and air exposure. To do this, I used binary multiple logistic regression mixed models ("lme4" package, Bates et al. [2015]). Note, I originally included interactions of the independent variables; however, they were not significant and were removed from the final analysis. There were no interactions between variables. Additionally, I included individual ID as a random effect because, unlike blood parameters, I had reflex scores for every individual.

For the second sampling period (i.e., immediate recovery experiment), I used binary multiple logistic regression models ("stats" package, R Core Team [2021]) to determine the effects of total length, fight time, and air exposure on either reflex or barotrauma impairment. I originally included depth and interactions of the independent variables in the model but removed them due to insignificance. Lastly, I compared reflex and barotrauma scores using a Pearson correlation ("devtools" package, Wickham et al. [2022]) to determine if the two response variables were associated.

Plate 2.1 Underwater footage of lake trout (*Salvelinus namaycush*) interacting with different bait types during winter angling.

Plate 2.2 Photo showing the sampling site organization during the immediate and extended recovery experiments on Clearwater Lake, Manitoba, Canada.

Figure 2.1 Images showing barotrauma assessment metrics including: (A) oral organ eversion, (B) Exophthalmia, (C) bloating and anal organ eversion, (D) hemorrhaging in the eye, and (E) hemorrhaging in the fins observed in lake trout (*Salvelinus namaycush*) following angling.

2.4 Results

2.4.1 *Extended Recovery*

Overall, I caught nineteen lake trout during the first sampling period. These fish had a mean (± S.D.) total length of 633 ± 149 mm with a range of 450–952 mm. The mean weight of the lake trout caught during the first sampling period was 3130 ± 2484 g with a range of 454–9667 g. There was a 36.8% mortality rate. Of the seven mortalities observed, only one occurred prior to the 0.5 h sampling point, three occurred after the 4 h sampling point, and three occurred shortly after the 6 h sampling point. In all fish, bleeding and injury were minimal, hooks were not swallowed, and fish were active upon hook removal.

Recovery time, total length, fight time, and air exposure did not have any effect on reflex scores (Table 2.1). Total reflex impairment immediately following capture was 4 and peaked at 18 at 4 h. Reflex impairment then began to decline at 6 h. Loss of orientation was the most observed reflex impairment with 84% of fish displaying it 4 h post-angling (Figure 2.2). At 4 h post-capture, cortisol was 70% higher than it was at 0.5 h (Paired t-test: $t_{12} = -5.7$, $P < 0.001$) and it doubled at 6 h (Paired t-test: $t_8 = -4.4$, $P = < 0.01$) with large effect sizes for both comparisons (Figure 2.3). At 4 h, lactate was 28% higher than it was at 0.5 h (Paired t-test: $t_{12} = -5.3$, $P = < 0.001$) and at 6 h it was 31% higher (Paired t-test: $t_8 = -6.5$, $P = < 0.001$) with large effect sizes for both comparisons. Glucose was not significantly higher at 4 h or 6 h post-capture when compared to the 0.5 h sample point. Extracellular pH decreased from 7.59 at 0.5 h to 7.43 (1%) at 4 h (Paired t-test: $t_{11} = 5.9$, $P < 0.001$) with a large effect size but not at 6 h post-capture. Intracellular pH did not significantly change at 4 h or 6 h post-capture when compared to the 0.5 h sample point. I found no relationships between blood metrics at any recovery time and mortality (Table 2.2). The most parsimonious models to predict cortisol, lactate, glucose, extracellular pH, and intracellular pH were found *via* AICc (Table 2.3). Thirty minutes after the angling event, fight time was a significant predictor of lactate ($R^2 = 0.42$), the interaction of fight time + reflex score was a significant predictor of glucose ($R^2 = 0.51$), and fight time was a significant predictor of plasma pH ($R^2 = 0.24$) (Table 2.3). Four hours after the angling event the interaction of fight time + reflex score was a significant predictor of lactate ($R^2 = 0.81$) and again at six hours ($R^2 = 0.80$).

2.4.2 Immediate Recovery

During the second sampling period, twenty-nine lake trout were angled. These fish had a mean total length of 599 ± 184 mm with a range of 310–1040 mm. The mean weight of the lake trout caught during the second sampling period was 2619 ± 3113 g with a range of 190–11310 g. There was a 3.4% mortality rate (one fish was hooked in the gill arches and died). Air exposure, total length, and fight time did not influence barotrauma scores. Totaled barotrauma scores peaked at 60 s of air exposure and then fluctuated throughout the rest of the timepoints up to 420 s. Bloating of the abdomen was the most observed barotrauma impairment with 20% of fish displaying it 60 s post-angling. Oral organ eversion was the only reflex indicator not observed in any fish captured. Only an air exposure time of 420 s influenced reflex score (Table 2.4). Total reflex scores continued to increase across the 420 s and loss of orientation was the most observed reflex impairment with 14% of fish displaying it 300 s post-angling (Figure 2.2). Reflex impairment and extent of barotrauma were not correlated (Pearson correlation: $t_{27} = 0.23$, $r = 0.05$, $P > 0.05$).

Table 2.1 Summary of binary multiple logistic regression models assessing the effects of recovery time (h), fish total length (mm), fight time (s), and air exposure (s) on whether lake trout (*Salvelinus namaycush*) showed impairment for any of the five reflex impairment indicators assessed after ice-angling during an extended recovery experiment (L.L. = effect estimate lower limit, U.L. = effect estimate upper limit).

Variable	Estimate	L.L.	U.L.
(Intercept)	-68.77	-158.66	21.11
Recovery Time 0.5	7.07	-2.75	16.90
Recovery Time 4	7.07	-2.75	16.90
Recovery Time 6	8.06	-2.46	18.59
Total Length	0.09	-0.03	0.22
Fight	-0.03	-0.07	0.02
Air Exposure	0.05	-0.04	0.13

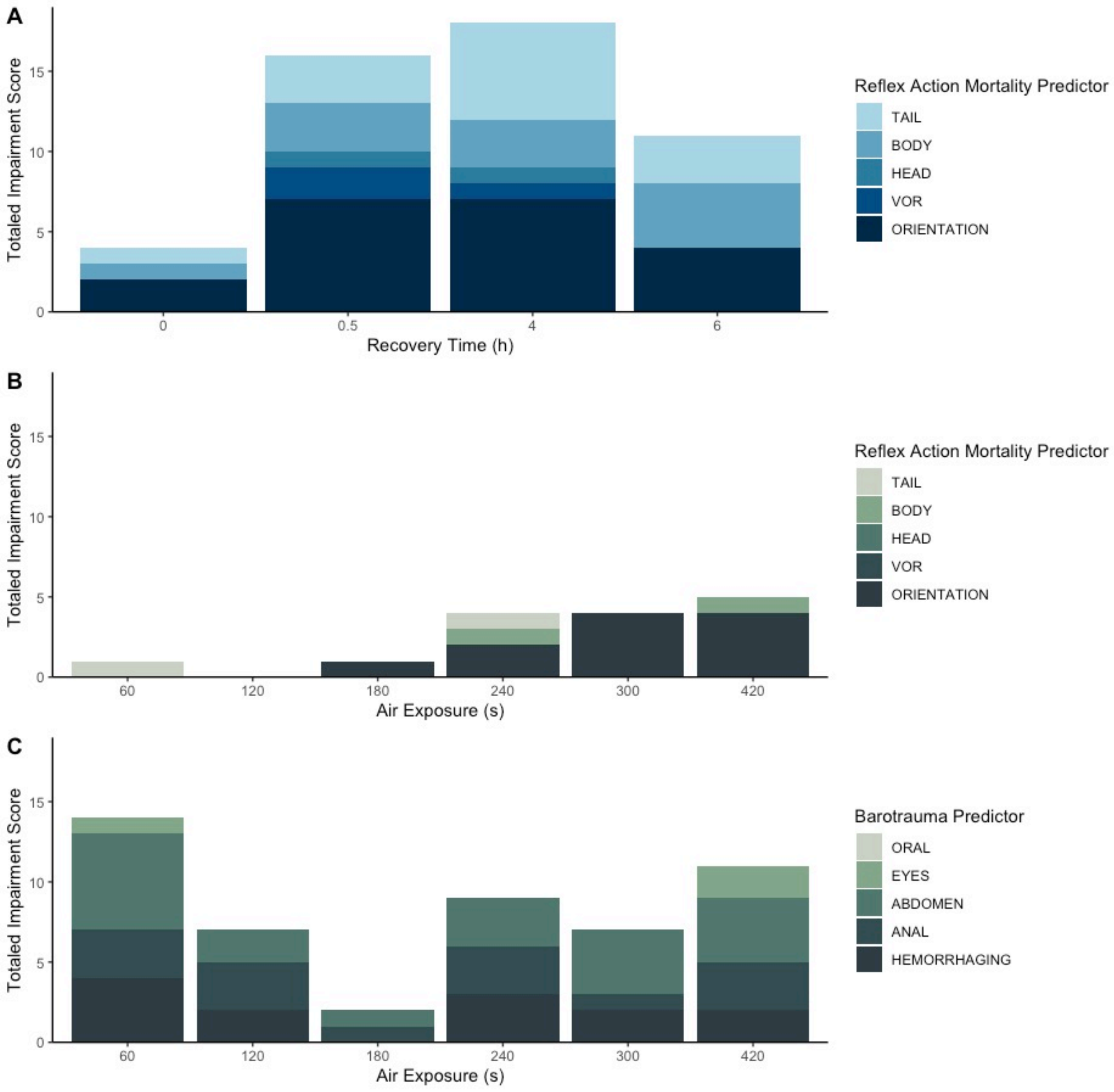

Figure 2.2 Totaled impairment scores for (A) extended recovery reflex impairment (n = 19), (B) immediate recovery reflex impairment (n = 29), and (C) immediate recovery barotrauma (n = 29) predictors in lake trout (*Salvelinus namaycush*) sampled following ice-angling. Reflex metrics include: (1) tail grab; (2) body flex; (3) head complex; (4) vestibular-ocular response; and (5) orientation. Barotrauma metrics include: (1) oral organ eversion; (2) exophthalmia; (3) bloating; (4) anal organ eversion; and (5) hemorrhaging.

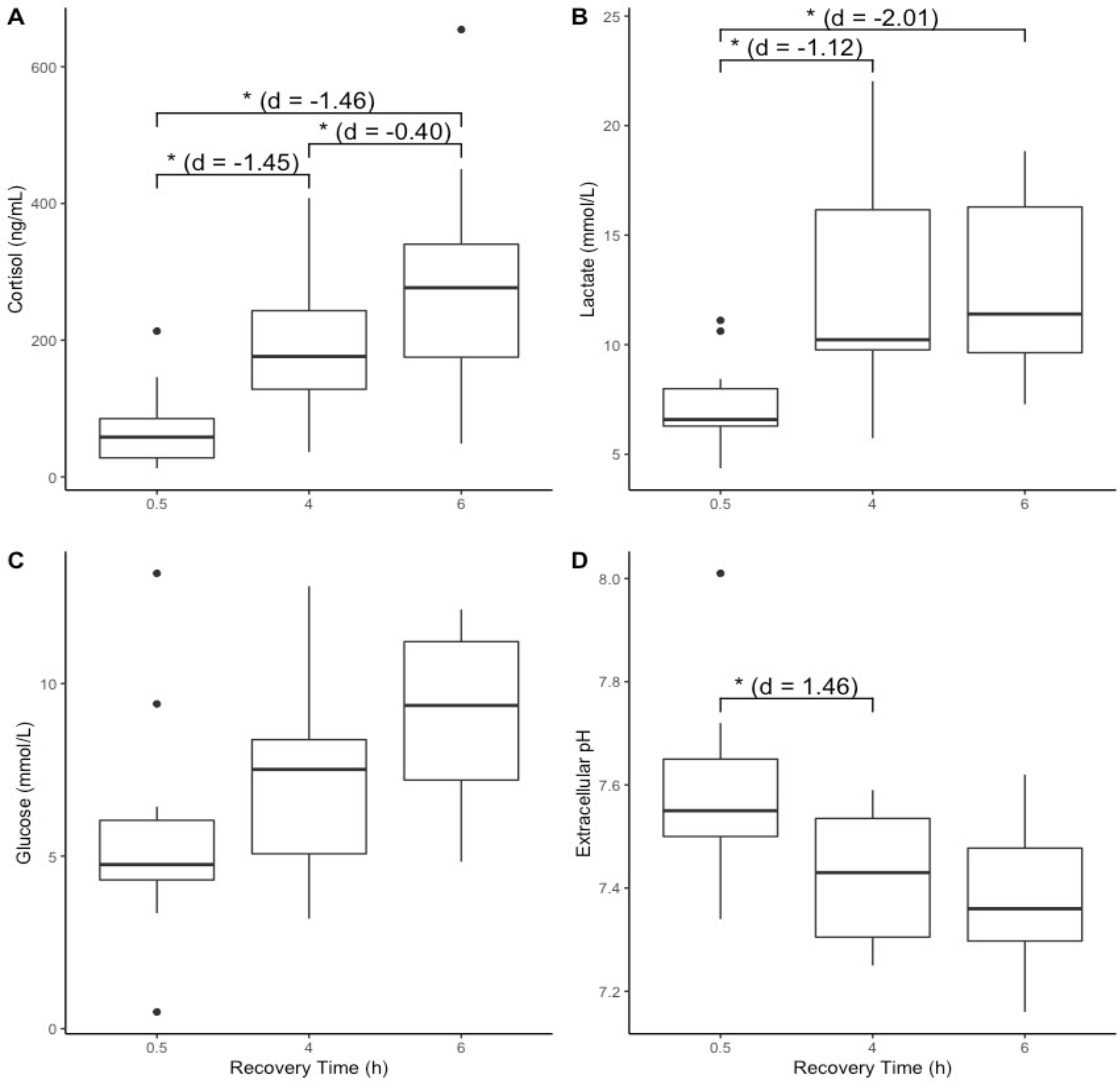

Figure 2.3 Concentrations of (A) plasma cortisol, (B) plasma lactate, (C) plasma glucose, and (D) extracellular pH in lake trout (*Salvelinus namaycush*) sampled at 0.5 (n = 13), 4 (n = 13), or 6 h (n = 11) following ice-angling. Thick black horizontal lines denote median values, boxes contain all data within the 25th and 75th quartiles, whiskers show the range of data, and outliers are depicted as black dots. Asterisks above horizontal brackets denote statistical significance at corrected $\alpha = 0.01$. Cohen's d values (i.e., standardised difference of the means) are within parenthesis.

