Life-history Characteristics of Recreational Lake Trout (*Salvelinus namaycush*) Fisheries in Manitoba

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Abstract

Contemporary data concerning lake trout (*Salvelinus namaycush*) populations have been lacking in the province of Manitoba for several decades. I compared life history characteristics (age, condition, growth, maturity, and survival) of lake trout from seven lakes in order to assess their present state. Furthermore, lake trout have been observed to have different ecotypes that exhibit different life-history traits and behaviours, therefore lake trout otolith morphology was compared to potentially identify suspected sympatric ecotypes in Clearwater Lake, Manitoba. Summer profundal index netting (SPIN) gillnets were set at varying depths during summer months in 2021 and 2022 to complete this project. Otolith morphology was compared using elliptic Fourier analyses. Length-at-age was back-calculated for lake trout individuals, and growth data was fitted by von Bertalanffy growth curves. Growth curves differed significantly across lakes based on several parameters (L_∞, K, t_0, and w). Northern lakes had the propensity to hold trophy-sized lake trout, while southern lakes did not. Significant otolith morphological differences between suspected lake trout ecotypes within Clearwater Lake. However, it is not possible to ascertain that otolith morphological differences are a result of different ecotypes or differing growth rates. There was a notable scarcity of lake trout in most southern lakes, while northern lake trout populations appear to be healthy. Historical high fishing pressure might be a culprit associated with the poor status of several southern lake trout populations. Fisheries Manitoba should consider using the SPIN program to further evaluate lake trout fisheries in Manitoba.

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List of Abbreviations

Abbreviation	**Full Name**
A_{50}	Age at 50% maturity
ACV	Average coefficient of variation
APE	Average percent error
B	Biomass density of a population
B_{MSY}	Biomass density of a population exploited at maximum sustainable yield
CW	Clearwater Lake
DL	Davidson Lake
GL	George Lake
HL	High Lake
K	Growth coefficient
L_{50}	Length at 50% maturity
L_{∞}	Asymptotic length
LDA	Linear discriminant analysis
M	Natural mortality rate
ML	Mantario Lake
nEFD	Normalized elliptic Fourier descriptor
PCA	Principal component analysis
SCL	Second Cranberry Lake
WHL	West Hawk Lake
Z	Instantaneous mortality rate

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Chapter 1: General Introduction

A fishery is defined as an assemblage of fish, regardless of whether it is being actively targeted or not for fishing purposes (Government of Canada, 1985). Canada's inland fisheries are supported by over two million lakes and rivers (DFO, 2012). The following literature review is aimed to give a brief overview of Canada's fisheries, but will focus in on the emergence of Canada's recreational fisheries sector, particularly in Manitoba.

Subsistence Fisheries

Before Europeans settled in Canada, fish were harvested by Indigenous peoples. Fish were a year-round staple in Indigenous peoples' diets (Heuring, 1993). Their subsistence practices, which consisted of a variety of techniques (e.g., gillnets, seine nets, dipnets, spears, and harpoons [Cleland, 1982]), aimed at catching fish for the consumption for their families, their community, and for trade (Berkes, 1988). Indigenous people have harvested a variety of fish across Canada including: Atlantic salmon (*Salmo salar*; Tiro, 2016), lake whitefish (*Coregonus clupeaformis*; Tough, 1984), lake sturgeon (*Acipenser fulvescens*; Cleland, 1982), and lake trout (*Salvelinus namaycush*; Whillans and Berkes, 1986). Larger fishing operations such as gillnetting, were a community-wide affair because they were labour-intensive. Men would set and retrieve nets, while women would repair nets and prepare fish for consumption (Cleland, 1982). They were able to sustainably harvest fish without damaging the ecosystem integrity (Castañeda et al., 2020; Menzies and Butler, 2007). For example, the Algonquin and Iroquois would only start fishing Atlantic salmon in Lake Ontario when tree leaves grew to a certain size (Tiro, 2016). Another example can be seen with the Gitxaala First Nation in British Columbia, who used fishing techniques that would allow the unharmed release of bycatch species, an issue later seen in modern day commercial fishing (Menzies and Butler, 2007).

Commercial Fisheries

Once European settlers arrived in Canada, and established themselves, Canada's aquatic ecosystems were consequently altered. Initial immigrants continued subsistence practices (e.g., Icelandic immigrants at Lake Winnipeg [Heuring, 1993]) until settlements expanded and the demand for food provisions, namely fish, grew considerably (Tough, 1984). Commercial fisheries, the act of fishing for profit, were established across Canada at the expense of Indigenous subsistence fisheries (Tough, 1984). Atlantic salmon, lake whitefish, and lake trout were some of the first major inland fisheries to develop in the early 19th century (Whillans and Berkes, 1986). These fisheries were part-time efforts, which mainly occurred in the autumn months using beach seines (Whillans and Berkes, 1986). Commercial fisheries spread west, with the development of commercial operations in the other Great Lakes between 1830–1850 (Whillans and Berkes, 1986), Lake Winnipeg in early 1870s (Heuring, 1993), and Great Slave Lake in 1945 (Kennedy, 1966).

The signing of land treaties and legislation was a crucial step for the expansion of commercial fisheries across Canada (Tough, 1984; Brenden et al., 2013). For example, The Fisheries Act (1868) was implemented to promote commercial fisheries, while directly managing and restricting Indigenous fishermen (McMillan and Prosper, 2016). Indigenous people were still allowed to fish in some ancestral waters, but they were often displaced and encroached on by commercial fishing operations who outcompeted them (Brenden et al., 2013; Castañeda et al., 2020). Some indigenous people joined commercial fishing efforts to have some control over their waters (Tough, 1984; Menzies and Butler, 2007), but tensions were high (Menzies and Butler, 2007).

Technological advancements helped not only grow commercial fisheries, but also the Canadian economy. Hooks, seines and weirs were used in early near-shore operations (Regier and Hartman, 1973). However, by the 1850s, cotton/linen gillnets and pound nets were used for fishing deeper depth sets in the Great Lakes region (Regier and Hartman, 1973). The adoption of nylon-mesh gillnets in the early 1950s further increased production across major Canadian fisheries due to its durability (Brenden et al., 2013). The conversion from sail boats to steam-powered, and gasoline-powered boats in the late 19th, and early 20th century allowed commercial fishermen to spend more time on the water and fish (Brenden et al., 2013). The construction of canals (e.g., the Erie Canal in 1825), and railroads, coupled with the invention of refrigeration, expanded commercial fishery markets (Regier and Hartman, 1973). Refrigeration was so important that it gave rise to the walleye fishery in Lake Winnipeg (Gislason et al., 1982).

As a result of technological advancements, urbanization, and increased harvest effort to meet regional as well as international demand, many fish stocks across Canada experienced boom and bust fates. Salmonids such as lake trout, and lake whitefish populations crashed as a result of overharvest (see Berst and Spangler, 1972; Christie, 1972; Heuring, 1993). Atlantic salmon were extirpated from Lake Ontario by the end of the 19th century as a result of overfishing, pollution, and invasive species (Dymond et al., 2019). Cisco (*Coregonus artedi*) was the most important fishery within Lake Erie between 1850 and 1925, until catches began to decline after 1925 (Kennedy, 1966). Once considered a nuisance species due to their tendency to break gillnets (Berst and Spangler, 1972), lake sturgeon were bycatch until the 1860s once fishermen learned how to smoke them and take caviar (Harkness and Dymond, 1961). By 1880, lake sturgeon was a major commercial fishery across Canada, and catch declines were observed by 1890 (Harkness and Dymond, 1961). Lake Winnipeg sturgeon experienced a 95% catch reduction between 1905 and 1910 (Manitoba Hydro, 2016). Blue pike (*Sander vitreus glaucus*) was another important commercial fishery in Lake Erie that experienced extensive harvest pressure in the early to mid-20th century, only to collapse in 1958 and never recover and lead to their extinction (Hartman, 1973). Today, commercial fisheries still exist in many lakes across Canada; however, its economic value is significantly less than recreational fishing, whereby the economic output of commercial fishing was estimated to $2.80 billion CAD (DFO, 2016), while recreational fishing generated $8.3 billion CAD in 2010 (Brownescombe et al., 2014).

Recreational Fisheries

Recreational fishing can be defined as fishing whose primary objective is for leisure, and the targeted species does not represent a significant proportion of a fisherman's caloric diet (Arlinghaus and Cooke, 2009). Traces of recreational angling in Canada can be found since at least the 16th century (Castañeda et al., 2020), and expanded when Europeans immigrated in the 1800s (Arlinghaus et al., 2007). 'Sportfishing', a competitive form of recreational fishing, had already been coined in the United Kingdom by the 1800s (Arlinghaus et al., 2007). The roots of 'catch and release angling', a strain of recreational angling whereby anglers will release the captured fish to promote the sustainability of fish populations, was developing at the same time during the 1800s (Arlinghaus et al., 2007). Unlike today, early adopters of recreational angling, could not tackle big lakes due to not having proper boats and equipment (Heuring, 1993). This led to anglers being constrained to tributaries and near-shore areas (Heuring, 1993). However, with the advent of gas-powered boats, GPS, and many other technological advancements, anglers have become more efficient (Brownscombe et al., 2014).

Nowadays, recreational angling is enjoyed by millions of Canadians. Total recreational angling expenditures from 1975 to 2010 contributes an average of $8.8 billion CAD per year to the Canadian economy (Brownescombe et al., 2014). Salmonids are the most caught and harvested groups of fishes by anglers, while walleye (*Sander vitreus*) was the most harvested fish in Canada between 1985 and 2010 (Brownescombe et al., 2014). Catch per unit effort (CPUE) (effort is registered as days fished) remained constant from 1990 to 2010 despite overall catch and harvests declines over the same timeframe (Brownescombe et al., 2014). This suggests that fishing opportunities have not declined; however, with technological advancements and angler proficiency, CPUE may not paint the whole picture (Post et al., 2002). The emergence of recreational fisheries has posed new problems to fisheries managers despite being a major economic force.

Recreational fisheries are complex socio-ecological systems (Brownscombe et al., 2019). They involve interactions between angler behaviour and aquatic ecosystems (Johnston et al., 2010). Angler behaviour can be quite diverse. Some anglers may be driven to select a lake that is known for an abundance of fish, while others are interested in 'trophy-sized' fish (Johnston et al., 2010). Conversely, anglers may be motivated to be immersed by nature as they find it relaxing (Fedler and Ditton, 1994). Because every angler is different, they view each waterbody differently. Harvest restrictions, and lakes deemed to be 'low-productivity' may not deter anglers if it becomes easier to target and locate fish with better technology (e.g., AquaVu® underwater cameras). If fish aggregate together in a low-productivity lake, and anglers are aware of these locations, trouble arises if fish harvest continues unchecked (Post, 2013). Many assumed that recreational fisheries were inherently different than commercial fisheries because they are self-regulating systems, but that may not be the case (Post et al., 2002).

Fisheries managers use a variety of strategies to sustainably manage recreational fisheries (Radomski et al., 2001). Seasonal closures, daily catch limits, minimum and/or maximum harvest lengths are used across Canada (Brownscombe et al., 2019; Cooke and Cowx, 2006). Seasonal closures are used during the critical parts of fish life cycles, typically spawning periods (Cooke and Cowx, 2006). Seasonal closures and openings are often tailored by species and geographical zones (ONGOV, 2021; QCGOV, 2021). Harvest size limits are intended to protect juvenile fish, and/or older mature individuals, especially old females who are vital to the spawning stock biomass (Gwinn et al., 2015). Gear limitation is a method aimed at reducing stress imposed upon fish during capture. An example of gear limitation can be seen in Manitoba where fisheries managers have banned the use of barbed hooks (MBGOV, 2021a). Creel and mail-in surveys are a common method to assess angler preferences, participation, effort and harvest rates (Brownscombe et al., 2019; Radomski et al., 2001). A combination of temporal and spatial data is accumulated which can inform managers of the state of individual fisheries, therefore impacting future management initiatives (Nieman et al., 2021).

In addition to angling-related harvest, recreational fisheries are threatened by several other factors. Sub-lethal stressors due to catch and release fishing is an emerging problem. Many factors including angler experience, gear types (i.e., hooks), hook location, hook removal, air exposure time, and duration of fight time can all influence physiological responses and mortality rates (Cooke et al., 2001). Climate change is a contemporary issue that currently plagues managers. Warming of waters is a major issue that threatens fish populations by reducing dissolved oxygen in water, and can negatively impact the survival rate of fish larva (Siefert and Spoor, 1974). Moreover, climate change has been estimated to alter the stratification phenology by accelerating the onset of lake stratification, while also delaying the break-up of lake stratification (Woolway et al., 2021). The accelerating rate of lake stratification can stunt the growth of cold-water adapted fish that benefit from long cold spring feeding regimes (King et al., 1999; Guzzo et al., 2017). Increased human connectivity and expanding trade routes have increased the opportunity of non-native species introductions (Reid et al., 2019). Non-native species have the capability to compete with (e.g., round goby (*Neogobius melanostomus*) [Reid et al., 2022]), predate (e.g., alewife (*Alosa pseudoharengus* [Madenjian et al., 2008]) and parasitize on native fauna (e.g., sea lamprey (*Petromyzon marinus*) [Regier and Hartman, 1973]), all of these interactions can alter ecosystem processes (e.g., dreissenid mussels [Karatayev et al., 2002]). While pathways of invasion can vary, recreational water activities have been implicated in several cases. Live baitfish is popular fishing method in eastern Canada and approximately 30% of anglers will release their live bait at the end of a fishing excursion (Drake and Mandrak, 2014). Furthermore, pleasure boat activity is the main source of overland transfer of non-native speciessuch as zebra mussels and Eurasian water-milfoil (*Myriophyllum spicatum*) (Johnson and Padilla, 1996). This can lead to competition of resources and habitat use between non-native and native juvenile fish.

Habitat degradation is another major threat to freshwater systems (Dudgeon et al., 2006). This can take form in many ways, namely deforestation which increases turbidity and sediment in waters (Dudgeon et al., 2006). This can ruin littoral habitats and reduce the viability of nearby spawning grounds (Dudgeon et al., 2006). Harmful algal blooms are another form of habitat degradation, which can reduce dissolved oxygen and lead to massive fish asphyxiation-related die-offs (Reid et al., 2019). Altered flow regime has been a long-standing issue in freshwater environments (Reid et al., 2019). Historically, dams have reduced river connectivity, isolated populations of fish, disturbed fish migration runs (Renöfält et al., 2010), and ultimately have contributed to the extirpation of fish populations (e.g. Atlantic salmon in Lake Ontario) (Dymond et al., 2021). Furthermore, altered natural flooding regimes from dams negatively impact fish communities by reducing viable spawning habitat (Junk et al., 1989), food availability (Benke, 2001), and nursery areas (Turner et al., 1994). All the aforementioned stressors are only some of the challenges that fisheries managers are required to deal with when managing recreational fisheries.

Overview of Data Chapters

While Canada boasts a huge number of inland fisheries, they pose a major challenge for fisheries managers countrywide. Manitoba is not exempt from this issue. About 12% (69100 km^2) of Manitoba's surface area is water (Butler, 1950). Despite this, Fisheries Manitoba is not equipped to monitor the health of every single waterbody, nor should they. While it is an impossible feat, some recreational fisheries are more valuable, therefore they take precedence over other fisheries, despite all lakes having intrinsic value. One type of fishery that has been largely ignored by the province are lake trout fisheries. Lake trout is the largest member of the *Salvelinus* genus (Redick, 1967), and can reach trophy-size length, otherwise known as 'Master Angler size' in Manitoba. Consequently, anglers are interested in catching these large fish, and outfitters have been able to sustain seasonal tourism businesses around the province for many decades (Butler, 1950).

Management of Manitoban lake trout recreational fisheries is essential to ensuring their sustainability and the subsequent economic revenue generated. Lake trout fisheries have been understudied for roughly three decades, therefore there is a lack of contemporary knowledge about the current state of these fisheries (Kroeker, personal communication, 2021). Thousands of anglers interact with these fisheries; thus, it is a necessary and lucrative undertaking for Fisheries Manitoba to better understand them. This thesis aims to unveil life history variation across seven different lake trout fisheries in Manitoba. Specifically, the second chapter of this thesis aims to compare life-history characteristics of lake trout fisheries from these lakes across a latitudinal gradient. Furthermore, the third chapter attempts to use otolith morphology to discriminate between different lake trout fisheries that have been historically stocked, while also seeking to identify intra-specific diversity.

Chapter 2: Life-history Characteristics of Recreational Lake Trout Fisheries in Manitoba

Abstract

Contemporary data concerning lake trout (*Salvelinus namaycush*) populations have been lacking in the province of Manitoba for several decades. I compared life history characteristics (age, condition, growth, maturity, and survival) of lake trout from seven lakes across a latitudinal gradient with differing degrees of fishing pressure. Summer profundal index netting (SPIN) gillnets were set at varying depths during summer months in 2021 and 2022. Populations were also assessed under the sustainability model proposed by Lester et al., 2021). Length-at-age was back-calculated for lake trout individuals, and growth data was fitted by von Bertalanffy growth curves. Growth curves differed significantly across lakes based on several parameters (L_∞, K, t_0, and w). Northern lakes had the propensity to hold trophy-sized lake trout, while southern lakes did not. Relative weight analysis indicated that all populations were below the 75th percentile of mean weight for the species. There was a notable scarcity of lake trout in most southern lakes. This was reflected by the Lester et al. (2021) sustainability model, which may be a relict of historical high fishing pressure

Introduction

Following devastating commercial fishery collapses, namely the Atlantic cod (*Gadus morhua*) collapse in eastern Canada in 1992, many researchers and fisheries managers began to scrutinize the impacts of recreational fishing had on waterbodies. In the early 2000s, Post et al. (2002) made a claim that Canada's recreational fisheries were experiencing similar collapses as commercial fisheries and called it an 'invisible collapse'. Due to the sheer quantity of lakes, a single collapse of a small lake would only impact local communities and not receive much attention, and therefore be invisible to many people (Post et al., 2002). Coupled with low funding, stocking, and spatial-temporal variability, the ability of fisheries managers to obtain an accurate snapshot of any particular fish stock are impaired (Post et al., 2002). A follow-up study using landscape-scale monitoring program from Alberta between 2000–2018 corroborated the central claim made by Post et al. (2002) that inland fisheries are in fact sensitive to overexploitation, and that angling regulations are fundamental to protecting fish populations (Cahill et al., 2022). A central idea that has revolved around these and subsequent papers is that there are wide knowledge gaps related to the impacts of recreational fishing on freshwater fish populations (see also Sullivan, 2003; Cooke and Cowx, 2004; Bartholomew and Bohnsack, 2005; Cooke and Cowx, 2006).

Recreational fishing can pose several unwanted ecological and evolutionary risks upon recipient fish populations. High harvest rates can lead to a decline in population size (Lewin et al., 2006). Size selectivity for larger fish is a common trait amongst anglers, therefore in fish stocks that are subjected to this angler behaviour often experience a shift from large and older age classes of fish to a smaller and younger fish (Lewin et al., 2006). This is a major concern due to the removal of the most fecund individuals (Gwinn et al., 2008), which can lower the reproductive potential of a population as well as reduce population resilience to exogenous stressors (Heyer et al., 2001). This pattern has been reported with the Eurasian trout (*Hucho taimen)* in northern Mongolia, whereby trout abundance, biomass, and weight have declined in response to recreational angling (Jensen et al., 2009). Fisheries-induced evolution has also been documented with older and larger wild zebrafish (*Danio rerio*) in an experimental study (Uusi-Heikkila et al., 2015). The group of individuals subjected to minimum harvest length simulations evolved significantly lower asymptotic lengths, matured at an earlier age, and had a reduced spawning frequency within five generations (Uusi-Heikkila et al., 2015). Fish behaviour can also be impacted. A lake with both anadromous and resident brook trout (*Salvelinus fontinalis*) populations in Quebec was studied in response to higher fishing pressure (Thériault et al., 2008). Their model predicted that brook trout facing higher levels of fishing pressure would decrease the probability of migration, while also increasing the age at which migration occurs (Thériault et al., 2008). Consequently, the reduction of migratory behaviour to access open niche space by the sea-run brook trout can reduce the growth rate, size and reproductive success (Thériault et al., 2008). The sum of evidence across all of these studies all inherently reduce a fisheries' economic value by potentially dissuading future anglers to travel to these compromised systems.

A recreationally important fish species in Canada is Lake trout (*Salvelinus namaycush*). Lake trout are a cold-water salmonid and are almost exclusively found in deep well-oxygenated oligotrophic lakes throughout Canada (Scott and Crossman, 1973; Martin and Olver, 1980; Muir et al., 2021). Lake trout are a late-maturing and slow-growing species that can live past 60 years and exceed lengths of 1 m (Campana et al., 2008; Gallagher et al., 2021). Lake trout express high phenotypic, morphological, and life history diversity and can inhabit several environmental and ecological niches, therefore facilitating multiple ecotypes within a lake (Chavarie et al., 2021). During the summer months in lakes that thermally stratify, lake trout will exhibit diel vertical migration, whereby they are typically restricted below the thermocline (Muir et al., 2021). Consequently, lake trout distribution is influenced by summer because of the physiological demands to minimize metabolic costs due to thermal preferences, while maximizing foraging opportunities (Guzzo et al., 2017; Binder et al., 2021).