Table 2.2 Summary of binary logistic regression models assessing the effects of cortisol (ng/mL), lactate (mmol/L), glucose (mmol/L), extracellular pH, or intracellular pH of lake trout (*Salvelinus namaycush*) sampled at 0.5, 4, and 6 h post-angling on whether a fish survived the angling event or not. Statistical significance was determined at a corrected α = 0.01.

Time	Blood Metric	Estimate	S.E.	*z* value	df	*P*
0.5	Cortisol	0.28	0.22	1.30	12	0.19
	Lactate	0.96	1.69	0.57	12	0.57
	Glucose	-2.10	1.70	-1.24	12	0.22
	Extracellular pH	13.76	21.17	0.65	12	0.52
	Intracellular pH	91.41	64.73	1.41	12	0.16
4	Cortisol	0.14	0.15	0.92	14	0.36
	Lactate	4.12	1.87	2.21	14	0.03
	Glucose	1.04	1.21	0.86	14	0.39
	Extracellular pH	10.23	24.52	0.42	14	0.68
	Intracellular pH	24.69	44.15	0.56	12	0.58
6	Cortisol	0.01	0.12	0.05	10	0.96
	Lactate	3.33	1.85	1.80	10	0.07
	Glucose	-0.19	1.31	-0.14	10	0.89
	Extracellular pH	-4.75	25.30	-0.19	10	0.85
	Intracellular pH	18.76	43.36	0.43	10	0.67

Table 2.3 Summary of model selection results based on second-order Akaike information criterion (AICc) for linear models predicting the cortisol (ng/mL), lactate (mmol/L), glucose (mmol/L), extracellular pH, and intracellular pH concentrations of lake trout (*Salvelinus namaycush*) sampled at 0.5, 4, and 6 h post-angling. The most parsimonious models are bolded.

Time	Metric	Model Name	K	AICc	ΔAICc	AICcWt	Cum. Wt	R^2
0.5	Cortisol	Null	2	61.90	0.00	0.41	0.41	-
	Lactate	**Fight**	**3**	**10.10**	**0.00**	**0.46**	**0.46**	**0.42**
		Length + Fight + Reflex	5	11.94	1.84	0.18	0.65	0.72
	Glucose	**Fight + Reflex**	**4**	**19.83**	**0.00**	**0.32**	**0.32**	**0.51**
		Reflex	3	20.64	0.80	0.21	0.53	0.24
		Null	2	20.92	1.09	0.19	0.72	-
	Plasma pH	**Fight**	**3**	**-53.07**	**0.00**	**0.22**	**0.22**	**0.24**
		Null	2	-52.86	0.21	0.20	0.41	-
		Air	3	-52.40	0.66	0.16	0.57	0.19
		Length	3	-52.28	0.78	0.15	0.72	0.18
		Fight + Air	4	-51.23	1.84	0.09	0.80	0.37
	Blood pH	Null	2	-65.80	0.00	0.56	0.56	-
4	Cortisol	Null	2	67.10	0.00	0.38	0.38	-
		Reflex	3	68.50	1.40	0.19	0.57	0.09
	Lactate	**Fight + Reflex**	**4**	**15.09**	**0.00**	**0.57**	**0.57**	**0.81**
		Length + Fight + Reflex	5	16.38	1.29	0.30	0.87	0.86
	Glucose	Null	2	19.61	0.00	0.23	0.23	-
		Air	3	19.63	0.02	0.23	0.46	0.19
		Reflex	3	20.14	0.53	0.18	0.63	0.15
		Air + Reflex	4	20.74	1.13	0.13	0.76	0.33
	Plasma pH	Null	2	-51.16	0.00	0.46	0.46	-
	Blood pH	Null	2	-64.13	0.00	0.30	0.30	-
		Fight	3	-63.81	0.32	0.26	0.55	0.10
		Length	3	-63.04	1.09	0.17	0.73	0.11
6	Cortisol	Null	2	65.09	0.00	0.53	0.53	-
	Lactate	**Fight + Reflex**	**4**	**13.75**	**0.00**	**0.85**	**0.85**	**0.80**
	Glucose	Null	2	16.91	0.00	0.35	0.35	-
		Fight	3	18.08	1.17	0.20	0.55	0.18
		Reflex	3	18.43	1.52	0.16	0.71	0.15
	Plasma pH	Null	2	-39.06	0.00	0.48	0.48	-
		Fight	3	-37.72	1.33	0.24	0.72	0.16
	Blood pH	Null	2	-49.86	0.00	0.48	0.48	-
		Fight	3	-48.61	1.25	0.26	0.74	0.17

Table 2.4 Summary of binary multiple logistic regression models assessing the effects of air exposure time (s), fish total length (mm), and fight time (s) on whether lake trout (*Salvelinus namaycush*) showed impairment for any of the five reflex impairment indicators or barotrauma metrics assessed after ice-angling during an immediate recovery experiment. Statistical significance was determined at α = 0.05 and is bolded.

	Variable	Estimate	S.E.	*z* value	df	*P*
Reflex	(Intercept)	-11.74	6190	-1.90	28	0.06
	Exposure Time 120 s	-19.21	4265	-0.01	28	1.00
	Exposure Time 180 s	1.68	3.12	0.54	28	0.59
	Exposure Time 240 s	1.88	2.18	0.86	28	0.39
	Exposure Time 300 s	2.97	2.13	1.39	28	0.16
	Exposure Time 420 s	**4.57**	**2.31**	**1.97**	**28**	**0.05**
	Total Length	0.02	1.10	1.48	28	0.14
	Fight	-0.00	0.02	-0.32	28	0.75
Barotrauma	(Intercept)	18.30	6389	0.00	28	1.00
	Exposure Time 120	-19.02	6389	-0.00	28	1.00
	Exposure Time 180	-22.70	6389	-0.00	28	1.00
	Exposure Time 240	-0.75	9544	0.00	28	1.00
	Exposure Time 300	-20.64	6389	-0.00	28	1.00
	Exposure Time 420	0.59	9804	0.00	28	1.00
	Total Length	0.00	0	0.02	28	0.98
	Fight	0.05	0.07	0.67	28	0.50

2.5 Discussion

2.5.1 Mortality

The 36.8% mortality rate observed in the extended recovery experiment was higher than I expected for a physostomous species, which are typically robust to stressors like barotrauma (Brown et al. 2014). However, these mortalities could not be confidently attributed to the hooking and retrieval, as immediately following capture, fish were responsive and had minimal injury or bleeding. Sampling and handling of fish, as well as holding the fish in tubs at surface rather than at capture depth, were additional stressors that could have contributed to the observed mortality (Ferter et al. 2015). Additionally, the low sample size during the extended sampling and the lack of variation in capture depth limit my interpretation of the mortality rate. Nonetheless, the mortality rate observed in this experiment is higher than what has been seen in other studies examining the effects of ice-angling on lake trout. For example, mortality rates in other studies were 10% (Dextrase and Ball 1991) and 24% (Persons and Hirsch 1994); however, fish in these studies were not held for extended periods of time like in my experiment and so delayed mortality was not assessed. Delayed mortality has been documented following exhaustive exercise or post-angling in other salmonids (Wood et al. 1983; Ferguson and Tufts 1992), with most angling-induced mortality occurring within the first 48h (Mongillo 1984; Dedual 1996). In my experiment, lake trout died within 6 h following capture at ~16 m. Holding conditions and handling can potentially exacerbate stress responses and behaviour (Portz et al. 2006; Mullen et al. 2020). Based on my higher-than-expected mortality rate, either angling caused a much more serious impact than found in other lake trout and ice-angling studies or some aspect of the fish holding induced unintended consequences. Due to fish capture depth, and my observation that lake trout were not releasing gas at the surface, I speculate that the fish may have suffered from barotrauma. Anecdotally, I observed swim bladder inflation in certain fish dissected after mortality had occurred. The addition of a barotrauma assessment during the second sampling period allowed me to deduce that pressure-related impairment was occurring in the lake trout, though based on observations between the two sampling periods, I do not think barotrauma was as severe as it was in the first sampling event. Holding fish to obtain physiological and reflex endpoints are one of the main challenges with C&R studies in the winter and refinement of methodology is needed to remove sampling and handling stressors (Lawrence et al. 2022).

2.5.2 Behaviour

Coupling behaviour with physiological parameters can provide insight to a fish's state following angling (Arlinghaus et al. 2009; Cooke et al. 2013a). Reflex indicator scores showed signs of behavioural recovery within 6 h. Loss of orientation was the most observed reflex impairment with 84% of fish displaying it 4 h post-angling during extended recovery and 14% of fish displaying it 300 s post-angling during immediate recovery. Impaired orientation has been shown to be a crucial predictor of mortality in other species (Gingerich et al. 2007; Raby et al. 2012) and is necessary for fish to return to desired depths upon release (Louison et al. 2023). Fish experiencing an orientation impairment are likely forced to float just under the ice surface after release and therefore experience low temperatures and potential tissue freezing (Card et al. 2022). Behavioural impairments, such as floating, force fish to continue exhaustive activity through the act of trying to return to depth, further perpetuating changes in physiological variables and possibly accelerating mortality (Wood 1991; Ross and Hokenson 1997).

Oral organ eversion is one of the most recognizable and commonly observed injuries resulting from barotrauma (Schreer et al. 2009). This occurs when the stomach is inverted and expelled through the esophagus due to the overexpansion of the swim bladder (Figure 2.1A). Physoclistous fish are typically more susceptible to barotrauma then physostomous fish like lake trout because their swim bladder is not connected to the stomach *via* a pneumatic duct (Saunders 1953; St. John 2003). These fish must instead diffuse gases through a capillary mesh that supplies blood to the swim bladder and is the interface for gas exchange (Ferguson 1989). Despite being physostomous, lake trout in my study exhibited barotrauma impairment which would not have been captured by using only the reflex assessment. I therefore recommend using both assessments in succession to provide a better estimate of the range of impairments.

Barotrauma may be exacerbated by varying factors. Other studies have found effects of depth and duration that fish were held at the surface on barotrauma (Schreer et al. 2009; Wegner et al. 2021). In my study, air exposure, total length, and fight time did not affect barotrauma scores. Angling for lake trout often occurs at depths > 40 m with bait either resting-on or jigging just above the bottom of the lake (Lamont 2017). Water pressure increases with depth and thus, fish angled from the bottom experience the full gradient of pressure changes on the way to the surface. Lake trout typically display their belching mechanism to expel excess gas through their mouths during an angling event. However, the high barotrauma scores observed in my study suggest that this mechanism was not entirely reliable during rapid decompression. Lake trout have previously been documented to display signs of barotrauma but not in relation to ice-angling (Ng et al. 2015; Sitar et al. 2017). Interestingly, reflex impairment and barotrauma were not meaningfully correlated despite similarities in certain impairment metrics such as orientation in the reflex assessment and abdominal bloating in the barotrauma assessment.

2.5.3 Blood Physiology

Ice-angling induced changes to plasma cortisol, plasma lactate, plasma glucose, extracellular pH, and intracellular pH in lake trout. Cortisol, lactate, and glucose were highest at 6 h post-angling when sampling ended. Despite below-ice water temperatures and the expectation that physiological processes, such as metabolism and the stress response, should be slowed (Davis et al. 1984; Barton and Schreck 1987; Guderly 2004; Louison et al. 2017b), the observed values for each variable were higher than what has been found in previous lake trout studies during summer months (Wedemeyer and Wydoski 2008; Pottinger 2010). These values may have been influenced by holding conditions, as described earlier. Typically, cortisol and lactate values peak between 0.5 h and 2 h before recovery after exhaustive exercise or handling (Milligan and Wood 1986; Barton and Iwama 1991). In female pink salmon, cortisol, lactate, and glucose peaked between 0.5 and 2 h after being exposed to 3 min of exhaustive exercise and 1 min of air exposure (Donaldson et al. 2014). Maximum intracellular and extracellular pH values were within similar ranges of other C&R studies (Brobbel et al. 1996; Mullen et al. 2020). The continued decrease in pH up to 6 h post-angling was expected because anerobic use of glycogen to meet energy demands leads to an excess of lactate and reduced pH (Milligan and Wood 1986). Quantifying maximum peak values for all other blood metrics was not possible since they increased continuously up to 6 h. The delayed onset of the stress response and heightened blood metrics after 4 h seen in my study has also been seen in other ice-angling research (Louison et al. 2017a; Louison et al. 2017b). Recovery profiles differ by species and context (Barton 2000; Ruane et al. 1999; Logan et al. 2019; Lawrence et al. 2022), so generalized physiological responses of ice-angled lake trout remains poorly characterized. Understanding fish recovery is important for conservation so further research is needed to understand the full amount of time required for fish to return to baseline physiological levels. Fish that continue to experience stress after being released can be more susceptible to other factors such as predation (Campbell et al. 2010; Holder et al. 2020). Therefore, quantifying physiological recovery time can improve understanding of delayed mortality.

Plasma cortisol, lactate, glucose, and pH were not predictors of mortality. All metrics examined in my study are physiological variables that are well explored in other fishes as physiological disturbance markers (Wood 1991; Suski et al. 2003; Cooke et al. 2013a; Twardek et al. 2018a). Cortisol is a primary stress hormone, lactate and glucose are metabolites, and pH indicates acid-base status (Wendelaar Bonga 1997). Collectively, they are a result of internal coordination to increase the availability of oxygen and energy (Rodnick and Planas 2016; Schreck and Tort 2016). Lactate is valuable in predicting mortality because it is a by-product of exhaustive exercise (Wood 1991). Lactate anion is produced *via* glycolysis while metabolic protons are produced during adenosine triphosphate (ATP) breakdown (Robergs et al. 2004). It has been implicated with post-exercise mortality and may play a role in mitigating pathological effects of exhaustion (Wang et al. 1994; Holder et al. 2022). Minimizing factors that influence changes in metabolites during collection and handling in field settings is difficult since the process of collecting blood itself inherently changes blood metabolite profiles through the stress of confinement (Kiilerch et al. 2018), handling (Sopinka et al. 2016), and technical ability (Lawrence et al. 2020). In my study, holding time was limited to mitigate effects from fasting and altered environment (Morata et al. 1982; Scarabello et al. 1991; Brobbel et al. 1996) but fish may have experienced increased handling due to logistical challenges with winter sampling.

Fight time and the interaction of fight time + reflex impairment were the only variables that predicted lactate at 0.5, 4, or 6 h post-angling. Longer fight times increase exhaustive activity and thus, lactate production (Holder et al. 2022). Exhaustion following line-fighting may also impair reflexes that require the depleted energy-stores such as body flex, orientation, and tail grab. In my study, only an air exposure of 420 s influenced reflex impairment score. A large body of research has previously demonstrated the effects of holding (Cooke et al. 2002b; Donaldson et al. 2013; Chhor et al. 2022b), fish size (Loftus et al. 1988; McLean et al. 2020), fight time (Cooke et al. 2016; Blyth and Bower 2022), and air exposure (Gingerich et al. 2007; Donaldson et al. 2014; Logan 2019; Chhor et al. 2022a) on reflex impairment. For example, brook trout > 328 mm with air exposure times > 10 s exhibit higher reflex impairment measures (Brownscombe et al. 2022).

2.5.4 Effect of size

While fish body length was not found to influence mortality or impairment in my study, larger rainbow trout (*Oncorhynchus mykiss*) have been shown to experience a higher degree of angling-induced stress (Wydoski et al. 1976) and hooking mortality (Schisler and Bergersen and 1996). The lack of effect observed in my study may be attributed to a low number of large individuals (i.e., 5 fish > 890 mm) captured during sampling periods. Larger fish may be more likely to fight to exhaustion and thus often experience negative survival outcomes after angling due to increased length of time fighting the line (Reeves and Staples 2011; Twardek et al. 2018a). Angler-induced C&R mortality is in direct conflict with fishery conservation aims and thus, management decisions should focus on methods to improve survivorship in released fish.

2.5.5 Management

The results of my study provide new information on the susceptibility of physostomes to angling-induced impairment during the winter. Specifically, lake trout exhibited delayed behavioural and physiological recovery in the extended recovery experiment and a high degree of impaired barotrauma metrics in the immediate recovery experiment. Understanding how to effectively manage this population during winter months is vital to prevent a decline in fish abundance. Generally, fisheries managers lack scientific information to inform decision making around winter C&R fisheries. Basic estimates of fish hooking mortality are necessary and can range from 1% to > 90% depending on species, angler skill, and environmental factors (Muoneke and Childress 1994; Arlinghaus et al. 2007). My study provides estimates of immediate and extended mortality following angling which may be used to inform strategies aimed at protecting and enhancing fishing opportunities. Additionally, I describe other factors such as physiological changes and reflex impairment that may predict mortality. Further research on ice-angling needs to explore extended impacts on spatial ecology (Lawrence et al. 2022). Monitoring after release is especially difficult due to a lack of pre-established telemetry infrastructure in many northern lakes in addition logistical difficulties associated with ice cover. General best practices must continue to be promoted for this fishery such as preventing air exposure, limiting fight times, and careful handling upon capture (Brownscombe et al. 2017; Danylchuk et al. 2018; Brownscombe et al. 2022; Chhor et al. 2022a). Wider implementation of commercially available descending devices may combat fish mortality by returning fish to a depth that allows them to relieve barotrauma pressure (Curtis et al. 2015; Bellquist et al. 2019; Davies et al. 2022; Louison et al. 2023). These devices are an alternative to more invasive methods such as fizzing which has the potential to harm vital organs if done improperly (Kerr 2001; Nguyen et al. 2009; Drumhiller et al. 2014). Further research should explore the efficacy of descending devices to relieve barotrauma in lake trout during winter months.

Chapter 3. Short-term impacts of recreational angling on lake trout

3.1 Abstract

It is crucial to understand the impact recreational angling has on fish populations and how stress can be observed through changes in behaviour or physiology. The assumption of high survival following catch-and-release can be impacted by external factors such as season. We therefore examined short-term impairment in lake trout (*Salvelinus namaycush*) angled during the summer (n = 74) and fall spawning period (n = 33). Immediately following capture or after having recovered for 0.5 h, fish underwent reflex and barotrauma assessment and provided a non-lethal blood sample. Fish were then fitted with a tri-axial accelerometer on a quick-release velcro harness and permitted to swim unhindered for 14 min. In the summer (23.3% mortality), reflex impairment and barotrauma were significantly correlated. Fish length, fight time, and angling depth influenced barotrauma score with bloating of the abdomen being the most observed impairment. Loss of orientation was the most observed reflex impairment with only one fish displaying oral organ eversion immediately after capture. Plasma cortisol, lactate, and glucose increased, and extracellular and intracellular pH decreased 0.5 h post-capture. No relationships were found between blood metrics and mortality. The time required to reach maximum depth was not impacted by fight time or air exposure while overall dynamic body acceleration (ODBA) was influenced by depth. During the fall, fish displayed no mortality or reflex impairment. Anal prolapse was the most observed barotrauma impairment (all signs displayed by females except for one male displaying exophthalmia), however, impairments captured in the barotrauma assessment were all likely a result of spawning (i.e., egg production) rather than pressure changes. Sex and recovery time influenced blood metrics, with length and depth being significant predictors of cortisol. The time required to reach maximum depth was not impacted by fight time or air exposure, ODBA was impacted by depth and males exhibited higher activity.

3.2 Introduction

In recreational fisheries, the use of catch-and-release (C&R) is widely implemented to promote practices that encourage high fish survivorship (Arlinghaus et al. 2007). The success of C&R relies on the assumption that angling does not induce major changes in behaviour, physiology, or long-term survivorship (Cooke and Schramm 2007). Stress is inherent for fish that are captured by angling, and sublethal effects may compound with abiotic conditions to affect recovery (Gingerich et al. 2007; McLean et al. 2020; Van Leeuwen et al. 2021).

Reflex scoring is a simple and inexpensive field-based assessment technique that measures fish vitality by examining behavioural reflexes that are present in unimpaired individuals (Davis 2007; Davis 2010). Scoring reflexes as either present or absent, one can effectively predict future survival of fish prior to their release since the assessment is a whole-animal indicator of compromised physiological state (Davis 2010; Raby et al. 2012). In addition to reflex impairment, fish can experience pressure-related injuries known as barotrauma (Carlson 2012). Lake trout are physostomous and possess a pneumatic duct which allows expulsion of excess gas through the esophagus, unlike physoclistous species which make use of an oval chamber and diffuse excess gas through a capillary mesh that supplies blood to the swim bladder (Saunders 1953; Ferguson 1989; St John 2003). Physoclistous species are known to be more susceptible to rapid changes in external pressure. When angled from depth, fish experience a gradient of external pressure change which in some instances may be too severe to be effectively expelled (Eberts et al. 2018; Stallings et al. 2023).

Coupling behavioural assessments with physiological markers of stress allows stronger conclusions to be drawn from C&R research (Arlinghaus et al. 2009; Twardek et al. 2018a). Stress from angling typically measured through changes in hormones, metabolites, or acid-base status from non-lethal blood sampling (Lawrence et al. 2020), however there has been recent exploration into other methods such as mRNA abundance (DePasquale et al. 2023). Physiological samples taken from wild fish following angling provide insight into the general stress response and allow researchers to understand correlates of mortality after release (Skomal et al. 2007). The process of angling involves many different variables that may be hard to distinguish in their effects on survival. Studies that incorporate both external and internal cues for monitoring stress in fish are therefore useful, not only for fisheries managers but also to individual resource users who wish to reduce their impact on the population.

Recently, coupling C&R studies and biotelemetry has become more prevalent (Donaldson et al. 2008). Understanding the energetic cost of angling on fishes is important in measuring their impairment and recovery. Accelerometery has been used to answer a wide breadth of questions relating to fine-scale movements, kinematics, and metabolic rate in both fresh and saltwater species (Gleiss et al. 2010; Brown et al. 2013; Brownscombe et al. 2014b; Metcalfe et al. 2015; Bouyoucos et al. 2017). Overall dynamic body acceleration (ODBA) is one method used as a proxy for energy expenditure, defined as a single integrated measure of body motion in three spatial dimensions (Halsey et al. 2009). ODBA relies on the link between acceleration produced by muscular contraction and energy consumption (Gleiss et al. 2011) because movement correlates with the energy expended to produce it (Wilson et al. 2006). Research exploring C&R with tri-axial accelerometers has validated ODBA as a useful tool in understanding how behaviour of certain fish can remain impaired even after a fish has been released as well as energy consumption (Lennox et al. 2018; Griffin et al. 2022). Swimming behaviours are good indicators of post-stressor survival (Beitinger 1990), and studies using ODBA to measure activity in both summer (Chhor et al. 2021) and winter (Larochelle et al.

2021; Bieber et al. 2022) illustrate how behaviour may be impacted not only by the angling event itself, but also by the environmental conditions that fish experience during recovery.

Seasonality can have a major impact on the scale of fish stress responses. The majority of C&R occurs during the open-water season, which is characterized by high air and water temperatures and elevated activity of target species (Kobler et al. 2008). During this time, metabolic processes are faster (Johnston and Dunn 1987; Anderson et al. 1998) yet environmental conditions may amplify physiological disturbances from C&R and increase susceptibility to impairment (Wilkie et al. 1996; Cooke and Suski 2005). Salmonid behaviour changes substantially during spawning, as they move towards shallower waters and display behaviours such as digging redds (females) or showing aggression towards other reproductive competitors (males) (Crisp and Carling 1989; Esteve et al. 2008). Behavioural impairment following angling is a concern because impacts of angling might prevent fish from engaging in typical spawning behaviours and thus, decrease individual fecundity. Understanding the effects on physiology is also important because during spawning, elevated baseline levels may leave less flexibility for additional stressors. Using genetic analysis, Richard et al. (2013) found that large Atlantic salmon produced less offspring when angled. The reproductive strategy of lake trout varies, with evidence suggesting that they do not reproduce each year and that certain morphologically distinct populations display adaptive strategies such as skipped spawning (Sitar et al. 2014). The sex hormone 17β-estradiol is important for fish reproduction (Piferrer and Donaldson 1994; Jeffries et al. 2012; Sinchak and Wagner 2012) and may become reduced in response to angling stressors (Donaldson et al. 2014). 17β-estradiol reduction may in turn influence reproductive output through less energy allocated into egg production.

In my study, I aimed to determine whether C&R angling induced short-term changes in reflexes, physiology, and behaviour of lake trout (*Salvelinus namaycush*) angled during the summer and fall spawning period. I accomplished this by assessing reflexes, barotrauma, and blood parameters 0 or 0.5 h post-capture before attaching a tri-axial accelerometer harness and monitoring their activity for 14 min. In doing so, I also examined interactions of variables that lead to impairment and mortality. Evidence suggests that external factors such as air and water temperature compound recreational angling stressors to influence survival (Gingerich et al. 2007; Donaldson et al. 2014; Logan 2019), lake trout were expected to display a more pronounced response to angling during the summer. Lake trout are a major component of recreational fisheries and numerous historical studies have attempted to quantify angling-related mortality (Falk et al. 1974; Loftus et al. 1988; Dextrase and Ball 1991; Persons and Hirsch 1994; Lee and Bergersen 1996). Contemporary estimates suggest that management policies based on an assumed 15% post-release mortality are likely underestimating the long-term effects C&R can pose to populations (Sitar et al. 2017). My study will therefore contribute to refining current management policies and explore this assumption.

3.3 Methods

3.3.1 Study location

I angled lake trout between June 23–July 20 and October 1–6, 2022, from Clearwater Lake, Manitoba, Canada (54.0570° N, 101.0564° W). The lake is 593 km^2 with an average depth of 13.1 m and clarity of 10 m. During the summer, air temperatures were between 13–30 °C (mean = 22.05 °C) (Environment and Climate Change Canada 2022) and surface water temperatures were between 15.9–21.3 °C (mean = 18.6 °C) (Pro20 model, YSI Inc., Yellow Springs, OH, USA; range = -5–55 ºC, accuracy = ± 0.3 ºC). Surface dissolved oxygen levels were between 4.20–8.01 mg/L (mean = 6.44 mg/L) and I angled fish between 10.05–42.4 m (mean = 26.02 m). During the fall, air temperatures were between 0–22 °C (mean = 12.90 °C) and surface water temperatures were between 10.8–14.4 °C (mean = 13.15 °C). Surface dissolved oxygen levels were between 11.2–13.4 mg/L (mean = 12.06 mg/L) and I angled fish between 1.5–13.7 m (mean = 3.37 m). A portion of the western half of Clearwater Lake is closed to all fishing from September 15 to October 15, to protect lake trout spawning (Province of Manitoba 2023a) since the natural population provides eggs and milt for the province's stocking programs (Province of Manitoba 2023b).

3.3.2 Fish capture and holding

Angling gear consisted of spinning rods spooled with 13.61 kg braided line and a 1.22 m 5.44 kg fluorocarbon leader on a size 35 reel. I rigged rods with either spoons, tubes, vertical jigs, crankbaits, jerkbaits, or quick-strike rigs with size 1/0 barbless treble hooks depending on angler preference and water depth. The angling location on the lake varied and I recorded water depth, temperature, and dissolved oxygen at each sample site from the boat (Plate 3.1).

Once an angler felt a strike (6 experienced anglers), they quickly raised their fishing rod to set the hook and lift the fish from the water. I recorded the time between hooking the fish and the fish fully clearing the water as well as the amount of time the fish was exposed to the air. Upon capture, I immediately unhooked fish, hooking location was noted, and level of bleeding was scored on a three-point scale (adapted from Falk et al. 1974): 0 score, none, no external bleeding near the hook entry point; 1 score, slight, a small amount of bleeding localized near the hook entry point; and 2 score, flowing, blood surrounding and obscuring the hook entry point. I also measured fish for total length and mass before placing them into a 378 L stock tank filled with fresh surface lake water to recover. Water temperature and dissolved oxygen within the tub fluctuated and was changed between fish. I placed fish into the tank to complete the reflex and barotrauma assessments, and phlebotomy (see below) immediately, or I left them to recover for 0.5 h before sampling them. A subset of fish underwent behavioural assessment without holding or subsequent phlebotomy for both seasons to test if assessment techniques would override angling effects.