Lake trout life-history characteristics have been explored across its geographic range, especially for Canada's largest lakes (see Burnham-Curtis and Bronte, 1993; Shuter et al., 1998; McDermid et al., 2010; Hansen et al., 2012; Chavarie et al., 2016; Hansen et al., 2021). While fish scales were chiefly used to age lake trout in older studies (Eschmeyer, 1955; Cable, 1956), contemporary studies have opted to use sagittal otoliths due to method being greater in accuracy in determining fish ages of a fish (Campana et al., 2008). Furthermore, otoliths revealed older age estimates, thus lowering formerly estimated mortality rates for older lake trout (Rahrer, 1965; Burnham-Curtis and Bronte, 1996). While gillnetting programs are biased by catching larger individuals in a population, back-calculated length-at-age study designs alleviate this problem to some degree by acquiring growth data for earlier life stages (Hansen et al., 2021). Life-history variation has been associated with several abiotic and climatic factors (McDermid et al., 2010). Colder mean annual temperature was associated with slower early year growth rates, later maturation, and increased longevity (McDermid et al., 2010). Furthermore, lake trout populations subjected to colder, but shorter winters exhibited faster early year growth rates and larger maximum sizes (McDermid et al., 2010). The physical characteristics of a lake also have been found to influence lake trout life-history. Lake depth was positively associated with age and length at maturity, while lakes with higher surface area were positively associated with lake trout max age and lengths (McDermid et al., 2010). Despite the plethora of knowledge concerning lake trout populations, few studies have examined the life history characteristics from lake trout fisheries in Manitoba (see Day, 1983).

The status of native lake trout populations geographically varies (Riley et al., 2021). Northern populations appear to be in a better state than southern populations (Riley et al., 2021), and lakes located closer to urban centres are typically subjected to more anthropogenic stressors (Arlinghaus et al., 2015) and habitat degradation (Riley et al., 2021). Historically, lake trout populations have not fared well in the face of human activity (i.e., overfishing and invasive sea lamprey parasitism [see Berst and Spangler, 1972; Christie, 1972; Pycha and King, 1975]). Lake trout life-history strategies (e.g., slow growth and late maturation relative to other species, e.g. percids) make them sensitive to anthropogenic stressors such as commercial and recreational fishing, which will in turn influence lake trout population structure and geographical distributions (Campana et al., 2020). Acquiring population information on lake trout fisheries is a fundamental first step for fisheries managers to assess their current conservation status. Furthermore, this information can provide managers with data to make informed decisions to meet sustainable management targets in recreational lake trout fisheries.

Manitoba is one jurisdiction where fisheries data is lacking for lake trout. Manitoba has a high angler participation rate compared to other North American jurisdictions, selling 190,000 angling licenses annually (MBGOV, 2021b). Lake trout are considered one of the premier sportfish in the province and can attain 'trophy-size' status, which is attractive to anglers. However, contemporary data regarding the state of lake trout fisheries across Manitoba has been lacking for roughly three decades (Kroeker, personal communication, 2021) despite several stocking events having taken place throughout the 21st century (MBGOV, 2021c), and increased fishing pressure targeting lake trout (Kroeker, personal communication, 2021). Lack of fisheries data also puts the fisheries at risk, which also puts at risk the local economies that depend on the activities surrounding recreational fisheries. Recreational angling contributed on average $8.8 billion CAD per year to the Canadian economy (Brownscombe et al., 2014). Furthermore, salmonids are the most harvested group of species in Canada (Brownscombe et al., 2014). Manitoba lake trout fisheries stimulate rural economies through tourism and angling-related purchases. Additionally, in Manitoba, the population is spread out and relies on fisheries-related tourism, which is worth approximately $600 million CAD annually (MBGOV, 2021b). Of all the lake trout fisheries across Manitoba, managers are most concerned with the status of the southern fisheries (Kroeker, personal communication). This concern stems from increased fishing pressure and increased social media exposure of high-quality lake trout fisheries in the province. It is therefore important to assess the present state of lake trout fisheries across Manitoba to better understand their status.

The objective of this thesis chapter was to compare life-history characteristics (age, growth, maturity, and mortality) between seven lake trout populations distributed along a latitudinal gradient in Manitoba, Canada. I hypothesize that growth rates would differ between the northern and southern populations. I predicted that northern lake trout populations would express slower growth rates than their southern counterparts because northern latitudes are associated with colder water temperatures and shorter growth seasons than southern latitudes. My secondary hypothesis was that mean age would differ across Manitoba. I predicted that northern lake trout populations would be older than southern lake trout populations, because of the known trend of lower mortality in northern lakes (McDermid et al., 2010; Hansen et al., 2021). Subsequently, my third hypothesis was that lake trout length would also differ between northern and southern populations, whereby northern populations attaining longer lengths than southern populations, because of the positive relationship between asymptotic length and lake size (Hansen et al., 2021).

Methods

Study area

Seven lakes containing lake trout were sampled in various locations across Manitoba from the southeastern region of the province and the northwest region (Figure 2.1). Lakes located in southeastern Manitoba included Davidson Lake (50°27'N 95°09'W, surface area = 2.25km^2, average depth = 9.11m), George Lake (50°13'N 95°29'W, surface area = 21.5 km^2, average depth = 12.0), High Lake (49°42'N 95°08'W, surface area = 8.04km^2, average depth = 12 m),

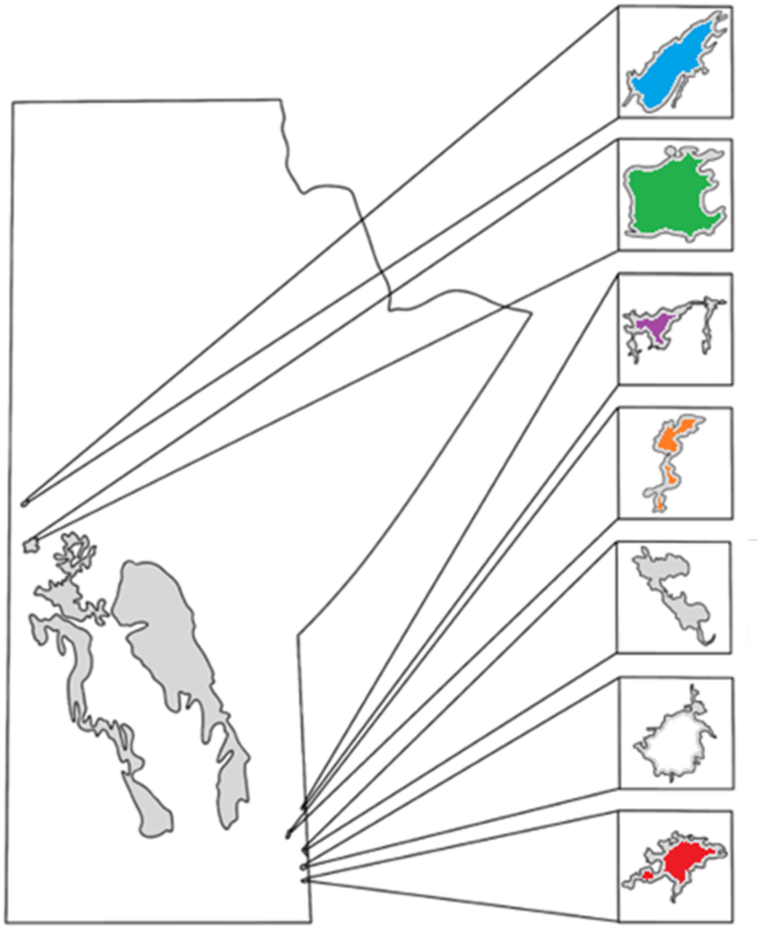

Figure 2.1. Map of all sampled Manitoban lakes. Blue = Second Cranberry Lake (54°38'N 101°11'W, surface area = 23.83 km^2, average depth = 19.81 m), green = Clearwater Lake (54°03'N 101°03'W, surface area = 285.07 km^2, average depth =13.10 m), grey = Mantario Lake (49°59'N 95°09'W, surface area = 4.12 km^2, average depth = 15 m), orange = George Lake (50°13'N 95°29'W, surface area = 21.5 km^2, average depth = 12.0 m), purple = Davidson Lake (50°27'N 95°09'W, surface area = 2.25 km^2, average depth = 9.11 m), white = West Hawk Lake (49°45'N 95°11'W, surface area = 14.60 km^2, average depth = 33.13 m), and red = High lake (49°42'N 95°08'W, surface area = 8.04 km^2, average depth = 12 m).

Mantario Lake (49°59'N 95°09'W, surface area = 4.12km^2, average depth = 15m) and West Hawk Lake (49°45'N 95°11'W, surface area = 14.60km^2, average depth = 33.13m). Sampled lakes in northwest Manitoba included Clearwater Lake (54°03'N 101°03'W, surface area = 285.07km^2, average depth =13.10m) and Second Cranberry Lake (54°38'N 101°11'W, surface area = 23.83km^2, average depth = 19.81m). All seven lakes stratify during the summer and are subjected to varying degrees of recreational pressure (Kroeker and Kitch, personal communication). Two fisheries managers were asked to qualitatively rank the sample lakes by fishing pressure and the results are as follows: CW>SCL>GL>WHL>HL>DL>ML. Clearwater Lake (hereafter CW) has the highest fishing pressure, while Second Cranberry Lake (hereafter SCL) has the second highest across all lakes (Kroeker and Kitch, personal communication, 2021). Both lakes are easily accessible by road and are both near the town of The Pas, Manitoba, although it takes about 10 min by boat to reach SCL. George Lake (hereafter GL) has the most fishing pressure amongst southern lakes (Kroeker, personal communication), despite needing to cross the Winnipeg River and hike about 2 km for access. This requires the use of another boat, and then travelling with your equipment to the lake. Davidson Lake (hereafter DL), High Lake (hereafter HL), and West hawk Lake (hereafter WHL) are considered by the province to experience low levels of angling pressure (Kroeker, personal communication). WHL is the most easily accessible lake due to its proximity to the Trans-Canada Highway and Whiteshell Provincial Park. Despite HL being close to WHL, it is harder to access because of need of a boat ride across Falcon Lake, and then 1 km portage, therefore this likely dissuades anglers from fishing HL. Consequently, HL likely has a lower fishing pressure over WHL. DL is situated in Nopiming Provincial Park and is accessible by gravel road but is not recognized as a productive lake. ML being situated in Manitoba's non-motorized zone is only accessible by a 6 h portage or float plane, and therefore likely has the lowest fishing pressure.

Lake substrate is important for lake trout biology, because of it's influence on optimal spawning grounds and pre-hatch embryo survivability (Marsden et al., 2005). In terms of lake substrate, SCL presents a mix of granite and other Pre-Cambrian formations in the northern half, while Paleozoic substrate such as limestone dominates the south (Butler, 1950; MBGOV, 2018). GL, HL and ML is also mainly Canadian Shield granite-based (Butler, 1950; MBGOV, 2018). Lastly, CW is also located in the Palaeozoic region, thus its substrate is more dolomite and limestone-based (Butler, 1950; MBGOV, 2018). WHL, however, it is a meteor crater lake, whose substrate is clay-based (Teller et al., 2008).

Gillnetting protocol

The gillnetting and fish sampling protocols used in this study were largely based on the Summer Profundal Index Netting (SPIN) manual created by the Ontario Government (Sandstrom and Lester, 2009). The SPIN methodology provides a rapid and low-mortality lake trout population integrity assessment tool that can be applied to both small and large lakes (Sandstrom and Lester, 2009). It operates throughout summer months once the water reaches 18°C to ensure that most fish are in the hypolimnion (Sandstrom and Lester, 2009). I used a YSI Pro20 probe (YSI Inc.©, Yellow Springs, OH, USA) to record the first 30 m of my study lakes' temperature and the dissolved oxygen depth profile to determine the hypolimnion depth, and therefore guide depth sets for lake trout. Gillnets used for sampling were 64 m long standard monofilament multi-mesh nets consisting of 8 x 8 m long panels, with mesh sizes ranging from 57 mm to 127 mm, arranged randomly in order (Sandstrom and Lester, 2009). This approach targeted lake trout at or greater than 300 mm fork length, a minimum length deemed to be captured by anglers

(Sandstrom and Lester, 2009). SPIN allocates net deployment based on lake surface area, depth strata (e.g. 0–10 m, 10–20 m), with the ultimate goal of ensuring complete coverage of the lake. Thus, I randomly set SPIN gillnets throughout lakes at various depths based on the strata available and the observed thermocline. While SPIN protocols call for nets to be soaked for strictly 2 h, only 30-min sets were allowed by local fisheries biologists (i.e., to avoid high non-target species mortality). High non-target mortality of lake whitefish (*Coregonus clupeaformis)* in both northern lakes SCL and CW was observed, therefore I primarily set nets for 30 min at these locations. Note that SPIN specific gillnets are set at the bottom of the lake, and only sample the bottom 1.8 m of a lake (the height of the gillnet). The number of nets to set in each lake is determined by an equation: number of sets = 0.0184 (Lake Area (ha)) + 24 (a maximum of 140 sets is used in large lakes; Sandstrom and Lester, 2009).

Captured lake trout designated for sacrifice were examined for, fork length (mm), total length (mm), weight (g), diet, sex, and maturity. Lake trout that were released were only examined for fork length (mm), total length (mm), and weight (g). I only sacrificed 10 lake trout individuals from every 5 cm size class encountered (starting from 300 mm with no maximum length threshold). However, some size classes had greater sample sizes due to gillnet-induced mortality. Furthermore, some weights of released individuals could not be accurately recorded due to the unsteady nature of the boat and certain weather conditions. For aging purposes, I collected sagittal otoliths from the lake trout that were sacrificed. I also supplemented SPIN sampling with angling in the southern lakes due to low catch rates (applies only to HL, ML, and WHL).

Otoliths thin-sectioning

I used procedures described by the ‘Ministère des Forêts, de la Faune et des Parcs Direction de l’expertise sur la faune aquatique’ (MFFP, 2018) to thin-section sagittal otoliths. I first cleaned the lake trout otoliths with distilled water to remove any remaining dried blood or endolymphatic fluid from the otolith. Afterwards, I used a stereo microscope (Motic SMZ-171 Stereo Zoom Microscope; Motic Instruments Inc.©, Richmond, British Columbia) to identify the core of the nucleus of the otolith (Figure 2.2). If the core could not be easily located, I gently polished the external side of the otolith with polishing paper (3M™ Wet-or-Dry™ 2000 µm, Saint Paul, Minnesota) to reveal the core (Gallagher, 2021). Once the core was identified, I marked it with a graphite pencil to align the core for subsequent thin-sectioning. Using silicon molds I embed each otolith into a 4:1 mixture of epoxy and hardener ratio (Buehler EpoxiCure™, Lake Bluff, Illinois). Otoliths were placed into molds sulcus side down and I removed excess air bubbles to avoid inconsistent cutting speeds when sectioning the otolith. Molds were given at least 48 h to harden and cure prior to sectioning.

To thin-section the embedded otoliths, I used a low-speed saw (Buhler Iso-met) with a single diamond wafering blade (M412L, MetLab, Niagara Falls, New York). To reduce friction between the blade and otolith I used a 3:2 glycerol to water lubricant mixture that I added into a liquid capture dish beneath the blade. I administered three incisions to create two 1 mm thin-sections of the otoliths (MFFP, 2018). I lined up the blade with the marked core of the otolith, and the blade moved 1 mm to the right of the core and the first incision was administered. I moved the blade 1 mm to the left, back to its original spot, and administered the second incision to create the first 1 mm thin section. I administered the final incision by moving the blade 1 mm to the left of the core, therefore creating the second thin-section. Thin sections were kept in microcentrifuge tubes prior to examination to avoid any potential unwanted damage. The thin-

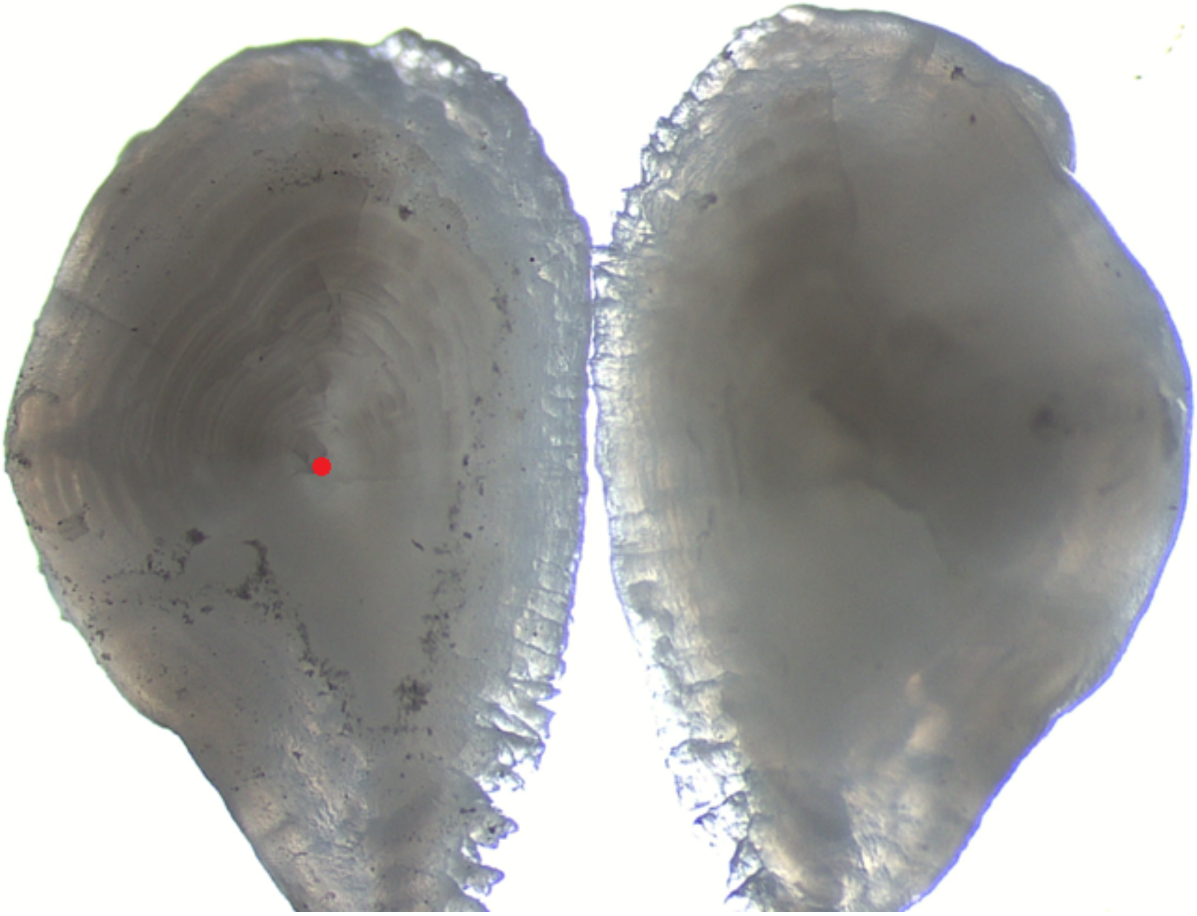

Figure 2.2. Comparison of sanded (left) vs unsanded (right) lake trout (*Salvelinus namaycush*) otoliths using 3M^{TM} Wet-or-Dry^{TM} 2000 μm polishing paper. The otolith core is identified with a red dot.

sectioning method allows for two opportunities for age analyses if one of the two sections are unsatisfactory (MFFP, 2018; Morissette, personal communication).

Otolith aging

To age sectioned otoliths, I placed them under a stereo microscope (Motic SMZ-171 Stereo Zoom Microscope with a built-in Moticam 1080BMH-U camera, Motic Instruments Inc.©, Richmond, British Columbia). I selected the section with the clearest annuli, and subsequently I lightly polished the otolith using polishing paper (3M™ Wet-or-Dry™ 2000 µm), followed by 5 µm and 1 µm micro-lapping aluminum-oxide lapping film (3M™, Saint Paul, MN) (Morissette et al., 2018). Afterwards, I placed the otolith under the microscope with an application of non-toxic mineral oil to enhance the clarity and resolution of the otolith's annuli. If necessary, these steps were repeated until the annuli were clear enough for photos to be taken. I took photos between a magnification range between 20X and 100X using both reflected and transmitted light. The magnification was recorded for each image to standardize the measurements between images. Transmitted light was primarily used for the edge of lake trout otoliths when annuli were condensed, a common feature in old lake trout (Campana et al., 2008). Because otoliths sections are still three-dimensional objects, it was necessary to take multiple photos at multiple magnifications and light intensities to ensure optimal photographs were obtained for aging purposes (Long and Grabowski, 2017). Lastly, I glued otolith sections on a glass slide and placed them in a reference collection box for archiving.