3.3.3 Behavioural assessments

I completed reflex assessments following previously established methods (see Chapter 2) within a stock tank filled with fresh lake water. My assessment included the following metrics: (1) tail grab, burst swimming response to caudal peduncle grab; (2) body flex, attempted escape when held out of the water by midsection; (3) head complex, opening of jaws in normal ventilation pattern when held out of water; (4) vestibular-ocular response, tracking of eye to remain level when rotated horizontally and held out of water; (5) orientation, vertical alignment after being placed upside-down in holding bin. I completed barotrauma assessments (see Chapter 2) in the same tank filled with fresh lake water. I checked for the presence of the following metrics: (1) oral organ eversion, gastric herniation into the buccal cavity; (2) exophthalmia, bulging eyes; (3) bloating, overinflation of the midsection; (4) anal organ eversion, prolapsed anus; and (5) hemorrhaging, redness in the mouth/gills/fins/anus. I completed both behavioural assessments for all fish to limit variation between samplers, with scores for each reflex recorded as either 0 (unimpaired) or 1 (impaired). I calculated overall reflex or barotrauma score for each individual as the proportion of the five reflexes that were impaired, with both assessments completed in under 120 s.

3.3.4 Phlebotomy

I held a subset fish for a period of 0.5 h within the stock tank. After this time had elapsed, following reflex and barotrauma assessments, I held fish ventral-side up with gills submerged in the water within the stock tank. A 1.5 mL of blood was drawn via caudle puncture with a 10 mL lithium heparin vacutainer and 21-G needle. Less than 10% of total blood volume was removed (Lawrence et al. 2020). I then immediately centrifuged blood at 6000 g for 3 min to separate plasma from other blood components. Plasma was then allocated into 3 separate 0.6 mL vials before being placed into a vapour shipper charged with liquid nitrogen along with the remaining red blood cells (Cryopro 3.6 L, VWR International, Radnor, PA, USA). Once transported back to the laboratory, I stored plasma and other blood component samples at – 80 °C. I released surviving fish with a coloured T-bar anchor tag inserted on the left side of the dorsal fin after they had been sampled to ensure each individual was only sampled once during the study. The vigour of release was scored on a three-point scale: 0 or poor, lethargic movement, and lack of consistent tail beats; 1 or good, regular movement and consistent tail beats; and 2 or excellent, energetic movement and fast-paced tail beats. No fish were recaptured.

In the laboratory, I determined cortisol concentrations in blood plasma using commercially available enzyme-linked immunosorbent assay (ELISA) kits (#402710, Neogen, Lexington, KY, USA) and a microplate spectrophotometer (SpectraMax i3, Molecular Devices, San Jose, CA, USA). The ELISA kits have been previously used for analysis of salmonid plasma samples (Raby et al. 2015). I ran samples in triplicate at a dilution factor of 200 after having completed a dilution series of 25, 50, 100, 200, and 400 to choose the appropriate factor based on a standard curve. Intra-assay variation (% CV) for summer and fall was 4.37% and 7.27% respectively, inter-assay variation was 9.92% and 23.23%. I determined plasma lactate and glucose concentrations following the enzymatic methods of Lowry and Passonneau (1972) with triplicates and a dilution factor of 3.75 for lactate. Intra-assay variation for lactate was 5.22% and 5.48%, inter-assay variation was 6.02%. Intra-assay variation for glucose was 9.43% and 6.69%, inter-assay variation was 13.94%. I measured extracellular pH from thawed plasma and intracellular pH from lysed red blood cells that went through five freeze-thaw cycles (Mullen et al. 2020) (HI98165 pH Meter, HANNA Instruments, Woonsocket, RI, USA).

3.3.5 Post-release behaviour

To evaluate post-release behaviour, I attached tri-axial accelerometer tags (Axy 5 S Depth, TechnoSmArt, Rome, Italy; Sampling rate: acceleration = 10 Hz, temperature/depth = 1 Hz; Resolution: acceleration = 8-bit, temperature = 0.1 °C, depth = 5 cm, G scale = 8; 36 × 14 × 9 mm, 6.03 g) around the midsection of the fish using a harness which I made by bonding the accelerometer to a waterproof 3D-printed plate (PET-G, Sakata 3D filaments, Granada, Spain; 36 × 22 × 2 mm, 0.96 g) with marine epoxy and then threading this onto a section of Velcro tape (One-Wrap Roll, Velcro Brand, Manchester, NH, USA; length = 35–68 cm, width = 2 cm). I used varying lengths of velcro tape to accommodate differing fish girths. I attached harnesses while fish were held out of water with Velcro tape wrapped once around the fish anterior to the dorsal fin, positioning the accelerometer on the lateral side above the left pectoral fin (Plate 3.2). Harness attachment took no longer than 30s and Velcro straps were attached as to not inhibit the normal range of motion in order to reduce the impact of the harness on fish behaviour. The accelerometer harness was connected to a rod and reel spooled with 13.61 kg braided line using a snap swivel clipped through a reinforced hole in the Velcro tape (see Chhor et al. 2022a; Chhor et al. 2022b). Fish were released by hand at the side of the boat and allowed to swim without resistance for 15 min on a "free-spool" before I retrieved the accelerometer harness by tugging the line, which released the Velcro. I checked for the presence of the fish on the end of the line before retrieving the accelerometer by feeling for motion and weight. Due to a lack of underwater structure, we observed no entanglement of the line.

3.3.6 Data processing

I trimmed raw acceleration data to include only the first 14 min to standardize the length recorded activity between all individuals. I calculated static acceleration by passing a 2 s smoother over each axis with the *rollmean* function in the "zoo" package (citation) and converted the values to degrees by multiplying values by 180 π^{-1} (Brownscombe et al. 2013). I then calculated dynamic acceleration (g) by subtracting static acceleration from raw acceleration values for each axis. Next, I calculated overall dynamic body acceleration (ODBA) by summing the absolute values of dynamic acceleration in each axis (Lennox et al. 2018).

3.3.7 Data analysis and statistics

I completed all statistical analyses in R version 4.1.2 (R Core Team 2021) with level of significance assessed at $\alpha \leq 0.05$, unless otherwise stated. I performed separate Wilcoxon tests to test whether plasma metrics differed across recovery times in the summer, for cortisol, lactate, glucose, extracellular pH, and intracellular pH using the "rstatix" package due to the data not meeting assumptions of homogeneity and normality (Kassambara 2021). Homogeneity of variance was assessed using Levene's test from the "cars" package (Fox and Weisberg 2019) and normality was assessed using the Shapiro-Wilk test from the "stats" package (R Core Team 2021). Outliers were identified using Grubbs' test from the "outliers" package (Komsta 2022) and effect size was calculated using Wilcoxon effect size from "rstatix" package (Kassambara 2021). A Bonferroni correction was used to account for multiple statistical tests being performed and significance was determined at $\alpha = 0.01$. To test whether plasma metrics differed across recovery times or sexes in the fall, separate two-way ANOVAs were performed using the "stats" package (R Core Team 2021). When the model assumption tests failed for cortisol and lactate, I used a log transformation prior to the two-way ANOVA. A Bonferroni correction was used to account for multiple statistical tests being performed and significance was determined at $\alpha = 0.01$.

I used binary logistic regression models to determine the relationship between cortisol, lactate, glucose, extracellular pH, and intracellular pH at both recovery times and the occurrence of mortality in the summer with the "stats" package (R Core Team 2021). Mortality was regressed against each blood metric independently for both recovery times. A Bonferroni correction was used to account for multiple statistical tests and significance was determined at $\alpha = 0.01$. Linear models were used to determine the effect of length, fight time, air exposure, depth, reflex score, and barotrauma score on cortisol, lactate, glucose, extracellular pH, and intracellular pH 0.5 h post-angling in the summer and fall using the "stats" package (R Core Team 2021). Blood metrics were used as the response variable in each model.

I used binary multiple regression models to determine the effects of recovery time, length, fight time, air exposure, and depth on whether any reflex or barotrauma impairment was observed using the "stats" package (R Core Team 2021). Interaction between reflex and barotrauma scores in the summer were tested with Kendall correlation using the “stats” package (R Core Team 2021). Generalized additive mixed models (GAMMs) were used to determine interactions between ODBA and capture depth in the summer, and capture depth and sex in the fall using the “gamm4” package (Wood and Scheipl 2020). Time post-capture, recovery time, fish length, fight time, and air exposure time were initially included in the model but removed due to correlation and sex was not included in the summer GAMM due to sexing not being possible during that time of year. Linear models were used to determine the effects of fight time and air exposure on the time it took lake trout to reach their maximum depth following angling using the “stats” package (R Core Team 2021).

Plate 3.1 Photo showing the boats where reflex assessment, phlebotomy, and recovery occurred within water-filled tanks on Clearwater Lake, Manitoba, Canada.

Plate 3.2 Placement of a tri-axial accelerometer harness on a lake trout (*Salvelinus namaycush*) to quantify behaviour following angling. The accelerometer was bonded to a waterproof 3D-printed plate using marine epoxy and then threaded onto a section of Velcro tape that was fastened anterior to the dorsal fin with the accelerometer on the lateral side above the left pectoral fin.

3.4 Results

3.4.1 Summer Angling

I caught 74 lake trout during the summer period and these fish had a mean (± S.D.) total length of 610.51 ± 113.19 mm with a range of 513–1073 mm. The mean weight of these fish was 2150.55 ± 1788.00 g with a range of 1090–10120 g. These fish had a 23.3% mortality rate. Of the 14 mortalities observed, 9 occurred immediately after capture and 5 occurred within 0.5 h of holding.

Lake trout displayed signs of reflex and barotrauma-related impairment. Recovery time, total length, fight time, air exposure, and depth did not influence reflex scores, but fish total length, fight time, and angling depth all influenced barotrauma scores (Table 3.1). Reflex impairment and extent of barotrauma were also significantly correlated (Kendall rank correlation: $z = 3.77$, $r = 0.44$, $P < 0.05$). Loss of orientation was the most observed reflex impairment with 31.9% of fish displaying it immediately after capture (Figure 3.1). Bloating of the abdomen was the most observed barotrauma impairment with 76.6% of fish displaying it immediately after capture. One fish displayed oral organ eversion immediately after capture.

Angling induced changes in physiological stress metrics. At 0.5 h post-capture, cortisol increased by 89.8% (Wilcox: $z = -6.08$, $P < 0.0001$, Cohen's $d = 0.80$), lactate increased by 67.5% (Wilcox: $z = -6.41$, $P < 0.0001$, Cohen's $d = 0.84$), glucose increased by 27.7% (Wilcox: $z = -3.35$, $P < 0.001$, Cohen's $d = 0.44$), extracellular pH decreased by 2.6% (Wilcox: $z = 4.76$, $P < 0.0001$, Cohen's $d = 0.62$), and intracellular pH decreased by 1.1% (Wilcox: $z = 4.23$, $P < 0.0001$, Cohen's $d = 0.56$) (Figure 3.2). Large effect sizes were found for all comparisons. No relationships were found between blood metrics at any recovery time and mortality (Table 3.2). The most parsimonious models to predict cortisol, lactate, glucose, extracellular pH, and intracellular pH 0.5 h post-angling were found by running linear regression models (Table 3.3). No variables were significant predictors of any blood metrics.

Upon release, fish were observed to descend quickly to depth with high ODBA scores before reaching a desired depth and remaining there with a low ODBA score all the way up to 14 min. The time it took to reach maximum depth was impacted by fight time and air exposure (Table 3.4). While statistical comparisons could not be made due to low sample size, fish that remained on the surface due to barotrauma impairment ($n = 9$) exhibited superficially higher ODBA scores (Mean score of 0.202 opposed to 0.131) than those that were able to return to depth ($n = 42$) (Figure 3.3). Swimming activity (ODBA) was significantly influenced by depth (Table 3.5, Figure 3.4).

3.4.2 Fall Angling

I caught 33 lake trout during the fall period and these fish had a mean (± S.D.) total length of 557.36 ± 57.14 mm with a range of 462–683 mm. The mean weight of these fish was 1471.52 ± 445.66 g with a range of 830–2480 g. These fish had no mortality or reflex impairment. Recovery time, total length, fight time, air exposure, depth, and sex did not influence barotrauma scores (Table 3.1). Prolapse of the anus was the most observed barotrauma impairment in the fall with 45% of fish displaying it immediately after capture. The entirety of fall barotrauma signs were exhibited by females except for one male in the 0 h recovery timepoint which displayed exophthalmia. Bloating of the abdomen, anal prolapse, and hemorrhaging are all likely a result of spawning (i.e., egg production) rather than pressure-related impairment.

Sex and recovery time influenced blood metrics (Table 3.6). Cortisol was 65.5% higher in females than males between recovery times (two-way ANOVA: $F_{1,17} = 9.99$, $P = < 0.01$) and

72.9% higher in the 0.5 h recovery time compared to the 0 h recovery time (two-way ANOVA: $F_{1,17} = 20.55$, $P = < 0.001$) (Figure 3.5). Lactate was 63.12% higher (two-way ANOVA: $F_{1,17} = 30.01$, $P = < 0.0001$), glucose was 19.22% higher (two-way ANOVA: $F_{1,17} = 11.36$, $P = < 0.01$), and extracellular pH was 2.39% lower (two-way ANOVA: $F_{1,17} = 17.48$, $P = < 0.001$) in the 0.5 h recovery time compared to the 0 h recovery time. Intracellular pH did not differ between sexes or recovery times. The most parsimonious models to predict cortisol, lactate, glucose, extracellular pH, and intracellular pH 0.5 h post-angling were found by running linear regression models. Length and angling depth were significant predictors of cortisol values (Table 3.7).

Again, fish were observed to descend quickly to depth upon release with high ODBA scores before reaching a desired depth and remaining there with a low ODBA score all the way up to 14 min. The time it took to reach maximum depth was not impacted by fight time or air exposure (Table 3.4). Swimming activity (ODBA) was significantly influenced by sex as well as depth (Table 3.5, Figure 3.6), with males exhibiting higher activity (Figure 3.7).

Table 3.1 Summary of binary multiple logistic regression models assessing the effects of recovery time, fish total length, fight time, air exposure time, and water depth on whether lake trout (*Salvelinus namaycush*) showed impairment for any of five reflex or barotrauma metrics assessed after angling in the summer and fall. Statistical significance was determined at Bonferroni corrected α = 0.008 for summer and α = 0.007 for fall. Significance is bolded with P-values rounded to the nearest hundredth.

Season	Assessment	Variable	Estimate	S.E.	z value	df	*P*
Summer	Reflex	Recovery Time 0 h	-0.23	0.83	-0.28	71	0.78
		Recovery Time 0.5 h	0.09	0.86	0.10	71	0.92
		Fish Total Length	0.01	0.01	1.55	71	0.12
		Fight Time	0.01	0.01	0.74	71	0.46
		Air Exposure	0.00	0.01	0.72	71	0.47
		Angling Depth	-0.00	0.05	-0.04	71	0.97
Summer	Barotrauma	Recovery Time 0 h	2.85	1.21	2.35	71	0.02
		Recovery Time 0.5 h	0.50	1.04	0.48	71	0.63
		Fish Total Length	**0.04**	**0.01**	**3.04**	**71**	**0.00**
		Fight Time	**-0.06**	**0.02**	**-3.05**	**71**	**0.00**
		Air Exposure	0.01	0.01	0.71	71	0.48
		Angling Depth	**0.12**	**0.07**	**2.66**	**71**	**0.01**
Fall	Barotrauma	Recovery Time 0 h	0.13	1.51	0.08	29	0.93
		Recovery Time 0.5 h	-0.82	1.72	-0.48	29	0.63
		Fish Total Length	-0.00	0.02	-0.04	29	0.97
		Fight Time	-0.05	0.08	-0.70	29	0.49
		Air Exposure	-0.04	0.04	-1.23	29	0.22
		Angling Depth	0.28	0.32	0.87	29	0.39
		Sex	2.11	1.84	1.15	29	0.25

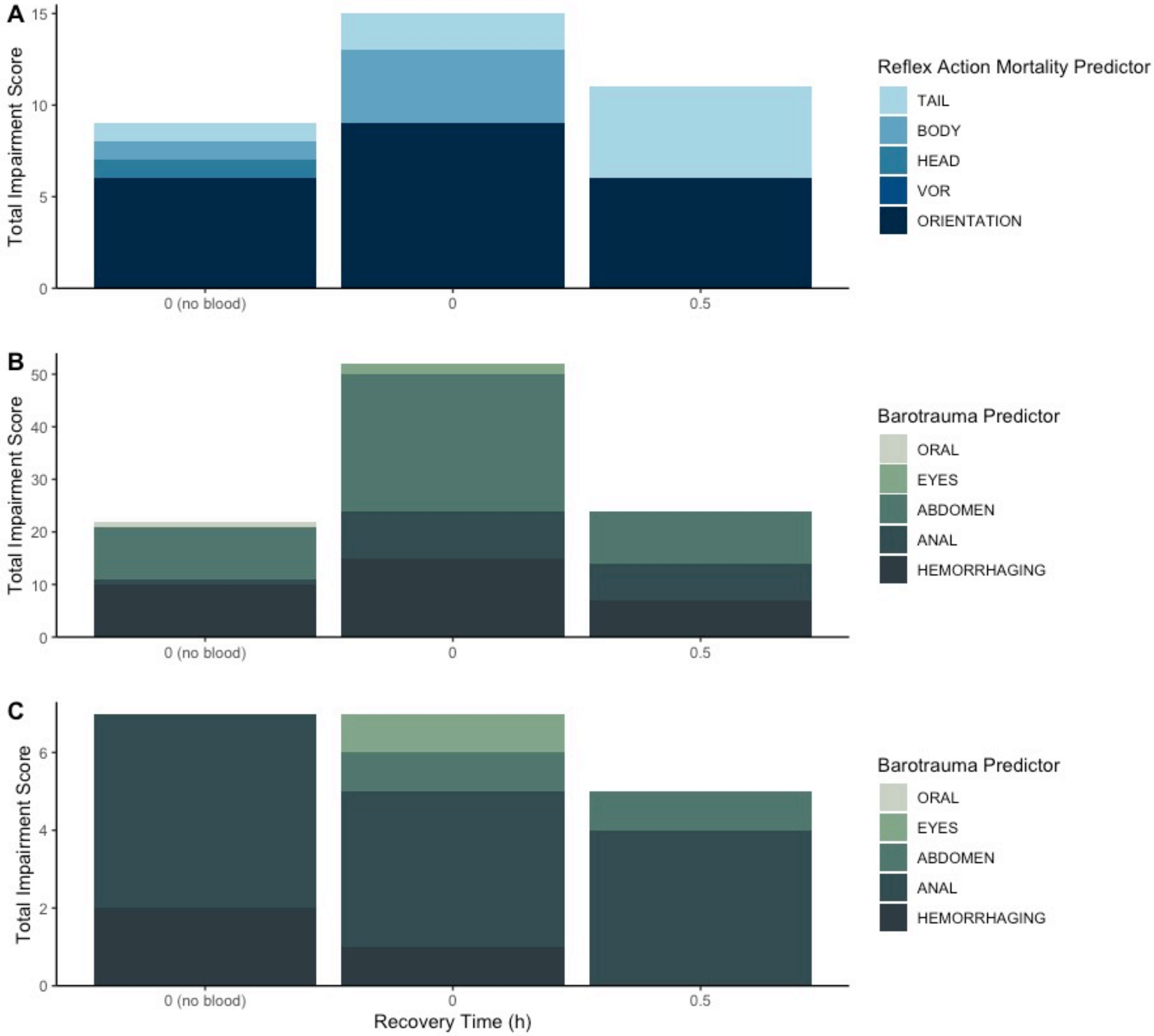

Figure 3.1 Totalled impairment scores for (A) summer reflex, (B) summer barotrauma, and (C) fall barotrauma predictors in lake trout (*Salvelinus namaycush*) sampled following angling. Reflex metrics include: (1) tail grab; (2) body flex; (3) head complex; (4) vestibular-ocular response; and (5) orientation. Barotrauma metrics include: (1) oral organ eversion; (2) exophthalmia; (3) bloating; (4) anal organ eversion; and (5) hemorrhaging.

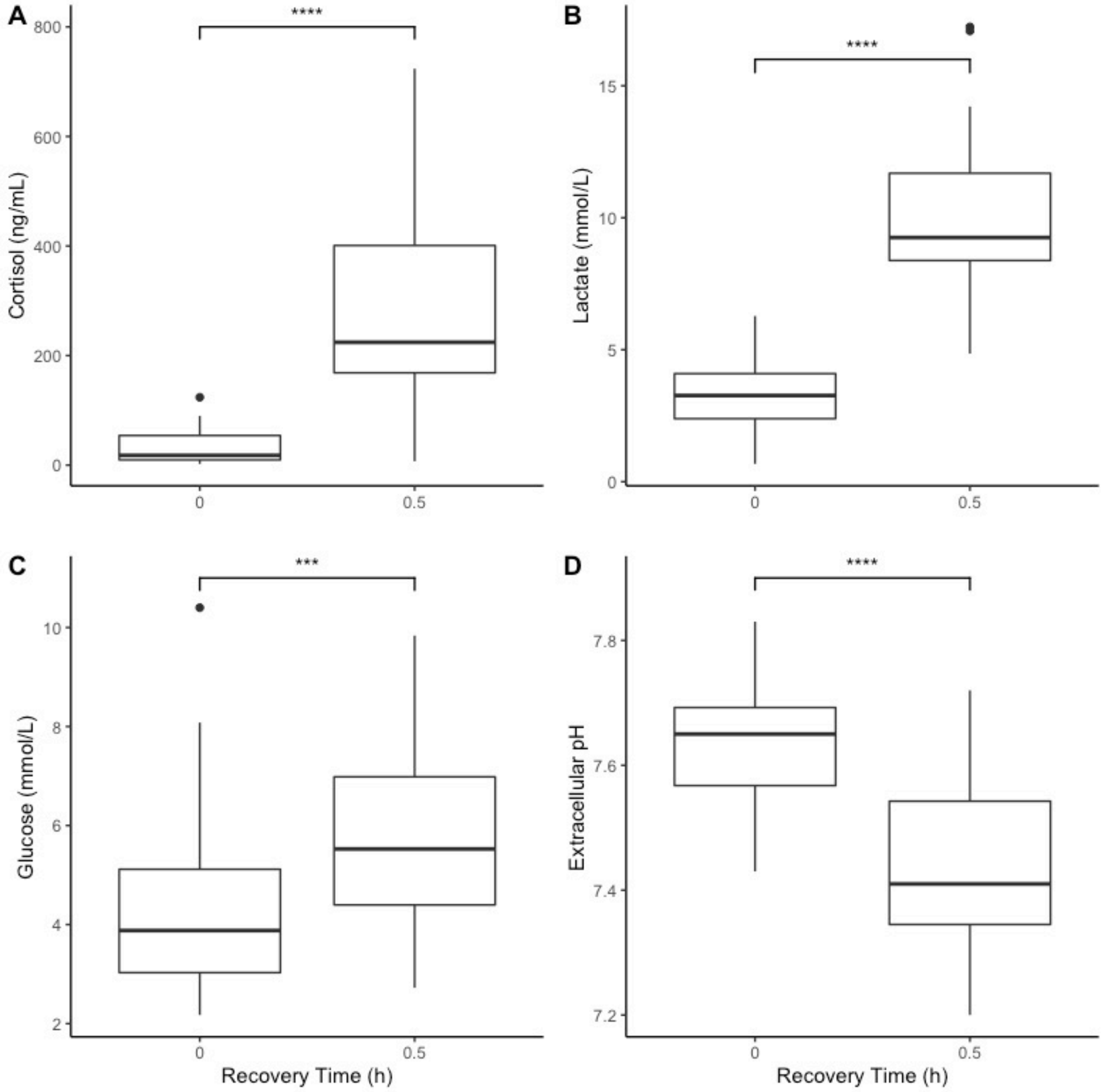

Figure 3.2 Concentrations of (A) plasma cortisol, (B) plasma lactate, (C) plasma glucose, and (D) extracellular pH in lake trout (*Salvelinus namaycush*) sampled at 0 (n = 32) or 0.5 h (n = 26) following summer angling. Thick black horizontal lines denote median values, boxes contain all data within the 25th and 75th quartiles, whiskers show the range of data, and outliers are depicted as black dots. Asterisks above horizontal brackets denote statistical significance at corrected $\alpha = 0.01$ ($P < 0.0001$ = ****, $P < 0.001$ = ***, $P < 0.01$ = **, $P < 0.05$ = *).

Table 3.2 Summary of binary logistic regression models assessing the effects of cortisol (ng/mL), lactate (mmol/L), glucose (mmol/L), extracellular pH, or intracellular pH of lake trout (*Salvelinus namaycush*) sampled at 0 or 0.5 h post-angling on whether a fish survived the angling event or not in the summer. Statistical significance was determined at a Bonferroni corrected α = 0.01 and is bolded with P-values rounded to the nearest hundredth.

Time	Blood Metric	Estimate	S.E.	*z* value	Df	*P*
0	Cortisol	0.05	0.03	1.46	31	0.14
	Lactate	-3.31	1.70	-1.95	31	0.05
	Glucose	-0.95	0.51	-1.87	31	0.06
	Extracellular pH	-13.97	8.30	-1.68	31	0.09
	Intracellular pH	-30.98	21.62	-1.43	31	0.15
0.5	Cortisol	-0.00	0.00	-1.14	25	0.26
	Lactate	-0.13	0.26	-0.49	25	0.62
	Glucose	0.09	0.40	0.23	25	0.82
	Extracellular pH	-19.80	12.21	-1.62	25	0.11
	Intracellular pH	23.03	16.96	1.36	25	0.17

Table 3.3 Summary of model selection results based on linear models predicting the cortisol, lactate, glucose, extracellular pH, and intracellular pH concentrations of lake trout (*Salvelinus namaycush*) sampled at 0.5 h post-angling in the summer. Statistical significance was determined at Bonferroni corrected α = 0.008 and is bolded with P-values rounded to the nearest hundredth.

Metric	Factor	Estimate	SE	df	*t*-value	*P*-value
Cortisol	(Intercept)	-610.32	771.67	19	-0.79	0.44
	Length	1.08	1.31	19	0.82	0.42
	Fight Time	-4.08	3.48	19	-1..17	0.26
	Air Exposure	-0.80	0.94	19	-0.85	0.41
	Angling Depth	22.80	8.91	19	2.56	0.02
	Reflex	-131.95	74.57	19	-1.77	0.09
	Barotrauma	10.78	55.78	19	0.19	0.85
Lactate	(Intercept)	22.95	11.46	19	2.00	0.06
	Length	-0.03	0.02	19	-1.75	0.10
	Fight Time	0.03	0.05	19	0.67	0.51
	Air Exposure	0.00	0.01	19	0.33	0.74
	Angling Depth	0.15	0.13	19	1.12	0.28
	Reflex	0.92	1.11	19	0.83	0.42
	Barotrauma	0.84	0.83	19	1.01	0.33
Glucose	(Intercept)	21.19	7.10	19	2.99	0.01
	Length	-0.03	0.01	19	-2.15	0.05
	Fight Time	0.07	0.03	19	2.11	0.05
	Air Exposure	-0.01	0.01	19	-1.02	0.32
	Angling Depth	-0.09	0.08	19	-1.09	0.29
	Reflex	-0.02	0.69	19	-0.03	0.98
	Barotrauma	0.23	0.51	19	0.44	0.66
Extracellular pH	**(Intercept)**	**6.78**	**0.49**	**19**	**13.89**	**0.00**
	Length	0.00	0.00	19	1.36	0.19
	Fight Time	-0.00	0.00	19	-0.81	0.43
	Air Exposure	0.00	0.00	19	0.66	0.52
	Angling Depth	0.00	0.01	19	0.76	0.46
	Reflex	-0.08	0.05	19	-1.74	0.10
	Barotrauma	-0.04	0.04	19	-1.24	0.23
Intracellular pH	**(Intercept)**	**6.86**	**0.20**	**19**	**34.35**	**0.00**
	Length	0.00	0.00	19	1.18	0.25
	Fight Time	-0.00	0.00	19	-0.20	0.84
	Air Exposure	-0.00	0.00	19	-0.30	0.77
	Angling Depth	-0.00	0.00	19	-0.03	0.98
	Reflex	-0.02	0.02	19	-0.81	0.43
	Barotrauma	-0.03	0.01	19	-2.22	0.04

Table 3.4 Summary of linear models assessing the effects of fight time and air exposure on the time it took lake trout (*Salvelinus namaycush*) to reach their maximum depth following angling. Statistical significance was determined at α = 0.05 and is bolded.