In this study, I and another observer aged all collected otoliths. As the primary observer (observer #1), I had some aging experience prior to aging lake trout; however, the second observer (observer #2) did not have any prior experience. We were both given an aging primer that I created before aging lake trout samples. The aging primer was a document that explains the general trends and patterns of lake trout otoliths. Furthermore, it covers common errors agers make, because of lake trout consistently having many false annuli (Osborne et al., 2022). We each had access to the photo files for all lake trout, and photos were aged using ImageJ (Schneider et al., 2012). If the photograph's clarity was required to be enhanced, we used the 'Brightness/Contrast' function on ImageJ to do so. We individually placed numbered points on each annuli on separate photos for cross-referencing purposes if there were discrepancies between age estimations amongst ourselves (Figure 2.3). We did not have access to biological data (i.e., total length, sex, and maturity) about fish other than the lake of origin. Furthermore, all fish were collected in summer months, so it was assumed that the formation of an annuli occurs during the winter periods of slow growth (Beckman and Wilson, 1995), therefore if there was no visible otolith growth from the spring, the edge was considered as an annulus (Osborne et al., 2022). Because lake trout otoliths commonly have subannular marks or checks between annuli (Campana et al., 2008; Osborne et al., 2022), it is important that we followed the same annuli identification criteria. Under reflected light, annuli were identified as dark translucent bands indicating winter growth, followed by bright white opaque bands indicating summer growth (Osborne et al., 2022). False annuli were identified as translucent bands, which appeared to be incomplete compared to true annuli (Morissette, personal communication, 2021). Additionally, false annuli were identified as translucent bands that have inconsistent thickness, darkness, and spacing with respect to adjacent bands (Morissette, personal communication, 2021). Because the first few annuli near the core of the otolith section can be difficult to identify, both observers were trained to read the otoliths at three different axes (Hansen et al. 2012; Figure 2.4). If 2/3 axes had the same age estimate, then it was considered to be the estimated age of the fish. We aged each otolith three times. A

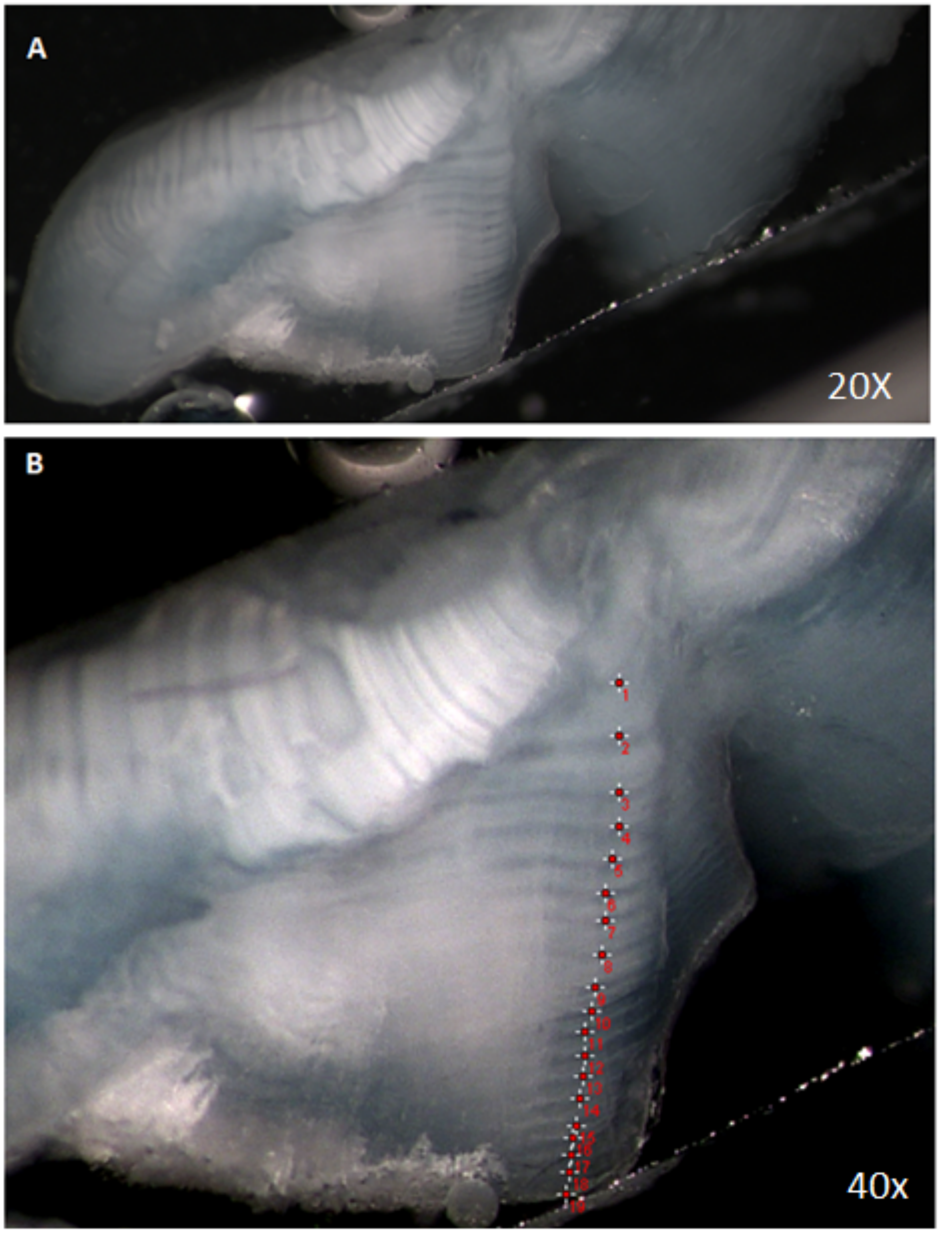

Figure 2.3. A) Picture of a 1mm thin-sectioned otolith from a lake trout (*Salvelinus namaycush*) estimated to be 19 years old. White opaque zones are the summer growth zones, while the black translucent zones are the winter growth zones. The combination of both growth zones equal one year of a lake trout's life. **B)** Contrast-enhanced image of the same otolith to enhance the clarity of growth rings. Red points represent the annual winter growth rings.

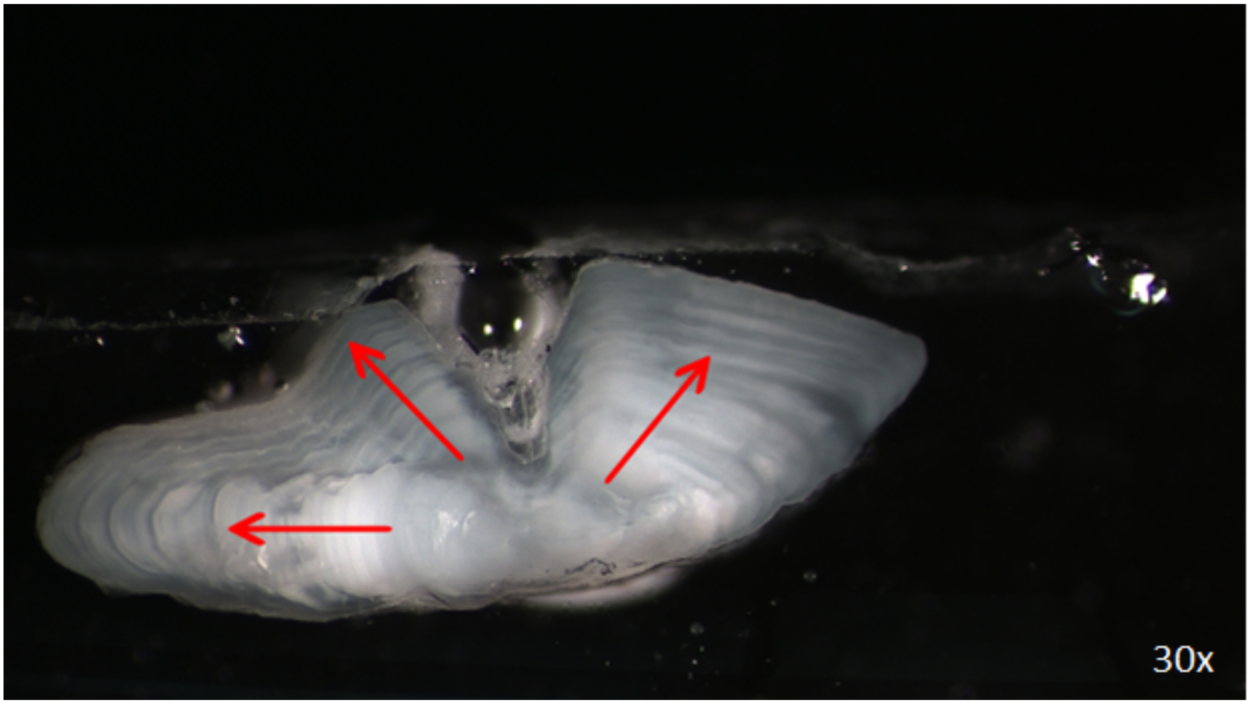

Figure 2.4. A picture of the three aging planes of a lake trout (*Salvelinus namaycush*) otolith.

minimum of a one week wait period between successive age estimations was used to avoid familiarity of specific samples (Gallagher et al., 2021). Moreover, the order of successive readings was randomized to further reduce aging bias. If we had difficulty aging an otolith, the photos were reexamined to decide whether more polishing or better lighting were required to create adequate photos. If this step did not yield better results, I sectioned the second otolith, following the previous steps. Once all three age estimations were completed, final ages for each observer was determined by majority (e.g., if a observer aged a fish 5, 6, and 5, then the final age for the observer is 5). If all three readings are different, then I selected the median value as the final age for the specific observer. In order to have an overall final age for the lake trout, each of the observers' final ages were compared and we discussed age discrepancies by comparing the marked photos, and a consensus age was reached (Burnham-Curtis and Bronte, 1996). This final consensus age was required for growth and age analysis (see below).

To assess the precision (replicability) of the three age estimations across observers and within observers, I calculated several measures of precision. I calculated the average percent error (APE%) using the 'Fisheries Stock Analysis' package in R (Ogle et al., 2022), which contains the *agePrecision* function that calculates APE%:

$$APE\% = 100 * \frac{\sum_{j=1}^{n} \sum_{i=1}^{R} (\left| x_{ij} - \bar{x} \right| / \bar{x}_j)}{nR}$$

where x_{ij} is the *i*th estimated age for the given *j* lake trout, $\bar{x}_j$ is the mean estimated age for *j*th lake trout, *R* is the number of age replicates for each lake trout, and *n* is the total sample size of the aging data set (Beamish and Fournier, 1981). Furthermore, I calculated the average coefficient of variation (ACV% or repeatability of age readings; Chang, 1982; Campana 2001), complete and partial agreement (+/-1 year), and created age difference plots to visualize the differences between observers. The ACV% was calculated using the 'Stock Analysis' package in R, which contains the *agePrecision* function that calculates ACV%:

$$ACV\% = 100 * \frac{\sum_{j=1}^{n} s_j/\bar{x}_j}{n}$$

where s_j is the standard deviation of the number of age replicates for the jth lake trout, $\bar{x}_j$ is the mean estimated age for jth lake trout, and n is the is the total sample size for the aging dataset (Chang, 1982). To evaluate where there was an aging bias amongst observers, I created age bias plots to determine whether systematic bias existed between the two datasets (Campana et al., 1995). Because I do not know the true age of the lake trout, the final age estimates from the observer with the most experience was used as the reference set (plotted on the x-axis). To measure bias between the datasets, I performed Evans-Hoenig symmetry tests, which is calculated from an age-agreement table based on its diagonal symmetry (Evans and Hoenig, 1998). I then performed multiple one-sample t-tests, which were corrected for multiple comparisons, to identify which estimated ages differed significantly between the two observers.

Growth, relative weight, maturity and survival

I reconstructed lake trout growth patterns by back-calculating length-at-age using a macro written for ImageJ version 1.53 (Spier, 2018). This method measures the distance between two annuli and assumes that there is a linear relationship between otolith growth and somatic growth (Vigliola and Meekan, 2009). To use the macro, I labelled the core and then the edge of each annulus until I reached the edge of the sectioned otolith, which was also labelled (Figure 2.5). The calculated length at age increment is based on the Dahl-Lea equation, which is a suitable equation for calculating length-at-age using otoliths (Shoup and Michaletz, 2017):

$$L_i = L_c * \ (S_i/S_c)$$

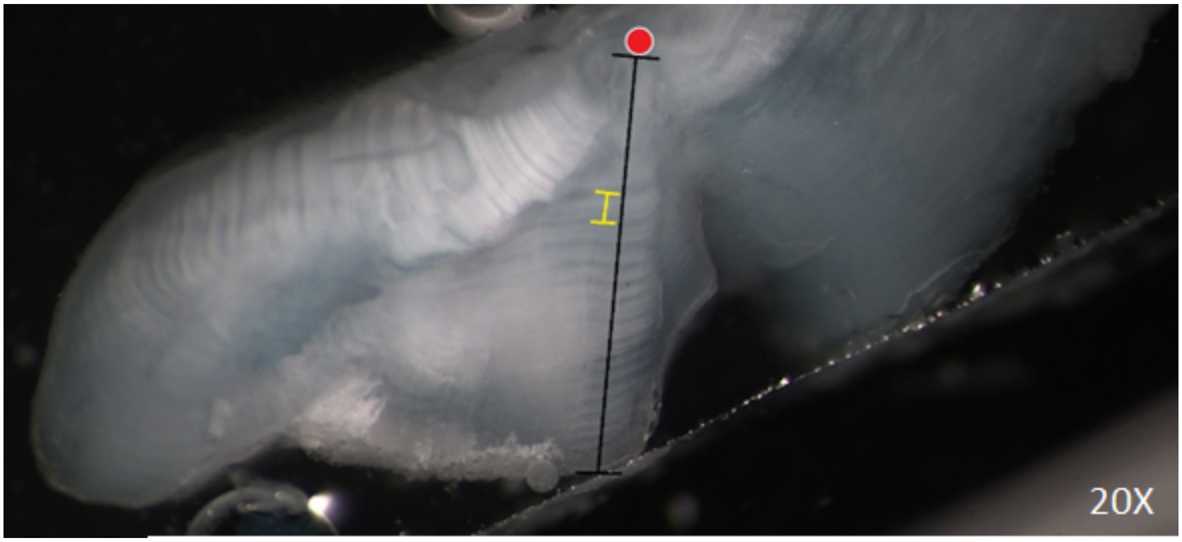

Figure 2.5. An example of procedure used to calculate annual growth. The core of the otolith, identified as a translucent spot (primordium), is marked with a red circle. The distance from one winter growth zone to the next is the length a lake trout grew in a single year, and is identified with the yellow line with hashmarks.

whereby L_i= length at age increment, L_c= length at capture, S_i= otolith radius at age increment, and S_c= otolith radius length at capture.

I then used the back calculated length-at-age data to generate von Bertalanffy growth functions (VBGFs) to model lake trout growth for each sampled lake, and plot age as a function of length (Ogle et al., 2016). I used the Beverton and Holt (1957) VBGF:

$$L = f(T, L_{\infty}, K, t_0) = L_{\infty}^{(1-e^{-K(T-t_0)})}$$

where L is length, T is age, L_{∞} is the asymptotic mean length of the population, t_0 represents the theoretical age when mean length is zero, and K describes the curvature of the VBGF. I used a hierarchical model to create growth functions for each population. This method was required as the back-calculated length-at-age data violates the independent observations assumption for non-nested growth models (Ogle et al., 2017). Under this maximum likelihood estimation framework, VBGF coefficients follow probability distributions for individuals in a population (Ogle et al., 2017; Gelman and Hill, 2007). As a result, the population-specific VBGF coefficients and predictions are not true parameters (Ogle et al., 2017). This ultimately leads to labelling these coefficients as partially pooled as opposed to other strategies such as pooled (i.e., assumed to be constant parameter values), or not pooled (i.e., assumed to be unique) in studies that examine multiple populations (Ogle et al., 2017).

I assessed relative body condition by using a weight-at-length model. Hansen et al. (2021) reviewed published literature related to lake trout population metrics across its native and non-native geographical range. They updated the logarithmic weight-at-length equation originally created by Piccolo et al. (1993) by using data from 97 populations: $log_{10}(g) = -5.589 + 3.210\ log_{10}(mm)$. This equation allows for relative body condition comparisons $K_n = (W/W')$, by comparing the measured weight of a lake trout at a given length (W) to the expected weight of a lake trout of the same length *(W')* (Neumann et al., 2012). A value below 100 represents a lake trout that weighs less than the 75% quantile of lake trout weights at the same length class across their geographical distribution (Piccolo et al., 1993).

I created maturity-at-age and length equations to model lake trout maturity schedules across populations. However, due to sample size restrictions, only CW, GL, and SCL populations were examined. Maturity at age or length curves can be calculated using logistic regressions, with from age or fork length, sex, and maturity using the equation:

$$p_{x1} = \frac{e^{(b_0 + b_1 * x_1)}}{1 + e^{(b_0 + b_1 * x_1)}}$$

where, p_{x1} is the probability that a lake trout is mature at a given age or length (x_1), b_0 is the intercept and b_1 is the slope of the curve (Hannah et al., 2009). I also calculated age at 50% maturity (A_{50}) and length at 50% maturity (L_{50}) from the maturity curves to more readily compare maturity schedules. A parametric bootstrapping approach was performed to generate confidence intervals for each variable associated with the maturity curves (Ogle, 2016). I selected 1000 bootstrap replicates to create my artificial dataset.

I used the Chapman-Robson method to estimate annual survival rate ($\hat{S}$) and instantaneous mortality ($\hat{Z}$) based on my cross-sectional age-frequency data (Chapman and Robson, 1960). This method involves involves analyzing the descending slope of the catch curve after the peak catch and is more robust than weighted regression methods (Smith et al., 2012). The Chapman-Robson estimate of annual survival rate is:

$$\hat{S} = \frac{T}{n + T - 1} = \frac{\hat{T}}{1 + T - 1}$$

where *S* is the annual survival rate, *n* is the total number of individuals observed along the descending slope of the catch curve, *T* is the total recoded age of individuals along the descending slope of the catch curve, and $\hat{T}$ is the mean recoded age of individuals along the descending slope of the catch curve. The Chapman-Robson estimate for instantaneous mortality is:

$$\hat{Z} = -\log(\hat{S}) - \frac{(n-1)(n-2)}{n(T+1)(n+T-1)}$$

where $\widehat{Z}$ is the estimate for instantaneous mortality, $\hat{S}$ is the annual survival rate, T is the total recoded age of individuals along the descending slope of the catch curve, and n is the total number of individuals observed along the descending slope of the catch curve. I then generated 95% confidence intervals for each population using the *confint* function in the 'stats' package in R (R Core Team, 2023). I deemed $\hat{S}$ and $\hat{Z}$ to be significantly different from each other if confidence intervals did not overlap (Rennie, personal communication, 2023).

Sustainable exploitation analyses

Lester et al. (2021) created a general life-history based sustainability model across a climactic gradient to sustainably exploit native lake trout populations based on 749 Canadian lakes. It was developed by pooling environmental and habitat data (i.e., lake size, mean annual air temperature, mean lake depth, and prey community make-up) with lake trout biomass data in order to further tailor the harvest model (Lester et al., 2021). This sustainability model can be applied to several maximum sustainable yield reference points including angling effort, biomass density, and total mortality rate, in order to account for the diversity of data that fisheries managers have on hand (Lester et al., 2021). For the purposes of this thesis, I decided to use biomass density and total mortality rate reference points to enumerate the current status of a lake trout population. There are four unique status levels (listed as stages in the chapter): stage 1 (healthy) – low fishing mortality and high biomass, stage 2 (overfishing early) – high fishing mortality and high biomass, stage 3 (overfishing, late) – high fishing mortality and low biomass, and stage 4 (overfished, recovering) – low fishing mortality and low biomass (Lester et al., 2021). To assign the aforementioned status designations several equations must be used. To determine whether a population is overfished, an exploitation ratio (*E*) must be used:

$$E = Z/M$$

,where *Z* is the total mortality rate of a population which is the sum of the natural and fishing mortality rates and *M* is the natural mortality rate of a population. If E > 2, then the population has high fishing mortality (Lester et al., 2021). While $\widehat{Z}$ was calculated from the Chapman-Robson equation, the natural mortality rate of a population can be estimated by using metabolic approach that incorporates life-history characteristics of a population derived by Lester et al. (2021):

$$M = \frac{91.8e^{0.021*T+0.0004*T^2}}{L_\infty^{0.96}}$$

, where *T* is mean annual air temperature and L_∞ is the mean asymptotic length of a population. Mean annual air temperature values were procured from Environment Canada. In order to assess biomass levels in a population, a biomass ratio (B_x) must be used:

$$B_x = B/B_{MSY}$$

,where *B* is the estimated biomass density of a population and B_{MSY} is the estimated biomass density when a population is exploited at maximum sustainable yield. In order to calculate B_{MSY}, the following equation derived by Lester et al. (2021) must be used:

$$B_{MSY} = 8.47 * D_{mn} * pV_{eb} * S * W_\infty^{-1.33}$$

, where D_{mn} is the mean depth of a lake, pV_{be} is the proportion of the lake volume in the epibenthic zone, *S* is the habitat suitability index for lake trout, and W_∞ is the mean asymptotic weight of the population. In order to estimate *B,* density must be first calculated. SPIN has created a density equation (number of fish/hectare) related to the observed CPUE in a given lake,

$$D = Adjusted\ CPUE * 4.86$$

, where the adjusted CPUE is sum of CPUE values at different strata (e.g., 10-20m) while accounting for the proportion of the lake that the strata occupy (Sandstrom and Lester, 2009). Since I did not have accurate bathymetric maps, being able to use the adjusted CPUE approach was not possible, therefore used a lake wide CPUE for the aforementioned equation to calculate density. Biomass density was calculated as follows:

$$B = \bar{x}_w * D$$

, where $\bar{x}_w$ is the mean weight of a lake trout population and D is the number of lake trout per hectare (density). If $B_x > 1$, then the population is deemed to have a high biomass (Lester et al., 2021). For the sake of brevity, equations that solve for the remainder of the aforementioned variables can be found in the Lester et al. (2021) chapter.