Season	**Variable**	**Variable**	**Estimate**	**S.E.**	***t* value**	**df**	***P***
Summer	Time to reach max depth	(Intercept)	10.47	206.3	5.08	37	<0.001
		Fight	**-10.13**	**4.67**	**-2.17**	**37**	**0.04**
		Air	**2.55**	**1.24**	**-2.05**	**37**	**0.05**
		Fight:Air	**0.05**	**0.02**	**2.33**	**37**	**0.03**
Fall	Time to reach max depth	(Intercept)	581.22	591.36	0.98	23	0.34
		Fight	-9.38	20.36	-0.46	23	0.65
		Air	-2.25	6.40	-0.35	23	0.73
		Fight:Air	0.14	0.23	0.62	23	0.54

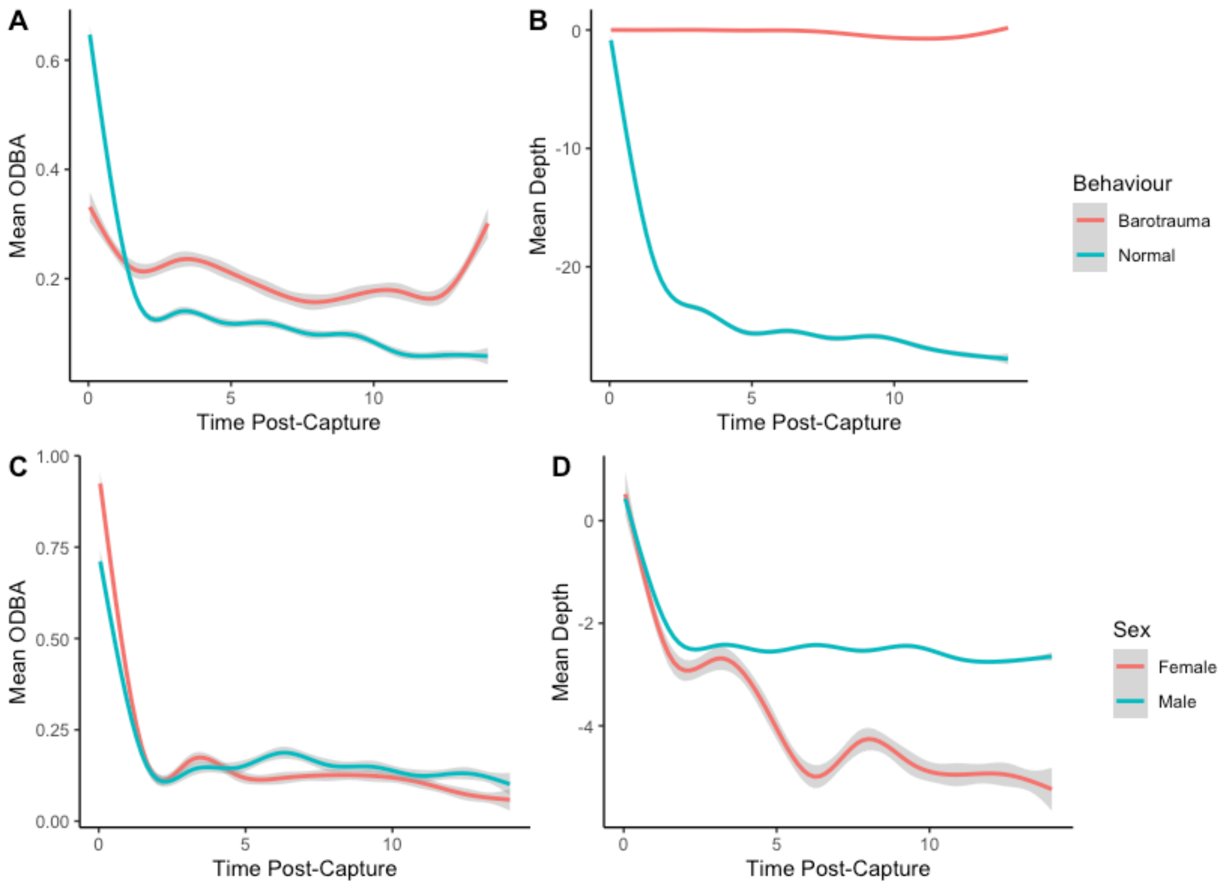

Figure 3.3 Mean (A) overall dynamic body acceleration (ODBA), and (B) depth use over time post-capture by lake trout (*Salvelinus namaycush*) exhibiting normal (n = 9) and impaired behaviour (n = 42) due to barotrauma injuries following summer angling. Also, mean (C) ODBA, and (D) depth use over time post-capture by male (n = 15) and female (n = 15) lake trout following angling during the spawning period.

Table 3.5 Summary of generalized additive mixed models (GAMMs) showing an interaction between overall dynamic body acceleration (ODBA) and capture depth in the summer, and sex and capture depth in the fall for lake trout (*Salvelinus namaycush*) captured via angling.

Season	Variable	Component	Term	Est	S.E.	*t*	*P*
Summer	ODBA	Param. Coefficients	(Int.)	0.90	0.00	186.3	<0.001
		Component	Term	edf	Ref. df	*F*	*P*
		Smooth Terms	**s(Depth)**	**7.83**	**7.83**	**2051**	**<0.001**
		Component	Term	Est	S.E.	*t*	*P*
Fall	ODBA	Param. Coefficients	(Int.)	0.89	0.00	179	<0.001
			SexMale	**-0.02**	**0.01**	**-2.97**	**0.003**
		Component	Term	edf	Ref. df	*F*	*P*
		Smooth Terms	**s(Depth)**	**8.43**	**8.43**	**1438**	**<0.001**

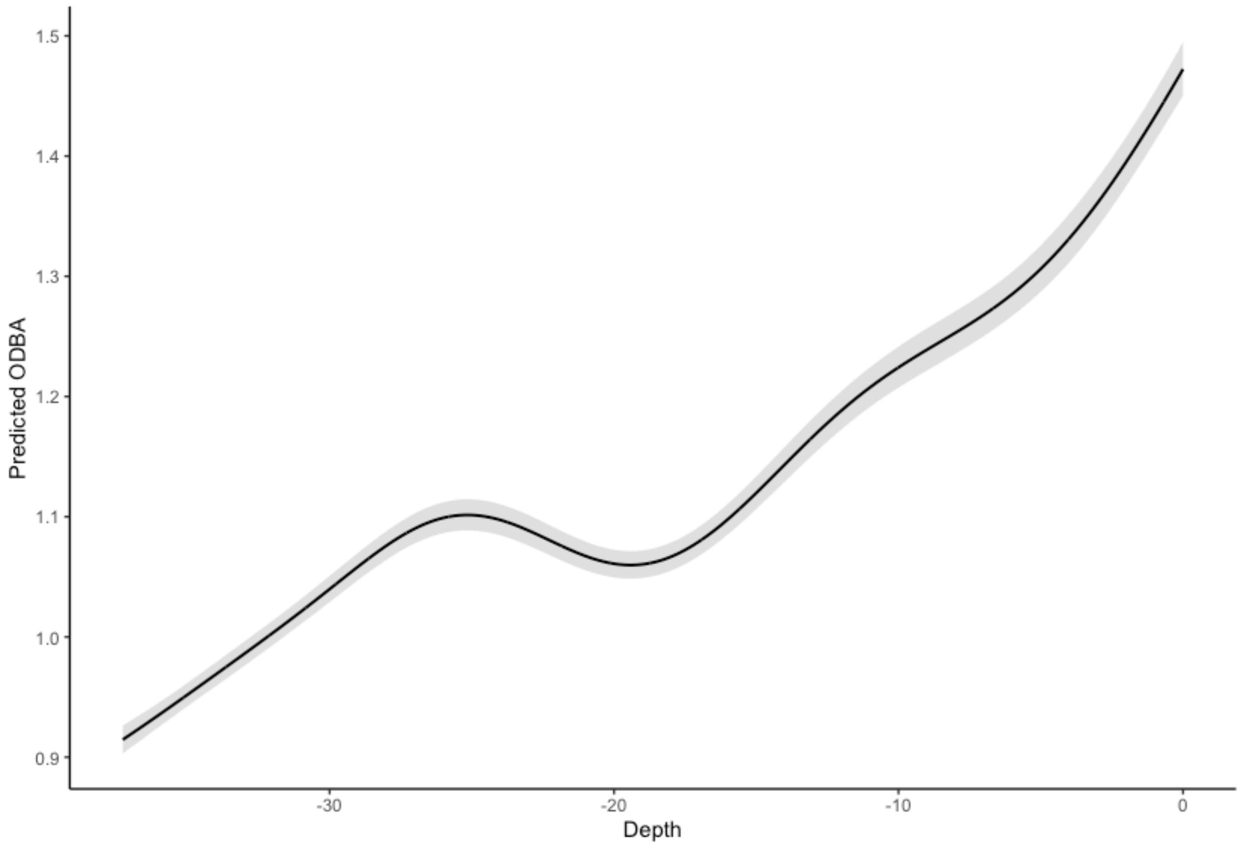

Figure 3.4 Predicted overall dynamic body acceleration (ODBA) values based on generalized additive mixed models (GAMMs) for lake trout (*Salvelinus namaycush*) (n = 51) angled during the summer.

Table 3.6 Summary of results from two-way ANOVAs on the effects of sex and recovery time (immediately after capture or 0.5 h) on cortisol, lactate, glucose, extracellular pH, and intracellular pH in lake trout (*Salvelinus namaycush*) following angling in the fall. Statistical significance was determined at $\alpha = 0.05$ and is bolded with all values rounded to the nearest hundredth. If an interaction was not significant it was removed, and the ANOVA was re-run.

Blood Metric	Variable	d.f.	SS	MS	*F* value	*P* value
Cortisol	**Sex**	**1,17**	**6.86**	**6.86**	**9.99**	**<0.01**
	Recovery Time	**1,17**	**14.12**	**14.12**	**20.55**	**<0.001**
Lactate	Sex	1,17	0.35	0.35	2.43	0.14
	Recovery Time	**1,17**	**4.36**	**4.36**	**30.01**	**<0.01**
Glucose	Sex	1,17	0.14	0.14	0.20	0.66
	Recovery Time	**1,17**	**7.64**	**7.64**	**11.36**	**<0.01**
Extracellular pH	Sex	1,17	0.00	0.00	0.09	0.77
	Recovery Time	**1,17**	**0.17**	**0.17**	**21.22**	**<0.001**
	Sex x Recovery Time	**1,17**	**0.04**	**0.04**	**4.64**	**<0.05**
Intracellular pH	Sex	1,17	0.00	0.00	1.93	0.18
	Recovery Time	1,17	0.00	0.00	1.14	0.30
	Sex x Recovery Time	**1,17**	**0.02**	**0.02**	**13.98**	**<0.01**

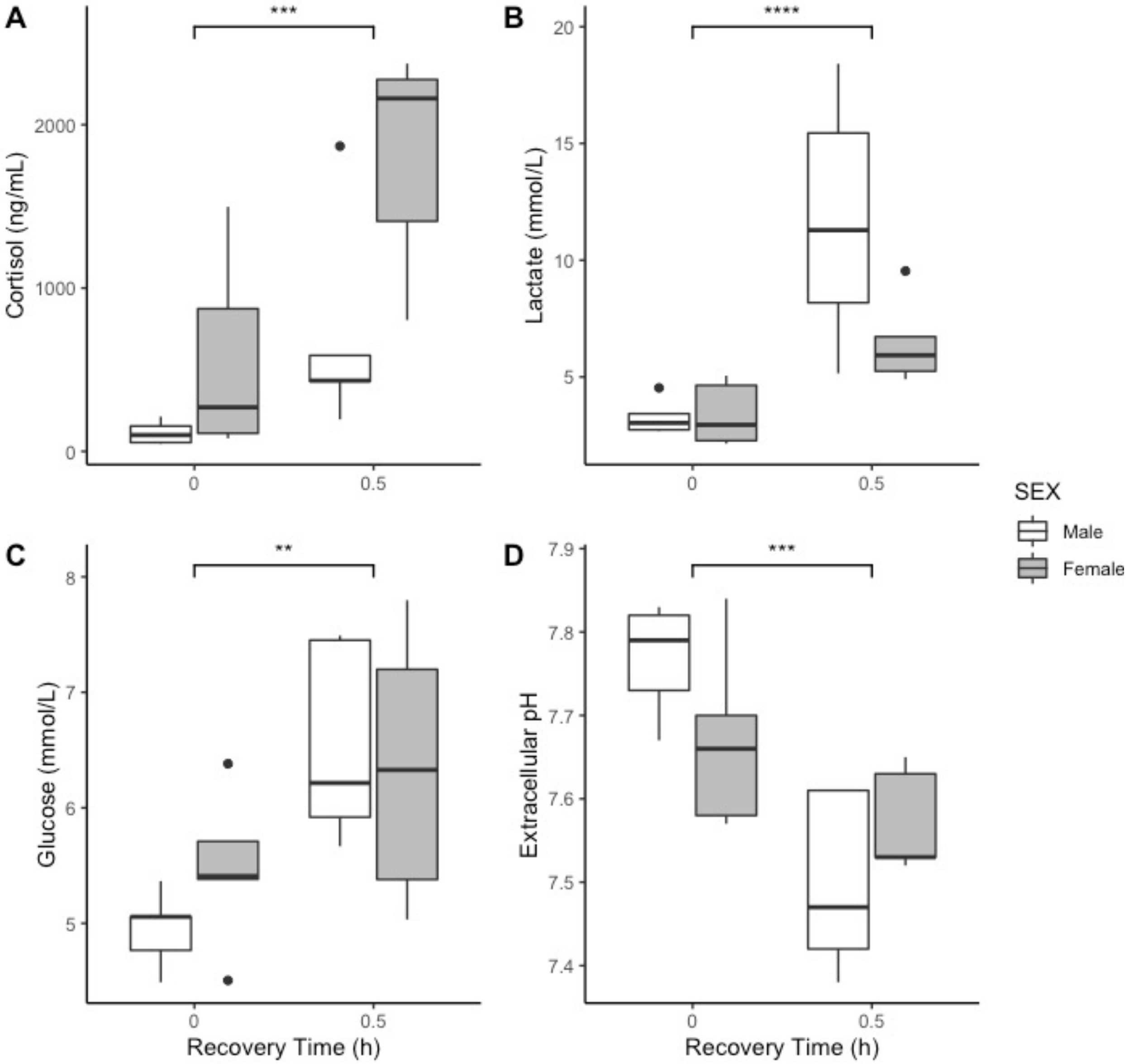

Figure 3.5 Concentrations of (A) plasma cortisol, (B) plasma lactate, (C) plasma glucose, and (D) extracellular pH in lake trout (*Salvelinus namaycush*) sampled at 0 (n males = 5, n females = 5) or 0.5 h (n males = 5, n females = 5) following fall angling. Thick black horizontal lines denote median values, boxes contain all data within the 25th and 75th quartiles, whiskers show the range of data, and outliers are depicted as black dots. Asterisks above horizontal brackets denote statistical significance at corrected $\alpha = 0.01$ ($P < 0.0001$ = ****, $P < 0.001$ = ***, $P < 0.01$ = **, $P < 0.05$ = *).