Statistical analyses

I used a Shapiro-Wilk and Levene's tests, respectively, to determine whether assumptions of normality and homogeneity of variance were achieved for every variable. All variables rejected the null hypotheses, therefore I used non-parametric tests. Length, weight, age, relative weight, VBGF parameters were compared across populations by using a Kruskal-Wallis test. I used Dunn tests to identify specific pairwise differences across populations. To test the relationship of lake size (surface area), latitude, and recreational fishing pressure on lake trout age, growth rate, length, and survival. I created several linear regression models. I calculated the coefficient of determination (R^2) to evaluate how much variability within my dependent variables could be explained by my independent variables. I also calculated the slope of the relationship and used a t-score test statistic to determine whether the relationship was significant between my variables. Admittedly, because I could only analyze these data with lakes as the sampling unit, power to detect statistical significance was low.

Results

A total of 468 lake trout were caught across all seven sampled populations in Manitoba, of which a subsample (n = 297) were sacrificed for aging (Table 2.1). The catch-per-unit-effort (CPUE) for lake trout was on average higher in northern Manitoba, whereby CW had the highest CPUE of 5.55, and SCL had the third highest CPUE value of 2.87. GL, a southern population, had the second highest CPUE value of 2.91 for lake trout caught (Table 2.1).

Fish size and relative weight

Northern lake trout populations were generally larger than their southern counterparts. Lake trout total length measurements varied significantly across populations ($X^2_{6,\,443} = 58.627$, $P < 0.001$). SCL had the highest mean length among lake trout populations (Figure 2.6). Omitting DL due to low sample size, GL had the lowest mean length among sampled populations. Both CW and SCL had lake trout caught above the master angler 'trophy-size' threshold of 890 mm. Three master angler-sized lake trout were caught in SCL (897 mm, 905 mm, and 925 mm), while four master angler-sized lake trout were caught in CW (909 mm, 944 mm, 944 mm, and 955 mm). SCL lake trout were significantly longer than all other populations including CW, GL, HL, ML, and WH (Table A.2.1). Lake trout weight measurements varied significantly across populations ($X^2_{5,\,312} = 48.484$, $P < 0.001$) (Figure 2.7). SCL had the highest average weight, while ML had the lowest mean weight. Similarly to length, SCL had significantly heavier lake trout compared to all southern populations as well as CW (Table A.2.2).

All lake trout populations had mean relative weight values below 100, indicating that the assessed Manitoban lake trout populations weight less than the 75th percentile of predicted

Table 2.1. Lake Trout Caught (SPIN/angling) in Manitoba. * indicate number of angled fish not aged, nor used in any other statistical analyses. Bolded lakes indicate that 30-minute net sets were used.

Lake	Nets Set	Lake Trout Caught	Lake trout sacrificed	SPIN Catch-per-unit-effort
Clearwater (CW)	150	254/2	120/2*	5.55
Second Cranberry (SCL)	58	47/0	47/0	2.87
Davidson (DL)	26	1/0	1/0	0.03
George (GL)	30	88/12	65/5*	2.91
High (HL)	21	12/10	11/10	0.58
Mantario (ML)	30	22/7	22/7	0.72
West Hawk (WHL)	48	12/1	12/1	0.24
Total	363	436/32	278/26	---

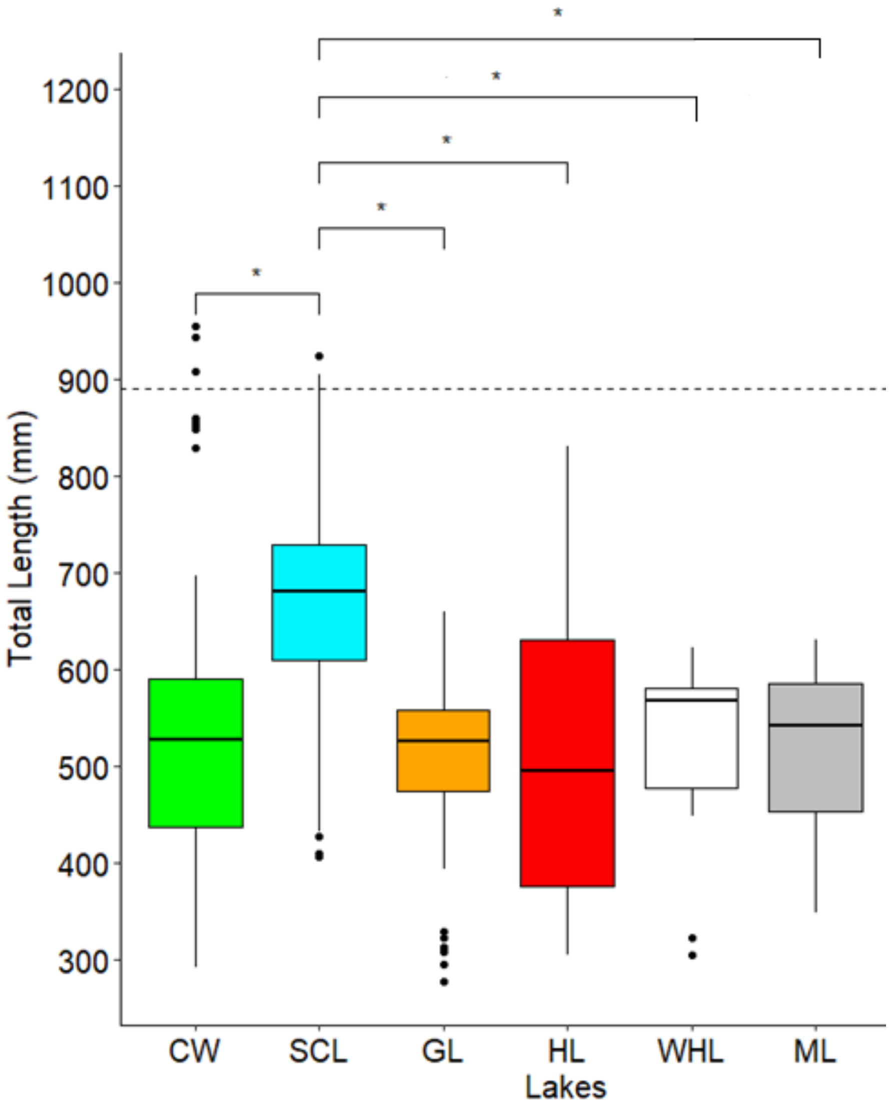

Figure 2.6. Boxplot graph representing total length distribution for seven Manitoban lake trout (*Salvelinus namaycush*) populations (Clearwater Lake = CW [n = 248], Second Cranberry Lake = SCL [n = 47], George Lake = GL [n = 86], High Lake = HL [n = 20], West Hawk Lake = WHL [n = 13], Mantario Lake = ML [n = 29], and Davidson Lake = DL [n = 1]). The dashed line represents the 89 cm threshold for trophy-sized lake trout in Manitoba. Using a Kruskal-Wallis test and a subsequent Dunn test, * indicate significant differences across populations at a threshold of α < 0.05.

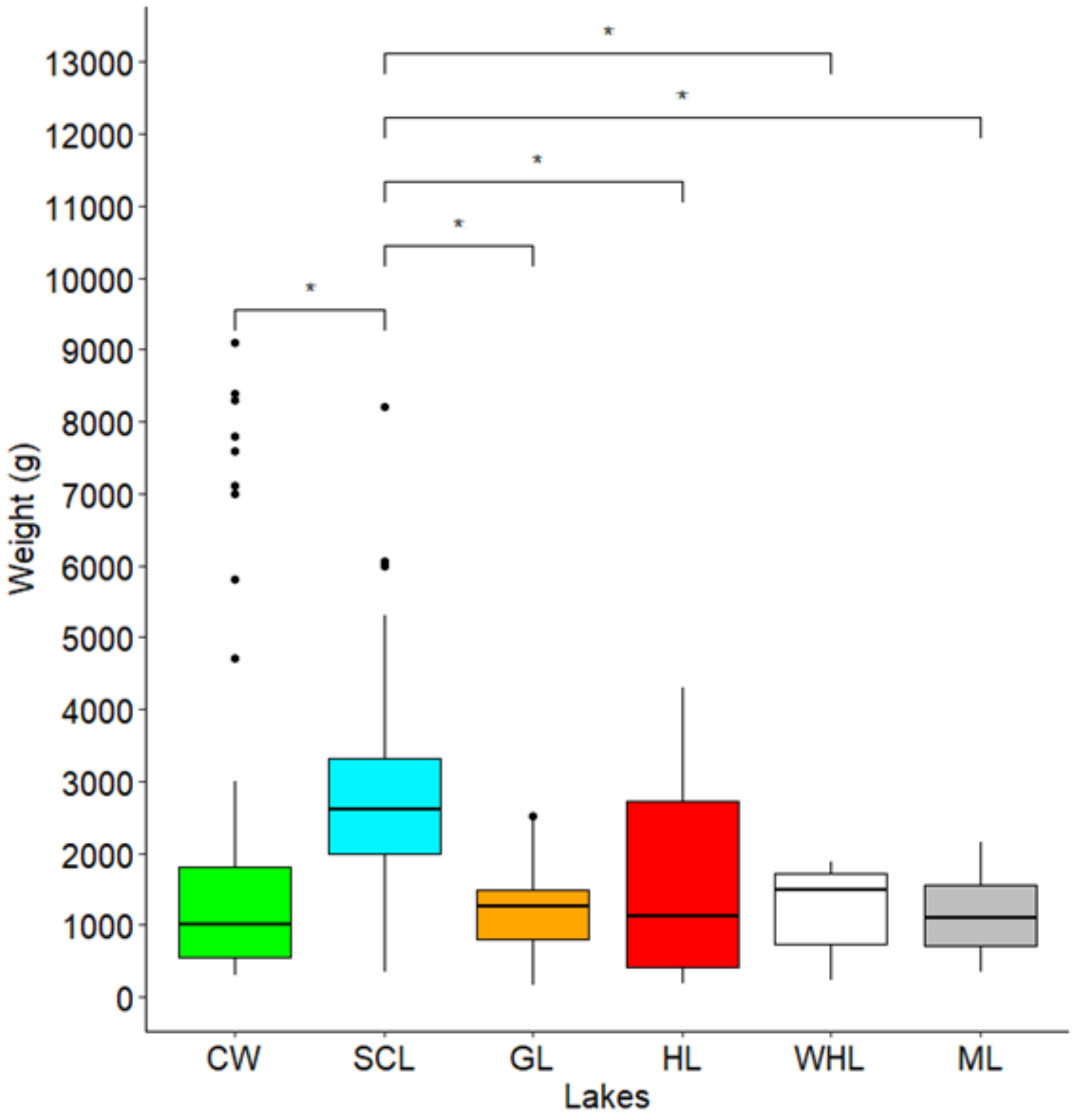

Figure 2.7. Boxplot graph representing weight distribution for six Manitoban lake trout (*Salvelinus namaycush*) populations (Clearwater Lake = CW [n = 117], Second Cranberry Lake = SCL [n = 47], George Lake = GL [n = 85], High Lake = HL [n = 21], West Hawk Lake = WHL [n = 13], and Mantario Lake = ML [n = 29]). Using a Kruskal-Wallis test and a subsequent Dunn test, * indicate significant differences across populations at a threshold of $\alpha < 0.05$.

weights across its geographical range (Figure 2.8). George Lake had the highest condition factor, while High Lake had the lowest score (Figure 2.8). Relative weight scores varied significantly across sampled populations (KW test, $X^2_{6,\,310} = 0.00238$, $P = 0.0238$). Mantario Lake relative weight scores were significantly lower than CW, and GL (Table A.2.3).

Aging precision

The precision of age estimates varied across the two observers (Table 2.2). Observer #1 had the highest percent agreement across the three age replicates of 57.2% compared to observer #2 who only had 34.9% percent agreement. Observer #1 had the lowest ACV of 2.7% and APE of 2.1% compared to observer #2 who had an ACV of 6.1% and APE of 4.6%. The age bias plot revealed a systematic bias between observer #2 and observer #1 (which was used as the reference age; Figure 2.9). Observer #2 (no experience) generally aged lake trout to be older than the reference age. This trend becomes apparent around the estimated 20-year mark. Despite this, the one-sample *t*-tests did not reveal significant differences at individual reference ages (Table A.2.4). Precision metrics between final ages of the observers revealed 47.3% agreement, but this value increases to 83.2% when expanding the percent agreement range to ±1 estimated year (Table A.2.5). The ACV% was estimated to be 5.4%, while the APE% was 3.8%.

Age and growth

The final consensus estimated ages from lake trout otoliths collected in all seven populations ranged from 4– 45 years old (Figure 2.10). SCL had the oldest fish aged (45 years old) as well as the highest average age, 18 years. Omitting DL, CW had the youngest mean age of 9 years. Amongst southern lake trout fisheries, GL had the oldest average age of 13 years. The final consensus estimated ages differed significantly across sampled populations (KW test, $X^2_{,\,291} = 67.799$, $P < 0.0001$). SCL had a significantly higher estimated age than several populations

Table 2.2. Age precision statistics between observer #1 (reference age), and observer #2.

Observer	N	Aging Replicates	% Agreement	Average Coefficient of variation (ACV%)	Average Percent Error (APE)	Average Standard Deviation (ASD)
Observer #1	292	3	57.190	2.746	2.072	0.326
Observer #2	292	3	34.930	6.131	4.561	0.709
Observer #1 vs #2 (Final ages)	292	2	47.260	5.425	3.836	0.603
Observer #1 vs #2 (all age replicates)	292	6	18.150	7.045	5.504	0.784

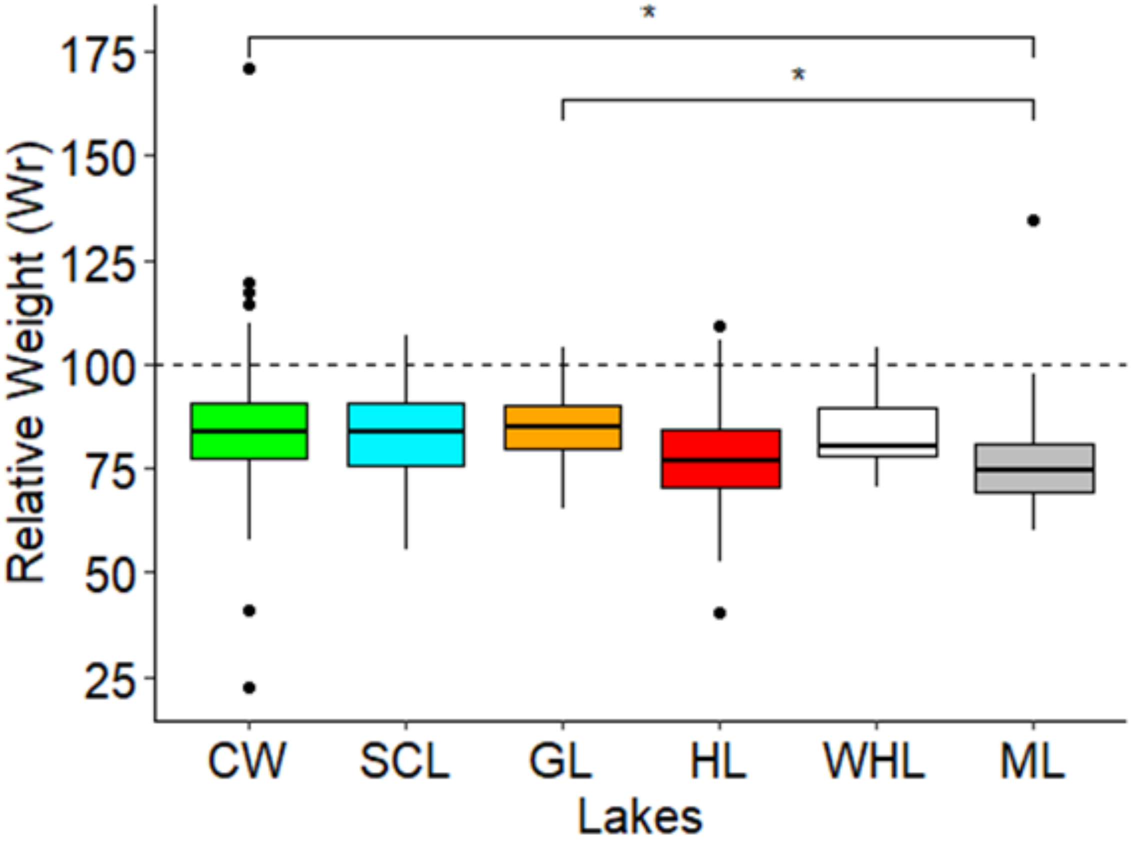

Figure 2.8. Boxplot graph representing relative weight scores for six Manitoban lake trout (*Salvelinus namaycush*) populations (Clearwater Lake = CW [n = 117], Second Cranberry Lake = SCL [n = 47], George Lake = GL [n = 85], High Lake = HL [n = 19], West Hawk Lake = WHL [n = 13], and Mantario Lake = ML [n = 29]). The dashed line represents the 75th percentile of expected weight for a given length of a lake trout across its geographical range. Using a Kruskal-Wallis test and a subsequent Dunn test, * indicate significant differences across populations at a threshold of $\alpha < 0.05$.

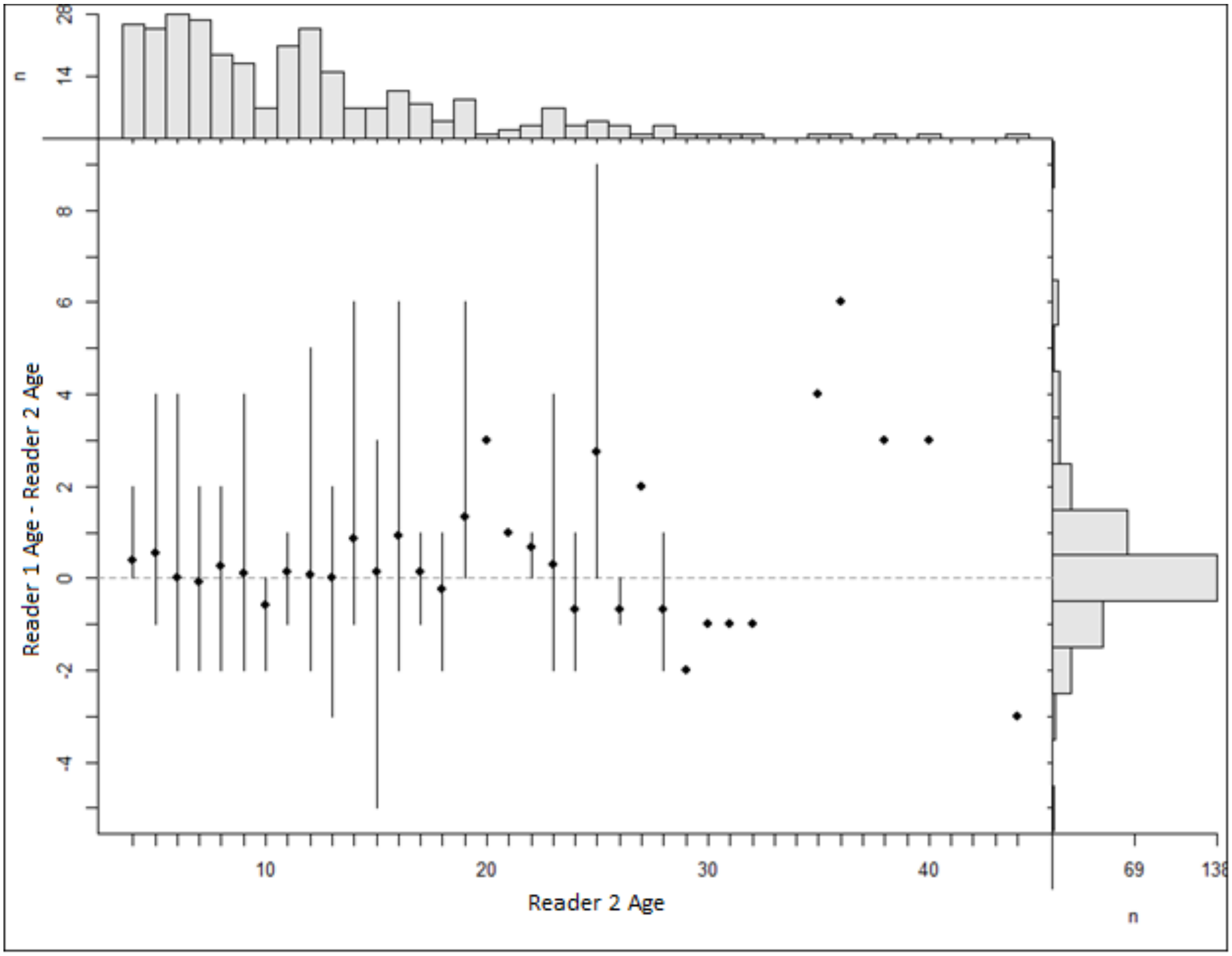

Figure 2.9. Age bias plot for observer #1 vs observer #2 (reference age set). The dashed line represents agreement in age, the points represent mean age difference at specific age groups. Lines represent the range of differences between observers. Histogram on the x-axis shows the frequency of individuals of each age group, and the y-axis histograms reveals the frequency of individuals in difference of age bins. Solid points represent non-significant differences of age estimates between observers at a threshold of α < 0.05.

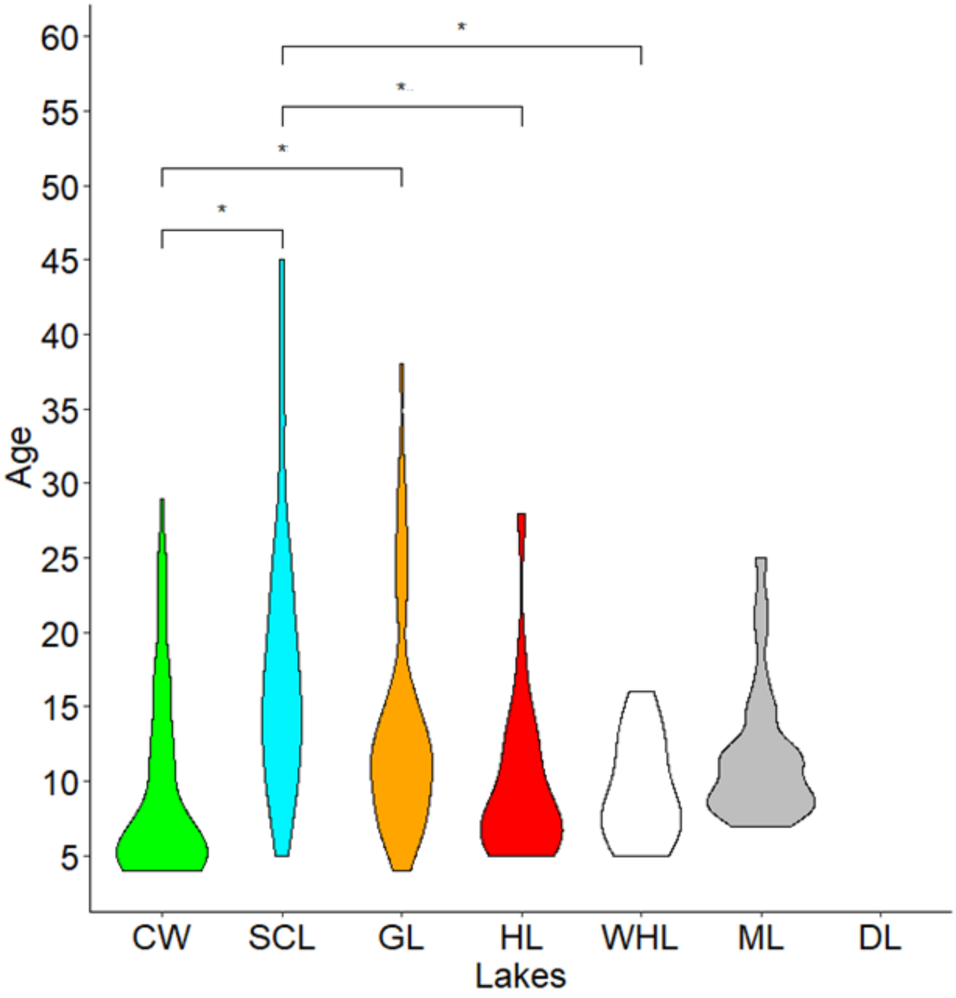

Figure 2.10. Violin plot representing the estimated age distributions for six Manitoban lake trout (*Salvelinus namaycush*) populations (Clearwater Lake = CW [n = 118], Second Cranberry Lake = SCL [n = 47], George Lake = GL [n = 64], High Lake = HL [n = 19], West Hawk Lake = WHL [n = 19], Mantario Lake = ML [n = 29] and Davidson Lake = DL [n = 1]). The wider the polygon, the more individuals for a given age class. Using a Kruskal-Wallis test and a subsequent Dunn test, * indicate significant differences across populations at a threshold of α < 0.05.

including CW, HL, and WHL (Table A.2.6). Lastly, GL mean estimated age was significantly older than CW ($Z_{1, 182} = 8.196$, $P < 0.0001$).

The von Bertalanffy growth curves differed across multiple parameters for several lake trout populations (Figure 2.11). L_∞ differed significantly across populations ($X_{25, 288} = 79.738$, $P < 0.0001$; Table 2.3). Of the two northern populations, only SCL reached a significantly longer L_∞ than some of the southern populations including GL, ML as well as the other northern population CW (Table A.2.7). GL had the lowest L_∞ value across all populations. *w* significantly differed across lake trout populations ($X^2_{5, 288} = 144.163$, $P < 0.0001$; Table 2.4). CW grew the fastest to reach L_∞, while SCL had the slowest growth rate of all lakes. CW reached a significantly higher w than GL, ML, and SCL (Table A.2.8). This pattern was also observed with *K*, whereby CW had the highest mean *K* value, while SCL had the lowest mean *K* value. *K* significantly differed across populations ($X_{25, 288} = 125.760$, $P < 0.0001$; Table 2.5). CW reached a significantly higher *K* than GL, HL, ML, SCL, and WHL (Table A.2.9). In addition to CW, SCL had a significantly lower mean *K* than GL, HL, and ML. T_0 significantly differed across populations ($X_{25, 288} = 109.117$, $P < 0.0001$; Table 2.6). CW had the highest mean t_0 value, while SCL had the lowest mean t_0 value. CW reached a significantly higher t_0 than GL, HL, SCL, and WHL (Table A.2.10). In addition to CW, SCL had a significantly lower mean t_0 value than, HL, ML, and WHL (Table A.2.10).

Age-at-maturity

Age-at-maturity curves and A_{50} values varied across populations (Figure 2.12). A_{50} estimates significantly differed across the lake trout populations ($X^2_{2,3000} = 2572.701$, $P < 0.0001$; Table 2.7). The bootstrapped mean A_{50} values suggest that lake trout from CW reached 50% maturity at the youngest age of 5 years and were significantly younger from the mean GL A_{50} of

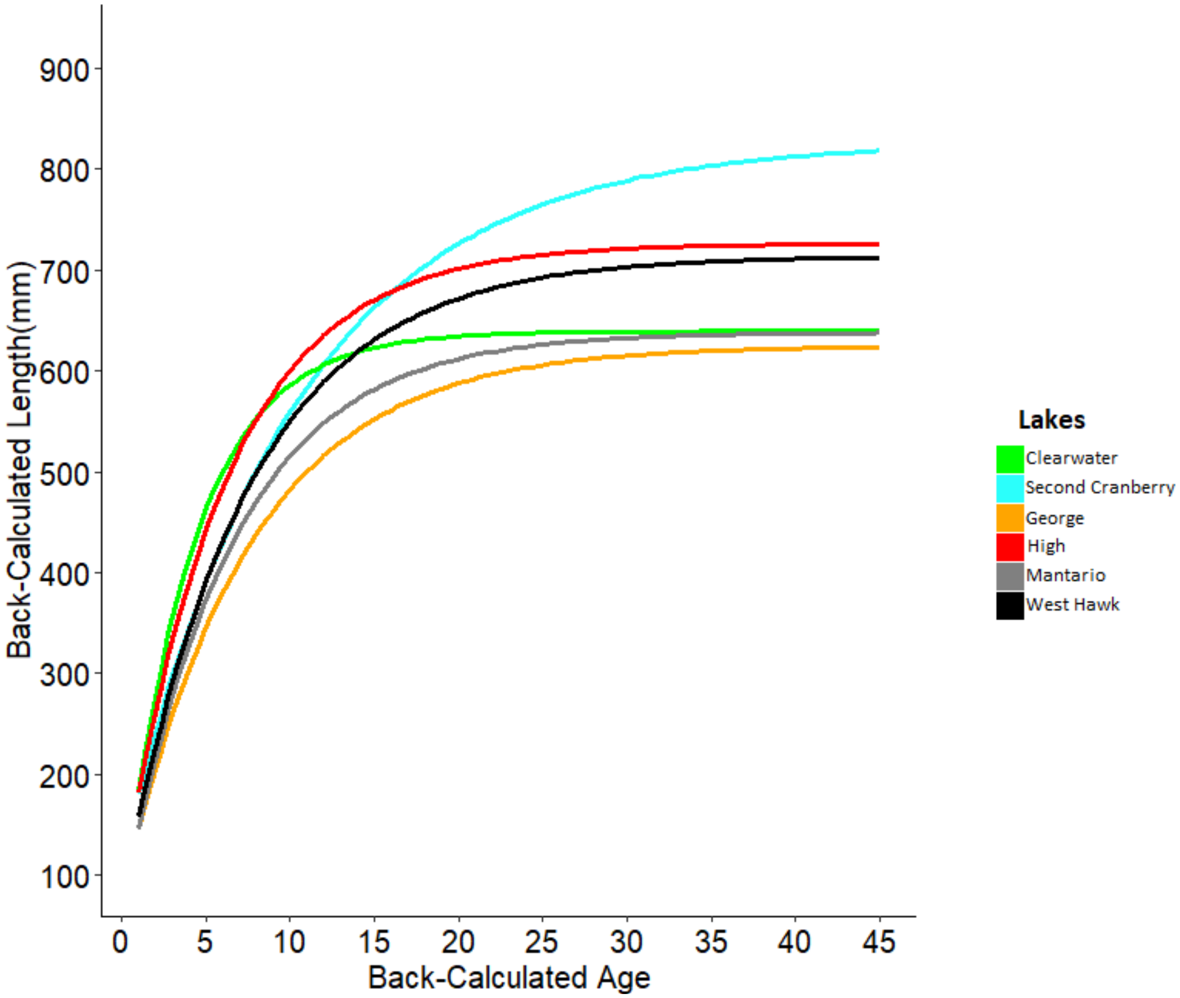

Figure 2.11. von Bertalanffy growth functions of the six Manitoban lake trout (Salvelinus namaycush) populations. (Clearwater Lake = green [n = 117], Second Cranberry Lake = turquoise [n = 47], George Lake = orange [n = 64], High Lake = red [n = 18], West Hawk Lake = black [n = 13], and Mantario Lake = grey [n = 29]).

Table 2.3. Asymptotic length *(L_∞)* parameter values for lake trout (*Salvelinus namaycush*) from six Manitoban populations. Letters denote statistical significance with an $\alpha < 0.05$.

Lake	N	Mean L_∞ (mm)	Standard deviation	Standard error	Upper confidence interval (95%)	Lower confidence interval (95%)
Clearwater (CW)	117	639.28^{a}	140.082	14.605	666.925	611.642
George (GL)	64	624.73^{a}	110.694	13.131	653.351	596.111
High (HL)	18	725.94^{ab}	221.898	54.185	832.061	619.838
Mantario (ML)	29	638.16^{a}	98.696	19.630	676.621	599.710
Second Cranberry (SCL)	47	826.72^{b}	119.91	18.611	863.190	790.251
West Hawk (WHL)	13	713.78^{ab}	28.849	15.188	743.521	684.050

Table 2.4. Early growth rate (*w)* parameter values for lake trout (*Salvelinus namaycush*) from six Manitoban populations. Letters denote statistical significance with an α < 0.05.

Lake	N	Mean *w* (mm/year)	Standard deviation	Standard error	Upper Confidence Interval (95%)	Lower Confidence Interval (95%)
Clearwater (CW)	117	144.818^{a}	36.301	3.356	151.465	138.171
George (GL)	64	79.545^{b}	18.670	2.333	84.209	74.882
High (HL)	18	101.945^{ab}	31.598	7.448	117.658	86.232
Mantario (ML)	29	95.445^{b}	19.824	3.681	102.986	87.904
Second Cranberry (SCL)	47	79.022^{b}	19.847	2.895	84.850	73.195
West Hawk (WHL)	13	96.723^{ab}	25.910	7.186	112.381	81.066

Table 2.5. Growth coefficient (K) parameter values for lake trout (*Salvelinus namaycush*) from six Manitoban populations. Letters denote statistical significance with an $\alpha < 0.05$.

Lake	N	K	Standard deviation	Standard error	Upper confidence interval (95%)	Lower confidence interval (95%)
Clearwater (CW)	117	0.218^{a}	0.0905	0.00997	0.257	0.238
George (GL)	64	0.134^{c}	0.0530	0.00704	0.148	0.121
High (HL)	18	0.123^{bc}	0.0805	0.0201	0.202	0.123
Mantario (ML)	29	0.154^{c}	0.0478	0.00923	0.172	0.136
Second Cranberry (SCL)	47	0.0976^{b}	0.0294	0.00467	0.107	0.0885
West Hawk (WHL)	13	0.136^{c}	0.0376	0.0117	0.159	0.113

Table 2.6. Age at length 0mm (t_0) parameter values for lake trout (*Salvelinus namaycush*) from six Manitoban populations. Letters denote statistical significance with an $\alpha < 0.05$.

Lake	N	Mean t_0	Standard deviation	Standard error	Upper confidence interval (95%)	Lower confidence interval (95%)
Clearwater (CW)	117	-0.516^{a}	0.487	0.0496	-0.321	-0.515
George (GL)	64	-0.980^{c}	0.531	0.00704	-0.841	-1.119
High (HL)	18	-0.963^{c}	0.372	0.0998	-0.572	-0.963
Mantario (ML)	29	-0.687^{ac}	0.478	0.0954	-0.499	-0.874
Second Cranberry (SCL)	47	-1.549^{b}	0.753	0.115	-1.323	-1.774
West Hawk (WHL)	13	-0.841^{bc}	0.502	0.154	-0.540	-1.142

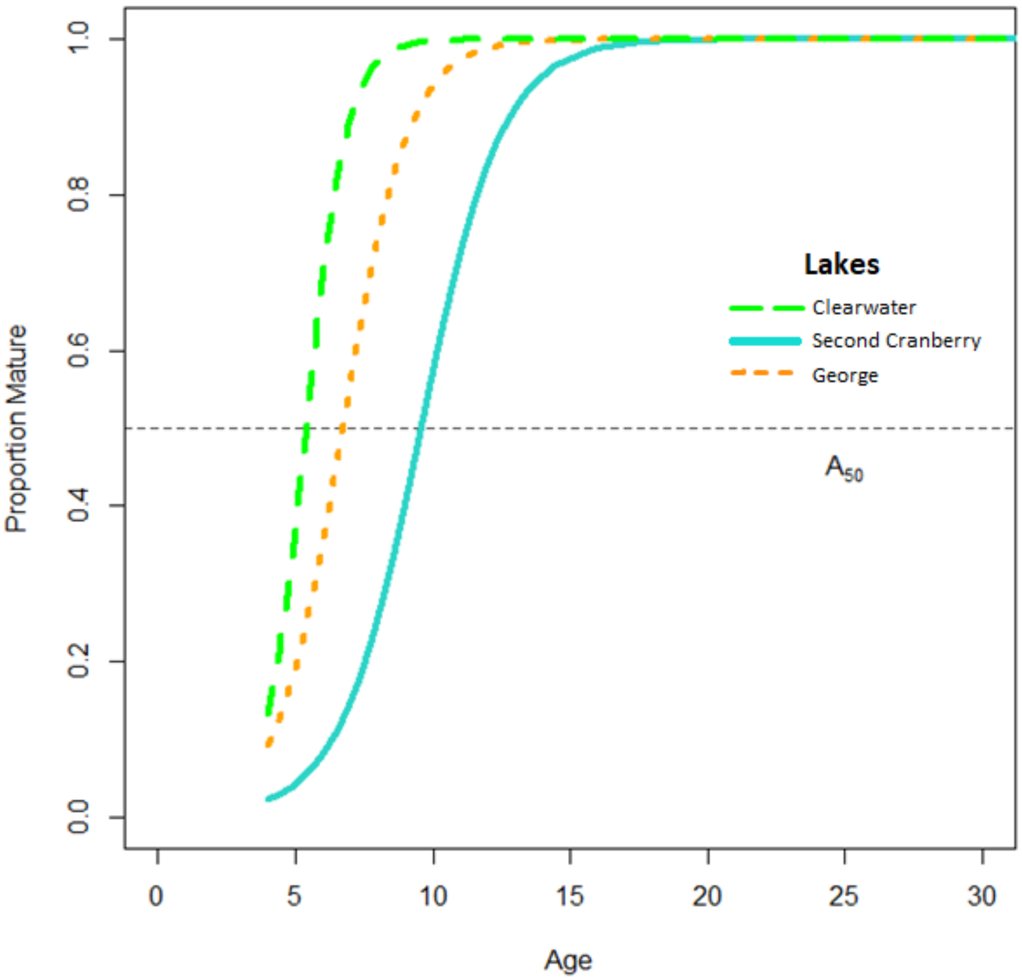

Figure 2.12. Age at maturity curves for Clearwater Lake, George Lake, and Second Cranberry Lake lake trout (*Salvelinus namaycush*) populations. Maturity curves are based on bootstrapped values. The dashed grey line represents the estimated age where 50% of individuals in the population will be mature (A_{50}). Clearwater Lake = green dashed line [n = 1000], George Lake = small dashed line [n = 1000], and Second Cranberry Lake = turquoise solid line [n= 1000].

Table 2.7. Age at which 50% probability individuals are mature (A_{50}), slope, and intercept values from the age-at-maturity logistic regression of three for lake trout (*Salvelinus namaycush*) populations. Parametric bootstrapping was procedure was conducted to recreate an artificial dataset of 1000 replicates. Letters denote statistical significance with an $\alpha < 0.05$.

Lake	Variable	N	Mean (mm)	Standard deviation	Standard error	Upper confidence interval (95%)	Lower confidence interval (95%)
Clearwater (CW)	A_{50}	1000	5.405^{a}	0.281	0.00889	5.422	5.387
George (GL)	A_{50}	1000	6.696^{b}	0.598	0.0189	6.733	6.659
Second Cranberry (SCL)	A_{50}	1000	9.599^{c}	1.239	0.0392	9.677	9.523
Clearwater	Slope	1000	1.534^{a}	0.709	0.0224	1.578	1.490
George	Slope	1000	1.371^{b}	2.166	0.0685	1.506	1.237
Second Cranberry	Slope	1000	2.787^{c}	3.664	0.116	3.014	2.559
Clearwater	Intercept	1000	-8.217^{a}	3.704	0.117	-7.987	-8.447
George	Intercept	1000	-9.090^{a}	14.162	0.448	-8.212	-9.969
Second Cranberry	Intercept	1000	-27.599^{b}	37.600	1.189	-25.266	-29.933

6 years, and the bootstrapped SCL mean of 9.6 years (Table A.2.11). Mean A_{50} values between GL and SCL also differed significantly, in which GL lake trout reach maturity at a younger age than SCL lake trout (Table A.2.11). The estimated variables associated with the logistic regression slopes and intercepts followed the same pattern. (Slope, $X^2_{2,3000} = 608.675$, $P < 0.0001$; Intercept, $X^2_{2,3000} = 236.463$, $P < 0.0001$, Table 2.7), indicating different maturity at age schedules. All logistic regression slope pairwise combinations for slope were significantly different from each other including CW-GL, CW-SCL, and GL-SCL (Table A.2.12). GL had a significantly different logistic regression intercept than CW, and SCL (Table A.2.13).