Table 3.7 Summary of model selection results based on linear models predicting the cortisol, lactate, glucose, extracellular pH, and intracellular pH concentrations of lake trout (*Salvelinus namaycush*) sampled at 0.5 h post-angling in the fall. Statistical significance was determined at Bonferroni corrected α = 0.01 and is bolded with P-values rounded to the nearest hundredth.

Metric	Factor	Estimate	SE	df	*t*-value	*P*-value
Cortisol	**(Intercept)**	**-6763.64**	**962.80**	**4**	**-7.03**	**0.00**
	Length	**15.48**	**1.75**	**4**	**8.84**	**0.00**
	Fight Time	10.27	8.68	4	1.18	0.30
	Air Exposure	-9.81	2.71	4	-3.62	0.02
	Angling Depth	**199.22**	**39.51**	**4**	**5.04**	**0.01**
	Barotrauma	-224.54	295.07	4	-0.76	0.49
Lactate	(Intercept)	34.69	12.85	4	2.7	0.05
	Length	-0.07	0.02	4	-2.95	0.04
	Fight Time	0.27	0.12	4	2.30	0.08
	Air Exposure	0.06	0.04	4	1.56	0.20
	Angling Depth	-0.85	0.53	4	-1.62	0.18
	Barotrauma	0.22	3.94	4	0.06	0.96
Glucose	(Intercept)	10.02	3.29	4	3.05	0.04
	Length	-0.01	0.01	4	-0.84	0.45
	Fight Time	0.03	0.03	4	0.93	0.41
	Air Exposure	-0.02	0.01	4	-2.33	0.08
	Angling Depth	0.27	0.13	4	2.02	0.11
	Barotrauma	-1.34	1.01	4	-1.33	0.25
Extracellular pH	**(Intercept)**	**7.22**	**0.36**	**4**	**20.28**	**0.00**
	Length	0.00	0.00	4	1.60	0.19
	Fight Time	-0.01	0.00	4	-1.58	0.19
	Air Exposure	-0.00	0.00	4	-1.23	0.29
	Angling Depth	0.01	0.00	4	0.76	0.49
	Barotrauma	0.04	0.11	4	0.32	0.76
Intracellular pH	**(Intercept)**	**6.88**	**0.12**	**4**	**58.47**	**0.00**
	Length	0.00	0.00	4	2.35	0.08
	Fight Time	0.00	0.00	4	2.07	0.11
	Air Exposure	-0.00	0.00	4	-3.97	0.02
	Angling Depth	0.00	0.00	4	0.32	0.77
	Barotrauma	-0.04	0.04	4	-1.08	0.34

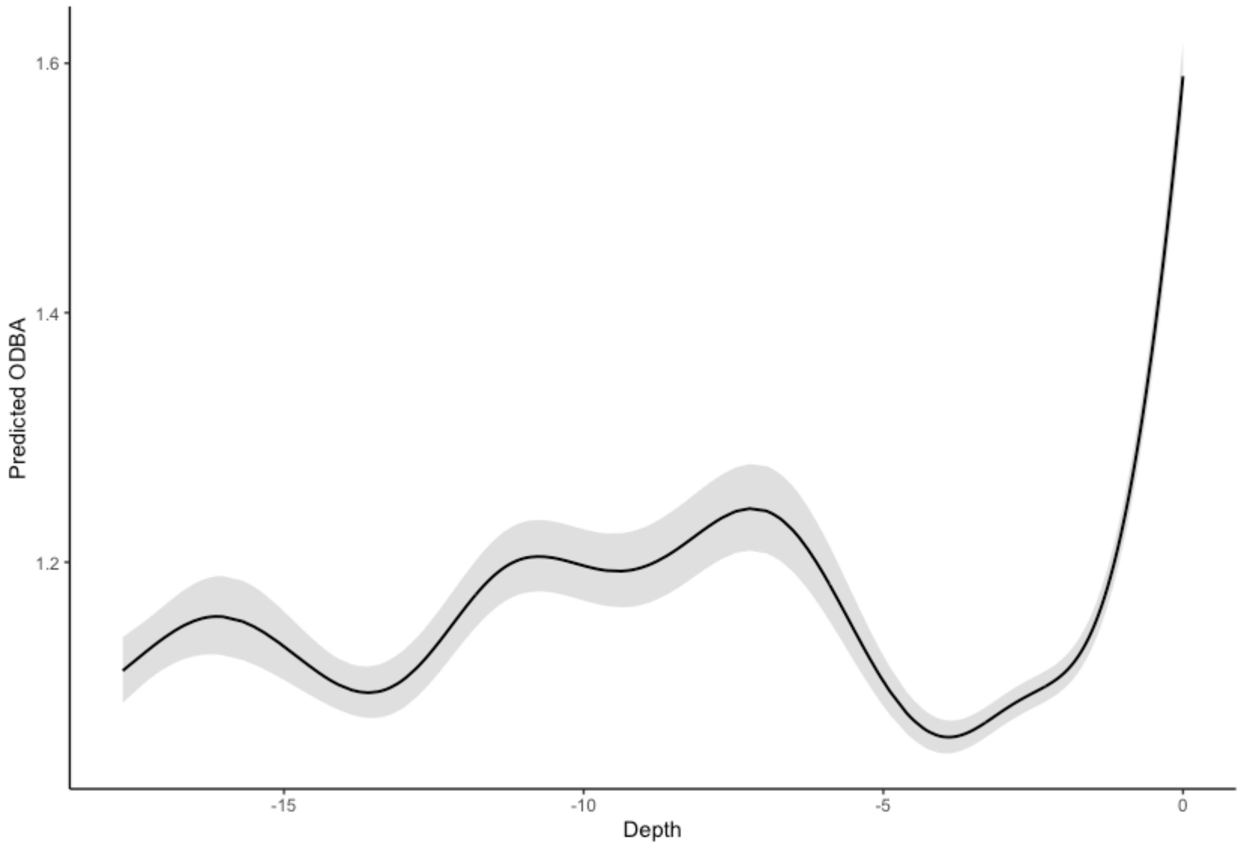

Figure 3.6 Predicted overall dynamic body acceleration (ODBA) values based on generalized additive mixed models (GAMMs) for lake trout (*Salvelinus namaycush*) (n = 30) angled during the fall.

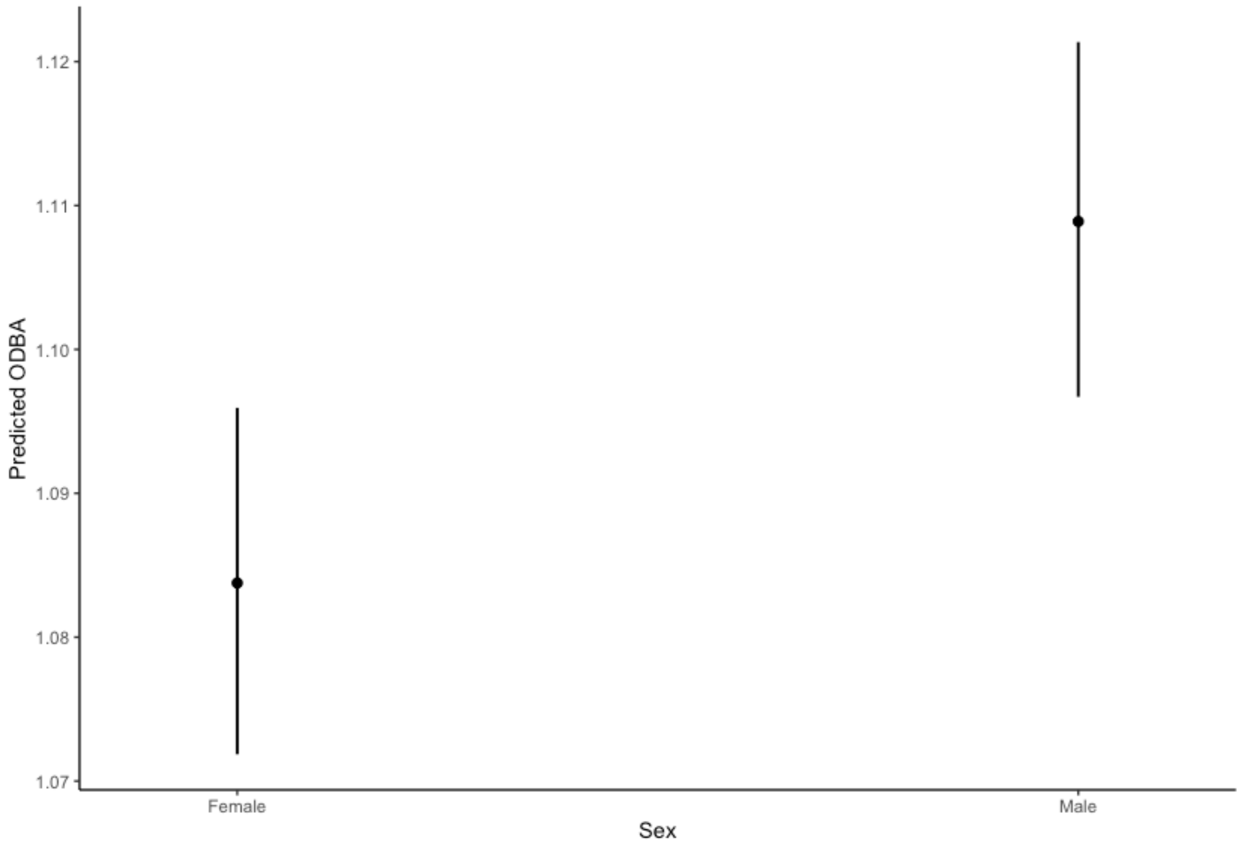

Figure 3.7 Predicted overall dynamic body acceleration (ODBA) values based on generalized additive mixed models (GAMMs) for male and female lake trout (*Salvelinus namaycush*) (n = 30) angled during the fall.

3.5 Discussion

3.5.1 Mortality

In the summer, nine mortalities occurred immediately after capture and five occurred within 0.5 h of holding (23.3% mortality). No relationships were found between blood metrics and mortality (Table 3), but high surface water temperatures may have been a contributing factor (mean = 18.6 °C). Water temperature is well understood to affect fish recovery (Cooke and Suski 2005; Arlinghaus et al 2007; Twardek et al. 2018a; Norin and Metcalfe 2019; Van Leeuwen et al. 2020) through pronounced effects on metabolism and growth (Clarke and Johnson 1999; Little et al. 2020). Atlantic salmon (*Salmo salar*) show increases in mortality following angling when water temperatures exceed 18 °C (Havn et al. 2015), and other studies provide evidence of the negative impact of temperature on post-release survival of salmonids (Meka and McCormick 2005; Gale et al. 2013; Sitar et al. 2017). Mortality rates in my study were higher than those previously reported for lake trout involved in C&R (6.98% in Falk et al. 1974; 14.9% in Loftus et al. 1988); however, these previous studies do not monitor fish for extended durations or account for delayed mortality. Regardless, mortality rates for salmonids are typically < 10% (Wydoski 1977; Muoneke and Childress 1994; Schisler and Bergersen 1996) and occur within the first 48 h post-release (Boyd et al. 2010). In the present study, fish were held at low densities in a large, covered stock tank and water was frequently exchanged. Thus, holding conditions were not expected to greatly influence stress responses or behaviour (Portz et al. 2006; Chhor et al. 2022b). Therefore, either surface water temperature inhibited sufficient metabolic recovery or the angling itself induced a larger effect than what has been seen in other studies. In the fall, no mortality was observed, and mean water temperature was 12.9 °C. Despite these findings, sub-lethal effects on reproductive success may still have occurred. In some cases, post-release mortality is higher for females (Crossin et al. 2008); however, research into the mechanisms that increase female sensitivity during reproduction should continue. Reflex impairment and barotrauma are likely not factors that would contribute to female mortality in the fall, due to the shallowness of spawning reefs, accelerated metabolic processes, and water temperatures during this time of year. In my thesis, the highest mortality was observed in lake trout that were ice-angled from depth (mean = 16.40 m) when air temperatures were well below 0 °C (see Chapter 2)

3.5.2 Behaviour

During the summer, lake trout experienced impairment of both reflexes and barotrauma. Reflex scoring has been used effectively to characterize impairment in closely related species such as brook trout (*Salvelinus fontinalis*) following angling (Kerr et al. 2017; Brownscombe et al. 2022). Most studies exploring angling-induced barotrauma focus assessments on freshwater physoclists or deep-dwelling marine species (Morrissey et al. 2005; McLennan et al. 2014; Eberts et al. 2018; Wegner et al. 2021). Evidently, only recent findings suggest that lake trout can experience pressure-related impairment following capture (Ng et al. 2015; Howell et al. 2023). In the present study, loss of orientation was the most observed RAMP impairment with 31.9% of fish displaying it immediately after capture. Similarly, bloating of the abdomen was the most observed barotrauma impairment with 76.6% of fish displaying it immediately after capture (Figure 3.2). One fish displayed oral organ eversion immediately after capture, which has been shown to be the most observed barotrauma-related injury in other fish (Schreer et al. 2009). Reflex impairment and extent of barotrauma were significantly correlated. Loss of orientation and bloating of the abdomen are similar in that they may impede fish from returning to depth and may prolong exposure to air and surface water temperatures as well as increase the likelihood of avian predation (Jarvis and Lowe 2008; Raby et al. 2014; Ferter et al. 2015).