Length-at-maturity

The length-at-maturity logistic regressions as well as L_{50} values varied across lake trout fisheries (Figure 2.13). The L_{50} values significantly differed across populations ($X^2_{2,3000} = 974.707$, $P < 0.0001$; Table 2.8). The bootstrapped mean L_{50} values suggest that lake trout from GL reached 50% maturity at the shortest length of 386 mm and is significantly different from both bootstrapped means of northern lakes CW and SCL (Table A.2.14.). Mean L_{50} values between the two northern lakes of CW and SCL also differed significantly, whereby CW reached maturity at a smaller size. Significant differences exist when comparing the slope and the intercept of each population's length-at-maturity logistic regressions (Slope, $X^2_{2,3000} = 188.459$, $P < 0.0001$; Intercept, $X^2_{2,3000} = 974.707$, $P < 0.0001$, Table 2.8). All pairwise combinations for slope and intercept comparisons were significantly different from each other, thus indicating different maturity at length schedules. All logistic regression slope pairwise combinations for slope were significantly different from each other including CW-GL, CW-SCL, and GL-SCL (Table A.2.15). All logistic regression intercept pairwise combinations for slope were

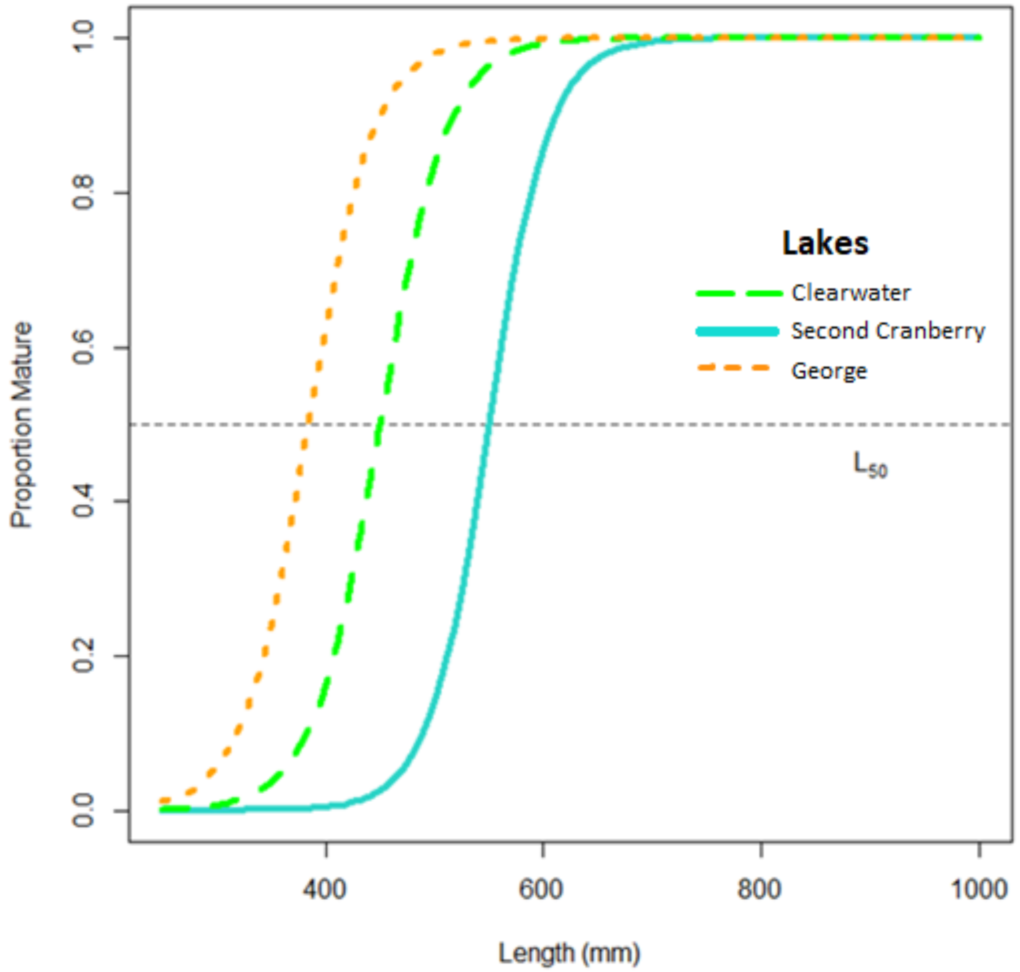

Figure 2.13. Length-at-maturity curves for Clearwater Lake, George Lake, and Second Cranberry Lake lake trout (*Salvelinus namaycush*) populations. Maturity curves are based on bootstrapped values The dashed grey line represents the length at which 50% of individuals in the populations are mature (L_{50}) . Clearwater Lake = green dashed line [n = 1000], George Lake = small dashed line [n = 1000], and Second Cranberry Lake = turquoise solid line [n = 1000].

Table 2.8. 50% maturity threshold (L_{50}), slope, an intercept values from the length-at-maturity logistic regression of three for lake trout (*Salvelinus namaycush*) populations. Letters denote statistical significance with an $\alpha < 0.05$.

Lake	**Variable**	**N**	**Mean (mm)**	**Standard Deviation**	**Standard Error**	**Upper Confidence Interval (95%)**	**Lower Confidence Interval (95%)**
Clearwater (CW)	L_{50}	1000	449.583[a]	9.768	0.309	468.882	430.591
George (GL)	L_{50}	1000	385.695[b]	19.180	0.607	420.776	348.450
Second Cranberry (SCL)	L_{50}	1000	553.689[c]	25.704	0.813	500.498	598.720
Clearwater	Slope	1000	0.0362[a]	0.00976	0.000309	0.0368	0.0356
George	Slope	1000	0.0633[b]	0.106	0.00335	0.0699	0.0567
Second Cranberry	Slope	1000	0.128[c]	0.168	0.00531	0.139	0.118
Clearwater	Intercept	1000	-16.245[a]	4.244	0.134	-15.981	-16.508
George	Intercept	1000	-24.445[b]	40.206	1.271	-21.950	-26.940
Second Cranberry	Intercept	1000	-72.367[c]	96.139	3.040	-66.401	-78.333

significantly different from each other including CW-GL, CW-SCL, and GL-SCL (Table A.2.16).

Annual survival rate and instantaneous mortality

Annual survival rates did not vary across populations, while instantaneous mortality rates did differ across populations. SCL had the highest annual survival rate, while ML had the lowest annual survival rate of 80.7 (Table 2.9). ML had the highest instantaneous mortality rate, while SCL had the lowest observable instantaneous mortality rate (Table 2.10). There were no significant differences in annual survival rates across populations based on 95% confidence limits overlapping. By contrast, instantaneous mortality rate did differ between populations as there was no overlap in confidence intervals between GL-SCL, ML-SCL, ML-SCL, and SCL-WHL pairs.

Age, Length, Growth Rate, and Survival Relationships

There were no significant relationships detected between the independent variables (recreational fishing pressure and lake surface area) and the response variables (mean total length, mean age, mean early growth rate). The variation of lake trout mean age could not be explained by any of the chosen independent variables and the regression equations were not significant for all independent variables including fishing pressure ($F_{(1, 5)} = 0.924$, $\beta = 0.701$, $P = 1.000$, adjusted $R^2 = -0.17$) and lake surface area ($F_{(1, 5)} = 0.139$, $\beta = -0.00609$, $P = 1.000$, adjusted $R^2 = -0.17$) (Figure 2.14AB). The variation of lake trout total length could not be explained by any of the chosen independent variables and the regression equations were not significant for all independent variables including fishing pressure ($F_{(1, 5)} = 1.744$, $\beta = 15.88$, $P = 1.000$, adjusted $R^2 = 0.110$) and lake surface area ($F_{(1, 5)} = 0.00803$, $\beta = 0.0261$, $P = 1.000$, adjusted $R^2 = -0.198$) (Figure 2.14CD). The variation of lake trout mean growth rate could not be

Table 2.9. Chapman-Robson estimated survival rates (*S*) from six Manitoban lake trout (*Salvelinus namaycush*) populations. Letters denote statistical significance with an $\alpha < 0.05$.

Lake	**N**	**Survival Rate (S)**	**Standard error**	**Upper confidence interval (95%)**	**Lower confidence interval (95%)**
Clearwater (CW)	118	84.448^{a}	1.483	87.355	81.541
George (GL)	64	88.325^{a}	2.294	92.820	83.829
High (HL)	19	84.932^{a}	4.216	93.194	76.668
Mantario (ML)	29	80.734^{a}	3.795	88.172	73.296
Second Cranberry (SCL)	47	89.636^{a}	1.615	92.802	86.470
West Hawk (WHL)	13	80.769^{a}	7.882	96.218	65.320

Table 2.10. Chapman-Robson estimated instantaneous mortality rates (*Z*) from six Manitoban lake trout (*Salvelinus namaycush*) populations. Letters denote statistical significance with an α <

Lake	**N**	**Instantaneous Mortality Rate (Z)**	**Standard error**	**Upper Confidence Interval (95%)**	**Lower Confidence Interval (95%)**
Clearwater (CW)	118	0.169^{ab}	0.0165	0.201	0.136
George (GL)	64	0.124^{a}	0.0184	0.159	0.0873
High (HL)	19	0.161^{a}	0.0354	0.231	0.0919
Mantario (ML)	29	0.212^{a}	0.0270	0.265	0.159
Second Cranberry (SCL)	47	0.109^{b}	0.0158	0.140	0.0781
West Hawk (WHL)	13	0.208^{a}	0.0324	0.271	0.144

0.05

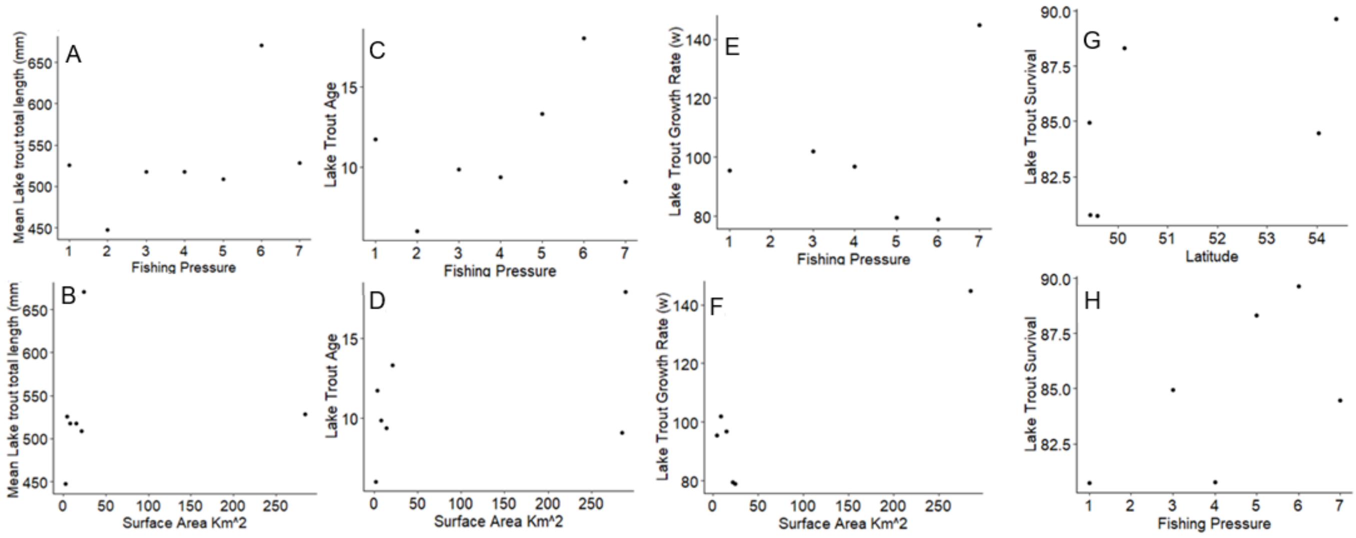

Figure 2.14 A) Scatterplot of lake trout (*Salvelinus namaycush*) total length plotted as a function of fishing pressure ($F_{(1, 5)} = 1.744$, $\beta = 15.88$, $P = 1.000$, adjusted $R^2 = 0.110$). The higher the fishing pressure number equates to a higher estimated fishing activity on the lake. **B)** Scatterplot of lake trout age plotted as a function of lake surface area ($F_{(1, 5)} = 0.00803$, $\beta = 0.0261$, $P = 1.000$, adjusted $R^2 = -0.198$). **C)** Scatterplot of lake trout age plotted as a function of fishing pressure ($F_{(1, 5)} = 0.924$, $\beta = 0.701$, $P = 1.000$, adjusted $R^2 = -0.17$). The higher the fishing pressure number equates to a higher estimated fishing activity on the lake. **D)** Scatterplot of lake trout age plotted as a function of lake surface area ($F_{(1, 5)} = 0.139$, $\beta = -0.00609$, $P = 1.000$, adjusted $R^2 = -0.118$). **E)** Scatterplot of lake trout early growth rate (w) plotted as a function of recreational fishing pressure. The higher the fishing pressure number equates to a higher estimated fishing activity on the lake ($F(1, 4) = 0.474$, $\beta = 3.63$, $P = 1.000$, adjusted $R2 = -0.118$). **F)** Scatterplot of lake trout early growth rate (w) plotted as a function of lake surface area ($F(1, 4) = 16.059$, $\beta = 0.195$, $P = 0.176$, adjusted $R2 = 0.751$). **G)** Scatterplot of lake trout survival plotted as a function latitude ($F_{(1, 4)} = 0.0371$, $\beta = 3.63$, $P = 1.000$, adjusted $R^2 = -0.118$). **H)** Scatterplot of lake trout survival plotted as a function recreational fishing pressure. The higher the fishing pressure number equates to a higher estimated fishing activity on the lake. ($F_{(1, 4)} = 2.298$, $\beta = 0.854$, $P = 1.000$, adjusted $R^2 = 0.122$).

explained by any of the chosen independent variables and the regression equations were not significant for all independent variables including fishing pressure ($F_{(1, 4)} = 0.474$, $\beta = 3.63$, $P = 1.000$, adjusted $R^2 = -0.118$) and lake surface area ($F_{(1, 4)} = 16.059$, $\beta = 0.195$, $P = 0.176$, adjusted $R^2 = 0.751$) (Figure 2.14EF). The variation of lake trout mean survival rates could not be explained by any of the chosen independent variables and the regression equations were not significant for all independent variables including fishing pressure ($F_{(1, 4)} = 2.298$, $\beta = 1.036$, $P = 1.000$, adjusted $R^2 = 0.206$), and latitude ($F_{(1, 4)} = 0.0371$, $\beta = 0.854$, $P = 1.000$, adjusted $R^2 = 0.122$) (Figure 2.15GH).

Sustainability reference points

The majority of the populations were deemed healthy populations (stage 1; Lester et al., 2021). All populations expressed low fishing mortality rates based on all Z/M ratios < 2 (Figure 2.15). Based on the $B/B_{MSY} > 1.0$ and Z/M ratio < 2.0, CW, GL, and SCL lake trout populations appear to be the healthiest populations (Figure 2.15). The aforementioned populations are deemed to experience low fishing mortality as well as high lake trout biomass levels. The three remaining southern lakes (HL, ML, and SCL) lie very close to the $B/B_{MSY} > 1.0$ threshold. This indicates that the estimated lake trout biomass densities of HL, ML, and SCL are very close to the biomass density when a population is exploited at the maximum sustainable yield level. These populations can be designated to be in a transitory state between being a healthy population (stage 1) and an overfished and recovering population (stage 4; Lester et al., 2021; Figure 2.15).

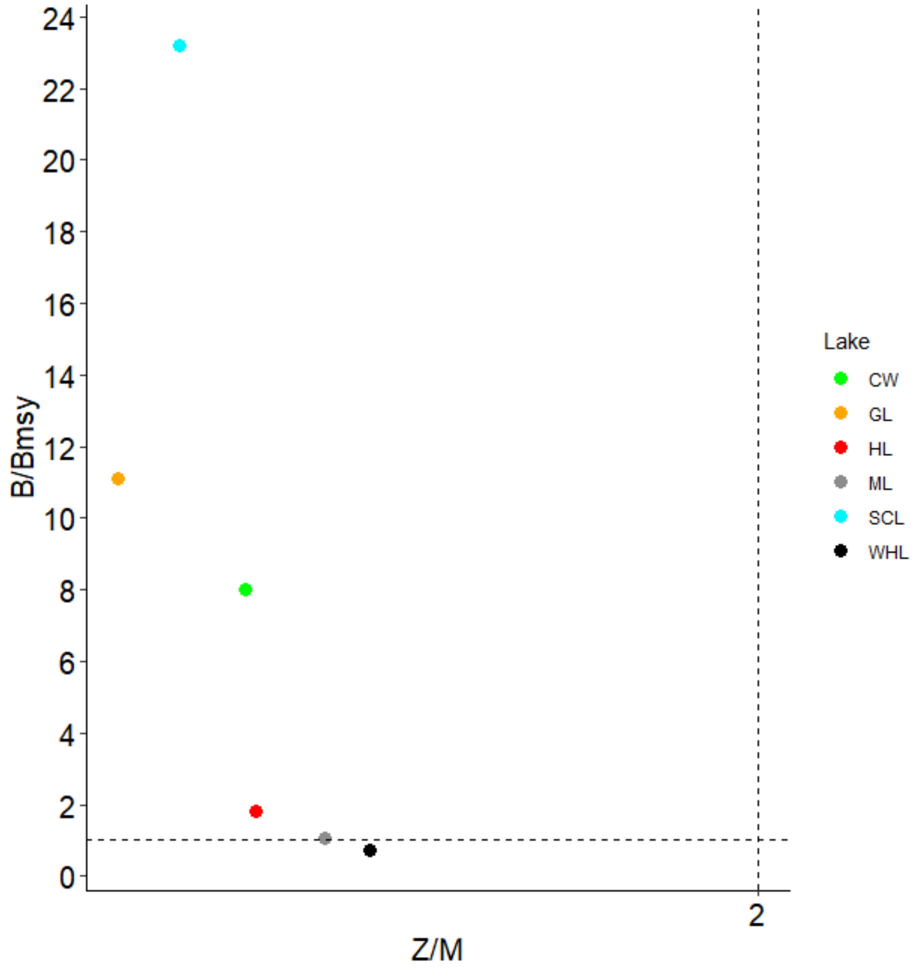

Figure 2.15. Implementation of mortality and biomass reference points for lake trout (*Salvelinus namaycush*) populations designed by Lester et al. (2021). Clearwater Lake (CW), George Lake (GL), High Lake (HL), Mantario Lake (ML), and Second Cranberry Lake (SCL) are considered stage 1 (healthy). West Hawk Lake (WHL) is considered stage 4 (overfished, and recovering).

Discussion

While I predicted that northern populations would have older lake trout than their southern counterparts, due to survival trends (Hansen et al., 2021), my survival results do not show a consistent trend based on my linear regression using latitude and fishing pressure as predictor variables. However, due to a small sample size (i.e., lakes as sampling units), it was hard to detect statistical differences. By analyzing individual fish in lakes, SCL lake trout were significantly older than fish from any of the southern populations; however, the other northern population, CW, was not. Furthermore, SCL had the lowest mortality rate, highest A_{50} and L_{50} estimates of all sample populations. These results are consistent with the life-history pattern of lake trout across its geographical range, where deeper lakes were associated with lake trout reach maturity at older ages and longer lengths (McDermid et al., 2010). Rather, CW had the youngest mean age of all sampled populations. This was also consistent with the A_{50} estimates, whereby CW had significantly earlier maturing individuals than GL and SCL populations. This suggests that CW's lake characteristics might be the most optimal for early life-stage lake trout growth and maturity relative to the other sampled lakes despite being in a northern latitude, which receives less solar radiation. The early maturation schedule for CW may indicate a potential adaptation to higher levels of recreational fishing pressure; however, the GL L_{50} values are significantly lower than CW, despite experiencing lower fishing pressure, therefore this is unlikely.

An identical pattern exists for growth rate, whereby southern populations do not necessarily grow faster than northern populations. I had predicted that southern populations would express faster growth rate than the northern populations, because northern latitudes are associated with colder water temperatures and shorter growth seasons than southern latitudes However, based on my linear regressions and growth rate analyses, my results indicate that it is case-specific. Though SCL had the slowest growth of all sampled populations, CW lake trout grew significantly faster than southern populations. This difference is interesting because both northern populations seem to have two different life-history strategies, whereby SCL lake trout growth slow, but attain a greater size based on L_∞, while CW lake trout grow fast relative based on t_0, K, and *w* parameters and reach a smaller L_∞. This difference in life history strategy is also reflected in the maturity schedules. CW and SCL have statistically significantly different L_{50} and A_{50} results, whereby the CW population reached maturity at a younger age and length than the SCL population. One explanation for this growth disparity is lake turbidity and light intensity. Light intensity can influence foraging efficiency and thus food consumption. Although Secchi depth was not recorded for this project, it is well known that CW is a very clear lake. This would theoretically aid lake trout finding prey compared to the other lakes sampled, which were more turbid throughout the summer months. This has been shown to be the case with lake trout, where their reaction distance to prey declined as light intensity declined as well in laboratory settings (Vogel and Beauchamp, 1999). This has also been examined in winter months, where low-light conditions limited lake trout spatial distribution, and increase foraging costs (Blanchfield et al., 2009). Despite these differences, both northern lakes are able to house large lake trout in contrast to the small southern lakes.