Fish total length, fight time, and angling depth all influenced barotrauma scores (Table 1). Angling depth is well understood to impact barotrauma expression as water pressure is greater in deeper areas of a waterbody, resulting in more severe changes in external pressure upon capture (Butcher et al. 2012; Hannah et al. 2012; Kerwath et al. 2013). Fish were angled from a maximum depth of 42.4 m and lake trout are known to exhibit phenotypic diversity with depth preferences (Zimmerman et al. 2006; Stafford et al. 2013). Larger fish may inhabit deeper sections of lakes and thus, when angled, are more susceptible to changes in pressure (Sitar et al. 2008). In addition, characteristics of large fish responses to capture such as increased fight times may combine with pressure changes and influence impairment (Thorstad et al. 2003; Reeves and Staples 2011; Twardek et al. 2018a). Conversely, research on fishes in the St. Lawrence River found no effect of fish length or fight time on barotrauma impairment (Schreer et al. 2009). However, these species inhabit shallower waters and are physoclistous, suggesting that their angling conditions and response to barotrauma may be different from that of physostomous species like lake trout.

Fish angled during the fall displayed no reflex impairment. There is limited knowledge on how angling impacts fish that have completed or are actively spawning. Sea-run brown trout (*Salmo trutta*) angled after a recent spawn displayed no reflex impairment immediately after capture in 48% of fish (Blyth and Bower 2022). In another study, reflex impairment increased predictably with air exposure during angling treatments on Pacific salmon caught after their arrival to spawning locations (Raby et al. 2013). In the present study, prolapse of the anus was the most observed barotrauma impairment with 45% of fish displaying it immediately after capture. However, due to (1) the comparatively shallow capture depths (mean = 3.37), (2) the observation that impairment was almost entirely displayed by females, and (3) the observation that most barotrauma impairment observed was anal prolapse, I have interpreted the metrics captured in the barotrauma assessment as spawning-related symptoms rather than pressure-related impairment. Physiological adaptations during spawning is commonly observed in salmonids (Flemming 1996; Bombardier et al. 2010). While angling was not observed to directly impact reflexes, other research suggests that the effects of angling can play a role in the reproductive process. Angling pre-spawn for Atlantic salmon showed an increase in sperm motility while females produced fewer eggs (Papatheodoulou et al. 2022). Egg viability in lake trout is determined by both maternal and environmental components (Johnston 2018). While parental exposure to C&R does not inhibit the growth of offspring (Duncan et al. 2023), the results of handling and air exposure continue to be a primary concern for adult survival (Smukall et al. 2019).

3.5.3 Physiology

Lake trout in my study displayed angling-associated impairment regardless of season, with changes observed in plasma cortisol, lactate, glucose, extracellular pH, and intracellular pH. In the summer, cortisol, lactate, and glucose remained elevated 0.5 h post-angling. Plasma cortisol values in my study are similar to those of Arctic charr (*Salvelinus alpinus*) which peaked at 2 h following a confinement stressor (Pottinger 2010). Lactate values were higher and glucose values were similar to those of the same arctic charr 0.5 post-stressor. Ultimately, the time scale of my study prevents quantification of the entire breadth of time required for physiological recovery. Thus, we do not report our blood metrics as peak values for lake trout. Fish must clear metabolites from the blood prior to regaining normal swimming performance (Milligan 1996). The recovery of plasma and metabolites is largely context-specific, with some studies showing return to baseline values ~ 6 h (Arlinghaus et al. 2009) or 9 h (Rapp et al. 2012) post-capture. Recovery may differ based on life history (Pankhurst and Dedualj 1994; Arkert et al. 2020; McLean et al. 2020; Pringle et al. 2020) and scale proportionately with the magnitude of the stressor (Schreer et al. 2001). The process of angling may result in metabolic and osmoregulatory disturbance that impair health and lead to mortality (Wedemeyer and Wydoski 2008). In the present study, blood metrics were not predictors of mortality. No variables were significant predictors of any blood metrics.

In the fall, plasma cortisol, lactate, and glucose remained elevated 0.5 h post-angling. Cortisol was 65.5% higher in females, suggesting that their baseline levels differ from males. In Pacific salmon, females are distinct from males in that they are less capable of responding to environmental stressors (Sandblom et al. 2009; Clark et al. 2011) and generally display higher levels of cortisol (Pottinger et al. 1996; Donaldson et al. 2010). Due to high maternal investment into gonadal development (Jastrebski and Morbey 2009; Johnston 2018), lake trout females are likely more susceptible to angling-related stressors than males. Female fish also display elevated levels of lactate and glucose (Jeffries et al. 2012). Increased lactate levels are generally associated with fight time (Meka and McCormick 2005; Twardek et al. 2018a; Blyth and Bower 2022), which is to be expected due to lactate being a by-product anaerobic exercise (Milligan and Wood 1986). Surprisingly lactate was not significantly higher in females in the present study. Females are particularly important to reproduction because they govern spawning success (Esteve et al. 2008). Previous research has found that C&R does not inherently prevent fish from surviving to spawn, specifically in Atlantic salmon (Keefe et al. 2022). However, Peregrin et al.

(2015) describe how angling fish during spawning can negatively affect subsequent gonadal development. Fish length and angling depth were significant predictors of cortisol values (Table 3.7). As mentioned previously, larger fish inhabit deeper waters and thus, when angled, tend to display longer fight times (Reeves and Staples 2011). Extended physical activity as a result of line fighting therefore increase the general stress response which includes the primary stress hormone cortisol.

3.5.4 Activity

In both seasons, fish descended quickly upon release and maintain similar depth once a desired depth was reached. This activity has been seen in other species such as Pacific cod (Nichol and Chilton 2006). While my study used accelerometers to observe fish behaviour for the first 14 minutes following release, other studies have used telemetry to monitor barotrauma relief over longer periods of time (Nguyen et al. 2009; Butcher et al. 2013; Curtis et al. 2015; Wegner et al. 2021). During spawning, C&R has a negligible effect on the movement of Atlantic salmon (Thorstad et al. 2007; Lennox et al. 2015) and rainbow trout (*Oncorhynchus mykiss*) (Nelson et al. 2005). The use of non-invasive tagging methods continues to be of interest to fisheries research (Chapple et al. 2015; Fontes et al. 2018; Chhor et al. 2022) but comes with caveats when drawing conclusions regarding activity and behaviour. External attachment can increase hydrodynamic drag and influence fish behaviour (reviewed by Donaldson et al. 2008), thus its implementation into management has been slow (Nguyen et al. 2021). In the present study, the time to reach maximum depth was impacted by fight time and air exposure in the summer but not in the fall. Extended activity during the beginning of an angling event may leave little energy reserved for post-release escape. While not statistically significant, fish with barotrauma appeared to exhibit higher ODBA scores on the surface of the water, likely indicating their continued activity as a result of attempting to return to depth. Maintaining normal swimming behaviors is critical to fish recovery and impairments that inhibit the return to depth or force fish to float at the surface can accelerate mortality (Gravel and Cooke 2008; Drumhiller et al. 2014). Swimming activity was influenced by angling depth in the summer and angling depth and sex in the fall (also seen by Hanson et al. 2008). Higher ODBA was likely associated with shallow depths due to fish displaying a burst of energy to escape once returned to the water. In addition, male fish have higher ODBA post-release likely due to having different spawning behaviours than females.

3.5.5 Management

My study builds upon knowledge surrounding the susceptibility of freshwater fish to recreational angling. Lake trout exhibited impaired reflexes, signs of barotrauma, physiological disturbance, and mortality in the summer. In the fall, reflex impairment and physiological disturbance occurred with sex playing a role in response. Fish movement was effectively measured in both seasons with depth influencing levels of activity. Water temperature is still a concern when angling during the summer and thus, best practices such as limited air exposure times should be promoted.

Spawning protection is mandated across Canada for multiple freshwater fishes but varies between provinces. The sensitivity of adult fish during spawning and the effects of broodstock collection methods on embryo viability continue to be of interest for fisheries management (Smukall et al. 2019; Howell et al. 2022; Duncan et al. 2023). Angling may coincide with the spawning period of multiple species and thus, understanding the impacts of such stressors are critical to protecting populations (Bade et al. 2019; Tufts et al. 2019). The Clearwater Lake population of lake trout provides eggs and milt for stocking lakes across Manitoba and other parts of Canada (K. Dyck, personal communication, April 19,2023). Ensuring the population remains healthy and does not experience negative effects associated with the recreational fishery is a current management aim. The results presented here represent population impacts of angling and while no major impacts were seen on fish during the reproductive stage, other factors associated with angling during the spawn such as angler wading could still have negative consequences (Roberts and White 1992). Thus, further research should explore prolonged effects of angling on reproductive success.

Chapter 4. General Discussion

4.1 Synthesis

My overarching hypothesis for this thesis was that responses to C&R would change according to season and be observable through behaviour, physiology, and activity. Chapters 2 and 3 explore responses to C&R during various seasons and time scales. I decided to group the experiments into two chapters according to time of year due to the expectation that physiological processes (i.e., metabolism) would be slowed during the winter (Davis et al. 1984; Barton and Schreck 1987; Guderly 2004; Louison et al. 2017b). In my extended recovery experiment in Chapter 2 I monitored fish up to 6 h, as delayed onset of stress has been seen in other ice-angling studies (Louison et al. 2017a; Louison et al. 2017b). The immediate recovery impairment only occurred up to 420 s since my aim was to measure the amount of barotrauma immediately experienced by fish which may in part, explain the high levels of mortality observed during the extended recovery experiment (36.8%). In Chapter 3, I only monitored fish up to 0.5 h since metabolism is faster during the open-water season, thus recovery was expected to occur. In all experiments, I was unable to quantify the maximum values for blood metrics as they continued to increase throughout all time scales examined. This means that values may continue to increase past the amounts of time examined and the timing of recovery remains unknown.

C&R is understudied in the context of winter conditions. In Chapter 2, I examined mortality as well as behavioural and physiological impairment across immediate and extended recovery experiments following ice-angling. Previous research has explored impairment following ice angling in other species (Louison et al. 2017b; Logan et al. 2019); however, my research addresses some of the key components missing in many winter studies to date (Lawrence et al. 2023 reference). Prolonged monitoring of recovery is one research gap that has yet to be solved, and in my extended recovery experiment I monitored fish for up to 6 h.

Barotrauma is also relatively understudied (Lawrence et al. 2022; Louison et al. 2023), especially for physostomous species in winter conditions. In my immediate recovery experiment, I quantified the first barotrauma signs to be reported in lake trout during the winter. Lake trout displayed reflex impairment in both experiments. During extended recovery, fight time was a predictor of physiological disturbance 0.5 h post-angling with longer fight times leading to higher lactate and glucose, and lower extracellular pH. Longer fight times typically increase the duration of activity and thus, increase lactate production (Holder et al. 2022). Blood metric values were superficially higher than what has been observed in other studies (Wedemeyer and Wydoski 2008; Pottinger 2010). In summary, recreationally caught lake trout showed behavioural and physiological impairment with such impairments magnified by extended air exposure.

In Chapter 3, I examined mortality, reflexes, behaviour, blood metrics, and activity following angling in both summer and fall. Open-water angling has been well-studied, however contextual gaps still exist for certain species. Lake trout displayed lower mortality in the summer (23.3%) and no mortality during the fall. In the summer, fish length, fight time, and angling depth all influenced barotrauma score. The characteristics of large fish make them more susceptible to pressure-related injury such as inhabiting deep sections of lakes (Sitar et al. 2008) and the tendency to fight for extended periods (Thorstad et al. 2003; Reeves and Staples 2011; Twardek et al. 2018). Plasma cortisol, lactate, and glucose increased, and extracellular and intracellular pH decreased 0.5 h post-capture. Typically, blood metric values peak between 0.5 h and 2 h before recovery after exhaustive exercise or handling (Milligan and Wood 1986; Barton and Iwama 1991). The time to reach maximum depth was not impacted by fight time or air exposure while overall dynamic body acceleration (ODBA) was influenced by depth. In the fall, fish displayed no mortality or reflex impairment. Sex and recovery time influenced blood metrics, with length and depth being significant predictors of cortisol. Female salmonids are typically less robust to environmental stressors (Sandblom et al. 2009; Clark et al. 2011) and may display higher levels of cortisol (Pottinger et al. 1996; Donaldson et al. 2010). Large fish inhabit deep waters and thus, when angled, display longer fight times (Reeves and Staples 2011). The time required to reach maximum depth was not impacted by fight time or air exposure, ODBA was impacted by depth and males exhibited higher activity. The use of non-invasive biologgers was shown to characterise post-release activity of angled fish as seen in other studies (Lennox et al. 2018; Chhor et al. 2022).

4.2 Future Work

Universal knowledge gaps pertaining to recreational fisheries have been recently highlighted, with (1) the current state of recreational fisheries, (2) the impact of recreational fishing, and (3) the life history attributes of recreational fish species being selected as the highest priorities (Bower et al. 2020). Knowledge in the field of C&R is largely contextual, with ample research available for many popular sportfish species (Arlinghaus et al. 2007). Less information is available for species that are targeted by more specialized anglers and for fish that are especially old and large in their populations (Card and Hasler 2021). Contrasting behavioural and physiological responses between different sized individuals is valuable and can be used to evaluate challenges faced by different age classes. Environmental context is also important when assessing responses to C&R (Gingerich et al. 2007; Van Leeuwen et al. 2021), therefore understanding processes in multiple seasons is necessary. Ice fishing is one area that lacks a volume of information, with research needs in physiological responses to air exposure, the effects of barotrauma, post-release behaviour, and spatial ecology (Lawrence et al. 2022).

The research presented here addresses multiple pitfalls stated above which limit our understanding, however further C&R research should continue to bolster our understanding of these sections. Within the context of the present study, further exploration into winter angling, the effect of angling on offspring survivorship, and long-term monitoring of post-release activity would be useful. Incorporating multiple metrics of assessing impairment and examining context-specific aspects of recreational angling will continue to improve fisheries management and resource protection.

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