What factors create trophy-sized lake trout?

One of my main predictions was that the northern populations would have bigger lake trout, and it is supported by the results. Both CW and SCL had the highest mean length and weight values across all populations, yet only SCL mean length was significantly different from the southern populations. Furthermore, L_∞ values indicated that SCL was the only northern population to reach a significantly higher L_∞ than the southern populations. Despite this, both

CW and SCL were the only lakes in which trophy-sized lake trout (>89 cm) were captured. Lake size and depth may be factors that lead to trophy-sized lake trout. CW and SCL were the biggest lakes in respect to surface area, and both lakes had deeper depths than most of the other lakes. These conditions are conducive to more complex prey communities, thus providing lake trout more diverse food sources (Chavarie et al., 2021). SCL was the only lake in which we caught cisco (*Coregonus artedi*), a food source valuable for lake trout growth (Martin and Olver, 1980). This might be a reason why despite CW being 10x bigger in surface area compared to SCL, SCL lake trout are significantly longer in length and significantly heavier in weight than CW lake trout. However, it is important to recognize that cisco are a pelagic fish, thus SPIN gillnets are not an appropriate gear type for cisco because they are they are of the sinking gillnet variant. Furthermore, SPIN gillnet surveys are not designed to examine prey communities, thus I cannot comment further on this. However, my linear regressions did not detect a significant trend between lake trout total length and lake surface area. Again, the sample size is small, therefore it is unclear if a trend does or does not exist. The fact that I did not catch a single trophy-sized lake trout in the southern lakes is consistent with geographical trends, where smaller and shallower lakes would reach maturity at smaller lengths and reach smaller asymptotic lengths than larger northern lakes (McDermid et al., 2010).

Another factor potentially influencing whether lake trout can attain trophy-size status can be shorter summers above the 54th parallel. In theory, the onset of lake stratification in northern lakes should be delayed compared to the southern lakes located between the 49th and 50th parallels due to less solar radiation to heat up the lakes. Furthermore, lake stratification should not last as long as the south due to the onset of colder temperatures earlier. This creates a wider growth window for CW and SCL lake trout as they inhabit waters that are closer to their thermal preference of 5–15°C (Blanchfield et al., 2009). While Secchi depth was not recorded, the aforementioned low turbid conditions may have promoted higher feeding rates in CW. All these factors probably play a role to some degree in promoting large lake trout. While the comparisons between northern and southern Manitoban lakes are important for fisheries managers, using geographical average life-history metrics of lake trout as a point of reference in deciding the population status is essential for the long-term sustainability of Manitoban lake trout fisheries.

Geographical Comparisons

In 2021, 462 lake trout population life-history metrics were compiled and evaluated across the entire native and non-native range for lake trout in order to identify large-scale trends and geographical averages (Hansen et al., 2021). Roughly 50% of the quantified lakes lied between the 46th and 54th parallel. This range includes all of my study lakes and should provide a good fundamental basis to determine where the sampled lake trout populations lie across many life-history metric distributions. However, it is important to note that I cannot attribute my findings to latitudinal differences due to only sampling seven lakes. Across 448 sampled lake trout populations, the average surface area was 5.73 km^2 (Hansen et al., 2021). CW, GL, HL, SCL, WHL are all above average sized lakes, with CW surpassing the 75th percentile threshold. Across 348 sampled lake trout populations, the average max depth was 43m (Hansen et al., 2021). All lakes except HL, and ML, had higher max depths, while WHL surpassed the 75th percentile threshold. Across 270 sampled lake trout populations, the average total length was 475mm (Hansen et al., 2021). Omitting DL, all sampled lakes surpassed the average length. Only SCL surpassed the 75% percentile mark of 544mm. Across 248 sampled lake trout populations, the average annual mortality was 0.205 (Hansen et al., 2021). All sampled lakes were below this threshold value. Furthermore, GL and SCL are in the bottom 25th percentile of average annual mortality for lake trout lakes, which makes sense, because these lakes housed the oldest fish in my dataset. Across 204 sampled lake trout populations, the average A_{50} was 8.00 (Hansen et al., 2021). SCL was the only lake to mature later than the average, while CW's mean A_{50} value of 5.405 is in the bottom 25% percentile. This furthers my theory that CW's lake characteristics and prey communities positively benefit lake trout growth and maturity. A_{50} estimates were positively related to both lake size and latitude (Hansen et al., 2021). Across 203 sampled lake trout populations, the average L_{50} was 420mm (Hansen et al., 2021). CW and SCL had above average L_{50} values, while GL had a below average L_{50}. SCL is situated in the top 75th percentile, therefore indicating it is a particularly slow maturing population.

VBGF parameters were also assessed by Hansen et al. (2021). Across 293 sampled lake trout populations, the average L_∞ was 717mm (Hansen et al., 2021). Only HL and SCL had higher than average L_∞ values than the geographic average. L_∞ values have been reported to be positively related to lake size (Shuter et al., 1998; Hansen et al., 2021). Although anecdotal, after my first six two-hour gillnet sets on CW, I changed the soak times down to 30 minutes due to high bycatch mortality, and to the request of the provincial government. Once this change was made, very few trophy-sized lake trout were caught in the nets compared to my first few sets. It appears the two-hour sets were more conducive to catching the bigger lake trout, which were always near lake whitefish in the net. This observation has been seen in other studies as well (see Rawson, 1961; Sellers et al., 1998). It is my belief that the mean L_∞ value of 639.283mm in CW is underestimated to due this sampling design. This can potentially be extrapolated to SCL as well; However I did not set any two-hour nets there, and cannot be as confident with this lake. Across 45 sampled lake trout populations, the average t_0 was -0.95 (Hansen et al., 2021). Only CW, ML, and WHL had higher t_0 scores than the average. Across 264 sampled lake trout populations, the average K was 0.130 (Hansen et al., 2021). CW, GL, ML, and WHL had above average K values in respect to the geographic average, while SCL's K value was in the bottom 25th percentile. CW was the only lake to exceed the 75th percentile in respect to the geographic average. Across 264 sampled lake trout populations, the average *w* was 89 mm/year (Hansen et al., 2021). CW, HL, ML, and WHL all had higher early growth rates than the average, while CW surpassed the 75th percentile threshold of 107 mm/year. *W* has been reported to be negatively correlated with latitude (Hansen et al., 2021), while being positively related with total dissolved solids (TDS), therefore implying higher productive lakes boost *w* levels (Shuter et al., 1998). While some of the Manitoban lakes examined were above or below average in different metrics, their mean relative weight scores indicate a singular trend.

The relative weight body conditions scores across all examined Manitoban lakes suggest slimmer lake trout in comparison to the 75th percentile benchmark across its geographical range. Despite this, all sampled lakes throughout this study had relative weight scores that the 50th percentile. From this metric alone, Manitoba's lake trout appear to be in better condition than 50% of individuals across its geographical range. Haberle et al. (2023) used an energetics model to better understand the relationship between individual fitness and stock status and found a negative correlation between individual fitness and stock status. Furthermore, as fishing mortality increases and reduces the population size, that would lead to an increase in individual body condition due to lower competition for limited food resources (Haberle et al., 2023). Curiously, while HL, ML, and WHL had low lake trout CPUE values, they did not benefit from depensatory effects of lower population sizes. Rather, ML's relative weight score was significantly lower than CW's score. This may indicate that lake trout hailing from these southern lakes may not be well suited for these lakes at this point in time. These inconsistencies with Haberle et al. (2023)'s research are concerning and warrants further research to better understand its stock status. In the cases of the CW, GL and SCL lake trout fisheries, the high relative CPUE and higher than the 50th percentile relative weight scores suggest a healthy population that can sustain the current fishing pressures. All of these findings are essential for Fisheries Manitoba to self-evaluate their past, current, and future management plans.

Otolith aging and precision

Lake trout otoliths are known to be difficult to age, especially older individuals (Osborne et al., 2022). Furthermore, there have been few known-age fish analysis studies conducted for lake trout (see Campana et al., 2008; Osborne et al., 2022). Consequently, because this study does not involve lake trout of known age, our age estimations cannot be validated. This can potentially obscure certain age classes that may be underrepresented due to the potential of aging error (Beamish and McFarlane, 1983). Furthermore, it can overestimate mortality and production of a fish stock, which hinders the ability fisheries managers to prevent overfishing (Burnham-Curtis and Bronte, 1996). Older lake trout are especially difficult to age due to the otolith annuli being very narrow and condensed (Campana et al., 2008). This is the result of lake trout reaching maturity, therefore lowering subsequent annual growth rates and creating the pattern of condensed annuli (Campana, 2001). Osborne et al. (2022) identified three otolith characteristics that are commonly responsible for aging errors: 1) difficulty identifying the first annulus, 2) incomplete annuli that resemble true annual growth marks, and 3) annuli near the distal edge of otoliths belonging to older lake trout. All three common error sources were reported by the two observers. This may have contributed to a systemic bias in observer #2, who generally aged lake trout slightly older than observer #1. Furthermore, this bias was not driven by a particular age class. Despite this, all ACV% metrics calculated for this study are below the general precision threshold of 7.6% (Campana, 2001). This value is species specific due to the varying age lifespans and species-specific otolith reading challenges (Campana, 2001).

Precision of age estimations in this study were both higher and lower compared to other lake trout studies that conducted aging studies in the past. An age-estimation comparison study in Great Bear Lake revealed individual observer ACV% scores ranging from 2.6 – 7.9%, and ACV% score between observers ranged from 3.3% –7.5% (Gallagher et al., 2021). Another age comparison study examining hatchery-origin lake trout from Lake Ontario, and ACV% scores between observers ranged from 7.9% – 9.2% (Osborne et al., 2022). While not many papers have disclosed their ACV% scores, despite the two observers having less experience than the observers from other studies. The precisions metrics within this study fall in line with the current published literature. Precise and accurate aging is fundamental in ensuring the validity of growth and survival rates, thus allowing effective management actions to be enacted.

In relation to lakes in similar latitudes, the average ages of the examined lake trout populations in this study are generally younger. Hansen et al. (2012) estimated the average age of lake trout located at Lake Mistassini, Quebec (50° 25” N) to be 27 years and 21 years for humper and lean ecotypes, respectively. Four lake trout ecotypes – lean, humper, redfin, and siscowet, were examined in Lake Huron, Ontario (49° 92” N), who’s average ages were estimated to be 13, 17, 20 and 19 (Hansen et al., 2016). Moshenko and Gillman (1983) surveyed Great Slave Lake, Northwest Territories (61° 45” N), and estimated lake trout mean age to be 17 years old. Only SCL’s lake trout population is older than some of the aforementioned populations, despite them being much larger than SCL.

It is also important to recognize that several back-calculation models exist. I used the oldest back-calculation model, the Dahl-Lea model, which assumes that there is a direct proportional relationship between fish length and otolith length growth rates (Dahl, 1907; Lea, 1910). Despite its simplicity, not every species may display such relationship, therefore a different model that accounts for the disproportional growth of fish length and otolith length is required. The Fraser-Lee equation was created for such purpose by adjusting the equation for that grow faster than their calcified structures (Fraser, 1916; Lee, 1920). After examining the lake trout and otolith length relationship for my dataset, lake trout total length does grow at a faster rate than otolith length. Due to the assumption of proportional growth being violated, the Fraser-Lea model appears to be better suited for my dataset. Another factor that influences the shape of growth trajectories is the error in age estimates. Aging error between observers was noted to increase as lake trout were estimated to be older. To alleviate this problem, one way is to remove some of the individuals where error was highest or to only keep the back calculation annuli that we are certain are correct. I decided not to incorporate this approach, because I did not want to reduce the already small sample sizes I had from some of our lakes.

Implications for fisheries management

In 2023, Manitoba angling regulations changed. A major change was a shift from region-based seasons to species-specific seasons (MBGOV, 2022; MBGOV, 2023). Furthermore, Fisheries Manitoba combined their conservation angler license and regular license into a singular angler license. Fisheries Manitoba had also instilled stricter harvest limits for many species including lake trout, in which anglers were previously allowed to keep two fish as a daily limit with one of them allowed to be kept above 65cm (this was not the case with the Northwest division where CW and SCL reside). Now anglers are only allowed to keep a single lake trout and anglers can only keep lake trout below the 65cm threshold (MBGOV, 2023).

Based on the estimated life-history characteristics of the sampled lakes, each lake has unique properties that can use tailored management strategies. Despite both residing in the north and only ~55 km away from each other, CW and SCL have two contrasting lake trout populations. SCL appears to be a slow growing and slow maturing population based on several metrics including above average geographic average L_{50}, and A_{50}, and below average K values. In contrast, CW appears to be a fast growing and maturing population based on similar metrics including a below average A_{50}, and above average w values. Their average ages were complete opposites when comparing them to the remainder of Manitoban lakes assessed for this study, whereby CW had the lowest average age of 9.076, while SCL had the highest average age of 18.043. While only two lakes, this comparison highlights the potential for high variability of lake trout life-history characteristics in northern Manitoba, thus lake specific angling regulations can be implemented. Manitoba does not employ minimum length for allowable lengths for harvesting. As a result, the onus is on the angler to decide whether they believe a lake trout they caught is a juvenile or not when deciding to release or keep a lake trout. However, a one size fits all approach may be ill-advised, because of the huge range of the maturity and growth schedules for my two examined lakes. Since SCL is the slowest growing and maturing population sampled for this study, an A_{50} value of 9.599 and an L_{50} value of 553.689 suggest that a slot-size limit between 55-64cm would be beneficial to protect this population. While the high survival rate of 88.325% suggests that the population is not overharvested (Healey, 1978), allowing anglers to dictate whether keeping a fish below 55cm when the data suggests that most individuals are not mature is not recommended. Based on Lester et al. (2021)'s sustainability model, SCL is well placed in the stage 1 zone of their sustainability model. With an estimated biomass density well above the estimated B_{MSY} threshold and well below the Z/M fishing mortality threshold, this population should be deemed a healthy population.

CW can use a different management approach. Based on CW lake trout life-history traits, it appears that the population is a fast growing and maturing population. With an A_{50} of 5.4 years, and an L_{50} of 449.6 mm, a slot-size limit between 45–64 cm is ideal. Furthermore, CW also exhibits very similar traits as SCL under the Lester et al. (2021) sustainability model. CW is also a healthy population whose estimate biomass is considerably higher than the minimum threshold to attain such designation. Considering that the fishing mortality rate is low, it is conceivable that this population is still suitable to maintain a higher harvesting intensity (i.e., daily bag limit of two) than the status quo because I sampled before the new regulations were implemented, therefore the population should exhibit patterns resulting from past management actions. With that said, CW receives a much higher volume of angler traffic than SCL (Kitch, personal communication), but because CW is a bigger lake, that might offset the increased fishing pressure. However, it is very important to recognize that during the summer months, based on CW's bathymetry, there are only two main spots that anglers as well as outfitters choose to target lake trout, because it is presumed that this is where many lake trout find refuge from warmer waters. This type of information could prove detrimental to the population if more anglers choose to target these locations in the future (Brownescombe et al., 2014).

CW has another interesting trait, and that is the potential for sympatric ecotypes. Based on Figure A2.1, there appears to be a split in growth trajectories. Lake trout ecotypes have been observed in several lakes across its geographical range including the Laurentian Great Lakes that can vary in physical appearance, life-history strategies, and genetics (Chavarie et al., 2021). Ecotypes are non-random sub-groups of a population that exist due to the opportunistic nature of individuals in a heterogenous environment, and ultimately develop unique traits (Lowry, 2012). The most common lake trout ecotype is the 'lean' lake trout; however, other ecotypes such as the 'humper', 'redfin' and 'siscowet' exist across its native range (Chavarie et al., 2021). Depth has been considered to be the main driver of this early stage of speciation (Marin et al., 2016; Chavarie et al., 2021). Moreover, growth rate differences have been identified as a key difference among lake trout ecotypes in Lake Mistassini, Quebec (Marin et al., 2016). The discovery of a slow-growing lake trout morph has significant implications surrounding the recreational fishery on CW. If this slow-growing ecotype is the main source for trophy-sized lake trout, then it has and will continue to be selectively targeted by anglers. Fisheries Manitoba already enforces a mandatory release of any lake trout above 65 cm, therefore the only other avenue to maintain these large fish is to increase awareness on proper fish handling and release methods. While it is feasible that sympatric lake trout exist in CW, further studies should investigate this potential phenomenon due to the underlying ramifications surrounding ecological, and economical areas of interest.

Based on the limited lakes I sampled, the southern lake trout fisheries appear to have a different problem – low lake trout numbers. Of the 5 lake trout lakes sampled in the southern region of Manitoba, only GL exceeded a CPUE value of 1.00, in which GL had the second highest value across all lakes with 2.91. GL has the second largest mean age score from my sampled lakes, below average A_{50} of 6.696 years and L_{50} of 386 mm, and an above average survival rate with respect to the geographic average. Of the sampled southern lakes, GL appears to be the best condition. What probably aids this population maintain a low mortality rate is the fact that GL is not accessible by road, and anglers must cross the Winnipeg River and walk 2 km to reach the lake. This is supported by GL's healthy designation by the Lester et al. (2021)

sustainability model. These barriers have conceivably contributed to potential lower fishing pressure compared to more readily accessible lakes like West Hawk Lake and High Lake, which appear to be in worse shape. Based on the general pattern of southern lakes being in bad shape, this lake should not deviate from the single lake trout daily bag limit. Furthermore, a minimum harvest length of between 40-45 cm is recommended, while the maximum should be reduced to 60 cm since those fish appear to be much older, and most likely very fecund.

WHL appears to be a case of an unproductive lake and potential historical overfishing. Across all sampled lakes, WHL had the lowest CPUE values for all other fish, and second lowest for lake trout. With that said, WHL has had an extensive stocking history, with lake trout and being both stocked as early as the 1930s (MBGOV, 2021c). According to Butler (1950), summer lake trout fishing was great for anglers. However, that does not appear to be the case anymore. Only catching 12 lake trout in 49 gillnets, and spending many hours angling to yield a single lake trout, WHL lake trout population appears to be impoverished. This population was classified as a stage 4 population that experienced overfishing and is now recovering based on the Lester et al. (2021) sustainability model. Taking into account of the low estimated biomass and past fishing pressure trends (Butler, 1950), this lake is no longer a lake trout fishing destination and may never be able to recover if current management practices (year-round fishing regulations in stocked trout lakes; MBGOV, 2023) persist.

HL, residing just south of WHL, appears to be in a slightly better state than WHL. While this lake was classified as a stage 1 (healthy) lake (Lester et al., 2021), it is very close to the biomass density threshold. This indicates that HL's lake trout population is in a transitory state between being a stage 1 and stage 4 lake. This mean that the population is experiencing low fishing mortality, with a biomass that can only just support maximum sustainable yield harvest rates (if they are met). HL's lake trout CPUE was estimated to be 0.557. As a result, HL might have been overfished in the past, thus explaining the low lake trout numbers as it is a small lake that has an outfitter operating on it. Unfortunately, without quantitative angling pressure data, I cannot comment further on this. Another reason exists that may be working synergetically to preventing lake trout recruitment. Carl and McGuiness (2006) have suggested that coregonines might be competing with juvenile lake trout or even predating on them at the larval and/or egg stages. Furthermore, lake whitefish might be imposing a survival bottleneck on the early life-stages of lake trout based on the CPUE values of juvenile and adult lake trout in lakes situated in the Algonquin Highlands of Ontario (Carl, 2008). If adult lake trout are in fact being selectively targeted and harvested in High Lake, then the trend of high lake whitefish numbers may be the result of a trophic cascade due to the inability of lake trout to regulate lake whitefish (Trippel and Beamish, 1993). In that case, it might be difficult for a depleted population of lake trout to recover when there is a large lake whitefish population present (Carl, 2008). Another curious finding was the presence of pelagic pike (50-60ft). This observation has also been seen throughout Ontario, whereby northern pike CPUE and life-history characteristics varied in response to off-shore prey abundances (Kennedy et al., 2018). This pattern suggests that pike can express generalistic foraging behaviours that extend to offshore prey communities (Kennedy et al., 2018), and may be influenced by low lake trout numbers allowing high lake whitefish concentrations. It is my recommendation that HL becomes a strict catch-and-release only lake, until further research and data is available to better understand the underlying ecological mechanisms dictating lake trout population dynamics.

The case of Davidson Lake is extremely concerning because it appears that there are virtually no lake trout left despite Fisheries Manitoba stocking lake trout in 2017. It has already been observed that competition with coregonids have potentially played a significant role is preventing stocking success of lake trout (Powell et al., 1986; Gunn et al., 1987). We caught large amounts of lake whitefish that had the highest average length across all sampled lakes. Lake whitefish might be preventing lake trout from persisting in the lake through competition of resources (Carl, 2008). It is my recommendation that stocking efforts cease, as this lake does not appear suitable for lake trout.

Mantario Lake is an interesting case study due to its location. Nested deep in Manitoba's non-motorized zone, the only ways to reach it by either portaging or float plane. There is a communal cabin that is run by a Nature conservation NGO and is the main source of human presence. It is therefore assumed, based on Fisheries Manitoba's information, that fishing pressure on this lake is close to zero. Prior to gillnetting in 2022, ML was stocked with lake trout fingerlings and juveniles 10 separate times between 1950 and 1975 (MBGOV, 2021c). Despite this, ML also appears to be in a transitory state between stage 1 and 4 (low fishing mortality and a biomass density that is just enough to withstand maximum sustainable yield harvest rates). If this lake is not productive and is not receiving much angling pressure, why is the biomass density not higher? Past gillnetting surveys were conducted by the province in 1993 and lake trout biomass and CPUE were considered adequate, whereby they accounted for 24% of the captured biomass in 1993 (Robert, 1994). Moreover, the mean length (529mm) recorded in 1993 was very consistent with our results (Robert, 1994). However, the mean weight dropped from 1636g in 1993 to 1143g in 2022 indicating a sizable shift in population weight (Robert, 1994), as well as a decline in body condition. Furthermore, the average age decreased from 14.540 in 1993 to 11.724 in 2022 (Robert, 1994). The conclusions from the report indicated that lake trout were infected with a parasite named *Traenopherous* (Robert, 1994), but that was not observed in our sampling. Furthermore, the lack of 8-year-old or younger fish and a lack of 45cm or smaller lake trout was brought up as a concern for diminished spawning success (Robert, 1994). These reasons may indicate why the CPUE and biomass values we low for ML, and that we had to resort to angling practices to supplement our samples. Pelagic pike were again observed in this lake when angling, thus suggesting low lake trout numbers in pelagic zones, allowing pike to be more opportunistic exactly like the pike in HL. Lastly, Robert (1994) indicated that Eastern Manitoban lakes are not well suited to house lake trout populations and low levels fishing pressure may be enough to disturb lake trout populations. It appears that the unsuitable waters, the presumed parasitic infection, and lack of spawning success has decreased the viability of this population.

Conclusion

Manitoba boasts many recreational lake trout fisheries with unique properties and should be managed accordingly. While both CW and SCL can generate trophy-sized lake trout, it takes significantly longer time for SCL lake trout to attain such lengths. Consequently, while current management regulations are homogenous, lake-specific regulations might be more effective if management wants to pursue this route. Furthermore, it is erroneous to assume all northern populations are inherently older than southern populations. Based on my aging data, southern lake trout individuals can survive for many years. Lastly, most southern populations do appear to be stressed based on the sustainability model (Lester et al., 2021). While current daily bag limits are reduced to one (MBGOV, 2023), further regulations may be required.

Chapter 3: Can otolith morphology analysis be a tool to identify different lake trout populations and ecotypes?

Abstract

Lake trout *(Salvelinus namaycush)* have been observed to have different ecotypes that exhibit different life-history traits and behaviours, have different genetic makeups, and live in different areas within a lacustrine environment. Otolith morphological studies have shown promise in their potential to identify different fish stocks. Otolith morphology is dually regulated by environmental and genetic factors; therefore, it is possible that otolith differences can be detected between different lake trout ecotypes. To test this, several multivariate analyses were conducted to examine whether multiple isolated lake trout populations in Manitoba would be separated by otolith shape. Furthermore, Clearwater Lake, which has been suspected to have sympatric ecotypes based on growth rate data, was also examined to identify potential clusters of individuals. Results showed moderate success in separating lake trout hailing from different lakes based on otolith morphological descriptors. Additionally, a multivariate Kruskal-Wallis test revealed significant otolith morphological differences between suspected lake trout ecotypes within a lake. However, it is not possible to ascertain that otolith morphological differences are a result of different ecotypes or differing growth rates. Future studies should conduct both morphological and genetic analyses to clearly identify lake trout ecotypes.

Introduction

Lake trout (*Salvelinus namaycush*) is a cold-water salmonid that lives almost exclusively in oligotrophic lacustrine environments in northern North America (Riley et al., 2021). Its native geographic range was largely influenced by the Pleistocene glaciations (Lindsey, 1964), whereby dissolved oxygen, lake depth, nutrient content, and water temperature are key environmental factors governing lake trout distribution (Muir et al., 2021). Lake trout ecotypes are common. Ecotypes are non-random sub-groups of a population that exist due to trait adaptations to heterogenous environmental factors (Lowry, 2012). Within lake trout, ecotypes often exist sympatrically within a waterbody and are distinguishable based on an array of biological factors (Chavarie et al., 2021).

Lake trout ecotypes vary in physical appearance, life-history strategies, and genetics (Chavarie et al., 2021). The most common lake trout ecotype is the 'lean' lake trout; however, other ecotypes such as the 'humper', 'redfin' and 'siscowet' exist across its native range (Chavarie et al., 2021). Depth has been identified as the main factor driving niche differentiation between sympatric ecotypes: lean lake trout are typically found in < 50m depths; 'humper' lake trout are found between 50–100m; and, 'siscowet' lake trout often reside in > 100m depths (Chavarie et al., 2021). As a result, lake trout morphology, diet, and ultimately, growth rates are also different between ecotypes (Eshenroder, 2008; Zimmerman et al., 2009; Chavarie et al., 2021). For example, 'humper' lake trout, who have a smaller head and larger eyes than 'lean' lake trout (Chavarie et al., 2021), have been observed to predate on macroinvertebrates more often than 'lean' lake trout (Hansen et al., 2012). Growth rate differences between 'lean' and 'humper' lake trout ecotypes in Lake Mistassini, Quebec were observed and attributed the differences to a more insect-centered diet for 'humper' lake trout in comparison to the piscivorous 'lean' lake trout diet (Hansen et al., 2012). Despite these ecotype differences, low genetic differentiation has been reported in several studies (Chavarie et al., 2016; Marin et al., 2016). However, lake trout genomic studies are relatively new, and methods are not refined, thus the probability of low genetic differentiation is plausible (Chavarie et al., 2021). Nevertheless, ecotype differences may be also observed in other contexts such as otolith shape. For example, otolith morphologies within a lake could provide a unique method for lake trout ecotype identification.

Otoliths are paired earstones that aid fish with balance and hearing (Campana et al., 1999). They are primarily composed of calcium carbonate in the form of aragonite (Degens et al., 1968). There are three pairs of otoliths, asteriscii, lapilli, and the largest, the sagittal otoliths (Campana et al., 1999). Sagittal otoliths have been used to age fish due to otoliths being metabolically inert and resorption rarely occurs (Mugiya and Uchimura, 1989). While many researchers are primarily interested about the inside of otoliths for aging purposes or for stable isotope analysis, morphology of the whole otolith may be an indicator to distinguish ecotypes.

Stock discrimination *via* examination of otolith morphology has occurred since the late 20th century (Casselman, 1981). Its application has been used for both inter- and intra-specific comparisons of species (see De la Cruz-Aguero et al., 2012; Stransky et al., 2008; Jónsdóttir et al., 2006). Sagittal otolith shape is unique for every species (L'Abee-Lund, 1988); however, intra-specific differences are observable across a species distribution (Casselman et al., 1981; Campana and Casselman, 1993; Khemiri et al., 2018). These differences in shape can be attributed to environmental variation (depth, temperature, prey), which are known to influence fish growth rate (Casselman et al., 1981; Campana and Casselman, 1993; Lombarte and Lleonhart, 1993). According to Campana and Casselman (1993), otolith morphology was highly correlated to fish growth rate. Atlantic cod (*Gadus morhua*) stocks with different growth rates could be successfully differentiated from each other by examining otolith morphology, through which otolith characteristics such as otolith area and perimeter differed significantly (Campana and Casselman, 1993). Similar results were observed in lake whitefish (*Coregonus clupeaformis*) stocks in Lake Huron, whereby unique stocks that had different levels of otolith ellipticity were identified only when their growth rate significantly differed from other potential stocks (Casselman et al., 1981). In addition to environment, there is also a genetic component that influences otolith shape (Cardinale et al., 2004). Cardinale et al. (2004) subjected two different anchovy stocks to similar environmental conditions and feeding conditions, and observed significant otolith morphological differences, whereby the finer details of the otolith shape were significantly different between stocks, therefore supporting the idea of genetics influencing intra-specific otolith morphology. It has also been noted that geographical distance between stocks has an influence on genetic differentiation and ultimately, otolith shape (Simoneau et al., 2000). Lake trout populations found within the same watershed only displayed subtle otolith shape changes, whereby the centroids (mathematical centre of the otolith) of the populations overlapped with each other (Simoneau et al., 2000). Alternatively, significant otolith length/height allometry otolith shape differences were observed between populations in different watersheds (Simoneau et al., 2000). Because lake trout ecotypes are exposed to different environmental conditions, and are somewhat genetically distinct from one another, otolith morphological analysis could be a worthwhile tool to identify suspected ecotypes within a lake.

Some population discrimination studies have also examined whether the shape of the otolith is related to genetics (Jónsdóttir et al., 2006; Libungan et al., 2015). For example, unique spawning groups of Atlantic Cod in northern and southern Iceland were identified based on otolith morphology (Jónsdóttir et al., 2006), which was congruent with a genetics study that indicated southern Atlantic Cod showed significant size, age, and genotype differences (Jónsdóttir et al., 2002). Similarly, significant shape differences between seven populations of Atlantic herring (*Clupea harengus*) were detected (Libungan et al., 2015), which were confirmed by prior genetic studies using microsatellite (McPherson et al., 2004) and mitochondrial DNA marker (Hauser et al., 2001) analyses. The consistency between shape analyses and genetic studies provides evidence that otolith morphological studies can be suitable in stock discrimination.

Otolith morphometric analysis has been mainly completed by examining the two-dimensional images of the otoliths (Afanasyev et al., 2017). While there are several different approaches to implement such analyses, the elliptical Fourier analysis is the most popular due to its flexibility and ability to fit any object shape (Bonhomme et al., 2014). Fourier analysis involves the comparison of otolith contours based on the summation of cosine and sine curves to generate an ellipse (i.e., harmonic), and consequently an estimation of the shape of the otolith (Kuhl and Giardina, 1982; Iwata and Ukai, 2002; Bonhomme et al., 2014). The result is a comprehensive reconstruction of the otolith contour by the summation of all the harmonics used to analyze the otolith (Afanasyev et al., 2017).

Freshwater fisheries management entities would benefit from knowing whether multiple ecotypes coexist within a lake, because high biodiversity increases an ecosystem's resilience and stability from stressors (Elton, 1958; Ives and Carpenter, 2007). There are no records of multiple lake trout ecotypes in Manitoba, Canada. It is assumed that the 'lean-like' ecotype is the only form of lake trout in the province. However, based on the von Bertalanffy growth curve findings from Navarroli et al. (Chapter 2, this thesis), biologists believe that there are potentially sympatric lake trout that exist in Clearwater Lake in northern Manitoba (Phillips, personal communication, 2023). Furthermore, lake trout originating from Clearwater Lake have been used as the brood stock for the provinces stocking efforts for decades (Butler, 1950; MBGOV, 2021c; Kroeker, pers. comm., 2021; Table A.3.1), therefore Clearwater Lake is debatably the most important lake trout lake in the province. It is assumed that lake trout from Clearwater Lake are the 'lean' piscivorous ecotype, but to my knowledge there is no information if that holds true for recipient lake trout populations when stocked. Consequently, it is important to know if multiple ecotypes exist within Clearwater Lake.

The aim of this chapter was to explore the potential of otolith morphological analysis on population discrimination of three lake trout lakes in Manitoba, in which two have been stocked from Clearwater Lake brood stock. This was done to determine whether otolith shape differences would be observed. I expected them to be different because these populations exist in different in environments and are at least somewhat genetically distinct based on past glaciation events coupled with their geographical distance from each other. Furthermore, my next objective was to examine a singular lake's otolith morphology distribution that is suspected to house multiple lake trout ecotypes to identify multiple clusters of individuals that may in turn be ecotypes. This would be the first study, to my knowledge, that would attempt to discern differences of potential sympatric lake trout ecotypes in Manitoba. Furthermore, this study would only be the second study to my knowledge using otolith morphological analysis methods on lake trout (see Simoneau et al., 2000). Ultimately, this study aimed to examine how stocking might impact otolith shape and consequently stock discrimination.

Methods

Study Areas

To collect lake trout otoliths, I sampled three lakes in Manitoba due to sample size limitations (Figure 3.1). The southeastern lake chosen was George Lake (GL) (50°13'N 95°29'W, surface area = 21.5 km^2, average depth = 12 m), while the northern lakes included Clearwater Lake (CW) (54°03'N 101°03'W, surface area = 285.07 km^2, average depth =13.10 m) and Second Cranberry Lake (SCL) (54°38'N 101°11'W, surface area = 23.83 km^2, average depth = 19.81 m). CW has been the site where provincial biologists have collected lake trout gametes for rearing and stocking purposes since 1943 (Dyck, personal communication, 2023). CW, GL, and SCL have been stocked with lake trout at varying intensities (30 times for CW, 34 times for GL, and two times for SCL) (see Appendix). All three lakes stratify during the summer and are subjected to varying degrees of recreational fishing pressure (Kroeker and Kitch, personal communication), but no commercial fishing operations exist on the study lakes. In terms of lake substrate, SCL is a mix of granite and other Pre-Cambrian formations in the northern half, while Paleozoic substrate such as limestone dominates the south (Butler, 1950; MBGOV, 2018). GL, which lies in the Whiteshell region of Manitoba, is also mainly Canadian Shield granite-based (Butler, 1950; MBGOV, 2018). Lastly, CW also resides in the Palaeozoic region, thus its substrate is more dolomite and limestone-based (Butler, 1950; MBGOV, 2018). All three lakes contain zooplankton and forage fish such as cisco (*Coregonus artedi*) based on my diet and gillnetting data, therefore classifying the study lakes as at least Class 2 lakes – lakes that present foraging opportunities in benthic and pelagic habitats (Rasmussen, 1990; Vander Zanden et al., 1999). *Mysis* shrimp were only present in one stomach of the collected lake trout in GL, therefore it is assumed that GL is a Class 3 lake, which further increases the trophic position due to a more complex food web (Rasmussen, 1990; Vander Zanden et al., 1999). GL was also the

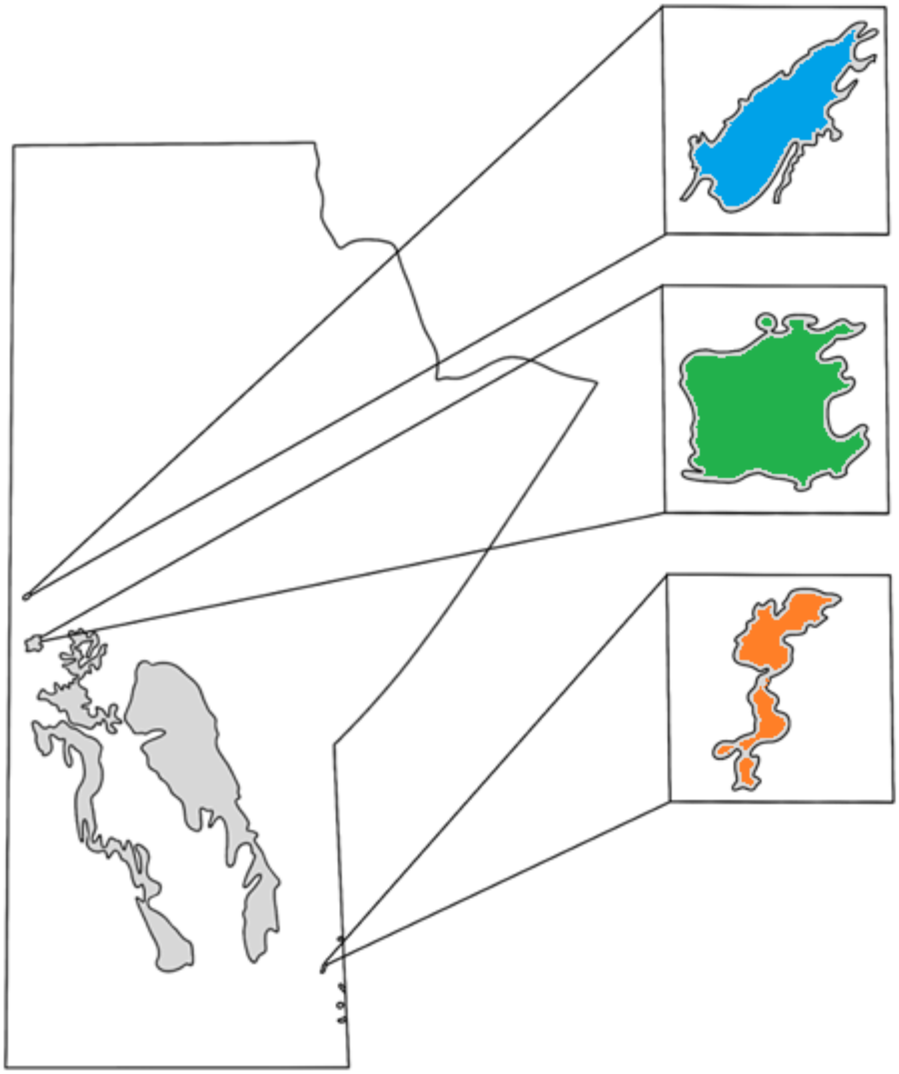

Figure 3.1. Map of sampled Manitoban lakes. Clearwater Lake (54°03'N 101°03'W, surface area = 285.07 km^2, average depth =13.10 m) [green], George Lake (50°13'N 95°29'W, surface area = 21.5 km^2, average depth = 12 m) [orange], and Second Cranberry Lake) (54°38'N 101°11'W, surface area = 23.83 km^2, average depth = 19.81 m) [blue].

only lake to contain invasive smallmouth bass (*Micropterus dolomieu*). SCL contained a population of walleye (*Sander vitreus*) and was the only lake where I caught cisco (*Coregonus artedi*). Lastly, CW was the only lake where lake trout were observed to predate on burbot (*Lota lota*).

Otolith Morphology Analyses

I removed the sagittal otoliths from lake trout caught using gillnet methods described in Chapter 2 of my thesis. The otoliths I collected were first cleaned with distilled water and inspected for damages such as chips and fractures. Otoliths with damage were omitted from the study. To limit the effect of potential confounding factors, the left sagittal otolith was selected for analysis. If the left otolith was not available, the right otolith was used and its image was mirrored to simulate a left otolith (Campana and Casselman, 1993). I placed otoliths on a black background sulcus side down with the rostrum pointing left under a stereo zoom microscope (Motic SMZ-171) with a built-in Moticam 1080BMH-U camera (Motic Instruments Inc.©, Richmond, British Columbia). Transmitted light was directed to the otolith at a high intensity to ensure that the SHAPE programs would register the edges of the otolith.

To analyze otolith morphology, I used the SHAPE package (Iwata and Ukai, 2002). The SHAPE package is a collection of programs designed to quantitatively evaluate the shapes of biological samples (Iwata and Ukai, 2002). It can determine the two-dimensional contour of an object through the use of harmonics, hereafter listed as Elliptic Fourier Descriptors (EFDs) (Kuhl and Giardina, 1982). EFDs are a series of sine and cosine waves used to describe the outline of a shape of interest through the stepwise creation of mathematical shape approximations (Kuhl and Giardina, 1982). This method has been tested and deemed successful for many otolith morphology comparisons (see Yu et al., 2014; Afanasyev et al., 2017; Khemiri et al., 2018). The first program, ‘ChainCoder’, converts the image of the otolith to a binary white and black composite and through edge detection, stores information about the contour of the otolith as chain code (Freeman, 1975; Iwata and Ukai, 2002). The second program, ‘Chc2Nef’, is used to convert the otolith chain code into normalized EFDs (Iwata and Ukai, 2002). The program recommends that the user analyses the shape of interest with 20 EFDs. Each subsequent EFD is more detailed than the last, thus generating a more accurate contour. Furthermore, each EFD contains four unique coefficients (A, B, C, D) that become normalized by using the first harmonic which is a simple ellipse, thus ensuring subsequent coefficients are invariant to size, rotation, and starting point (Figure 3.2; Kuhl and Giardina, 1982; Iwata and Ukai, 2002). ‘PrinComp’ is the final program in the SHAPE package and it carries out a principal component analysis (PCA) to reveal the variation within the normalized EFD (nEFD) coefficient data (Iwata and Ukai 2002). However, this study was conducted using R (Version 1.4.1717, R Core Team, 2023), therefore PrinComp was not entirely used. Rather, the only point at which I used this program was to extract the EFD coefficient data that is available in a text file. The text file data was then converted into an excel sheet for further analysis

Several studies have highlighted the potential confounding effects of several variables on otolith shape. Fish length, age, and maturity are potential covariates that may skew the results of discriminating different fish stocks due to allometric effects on otolith shape (Lombarte and Lleonhart, 1993; Simoneau et al., 2000; Galley et al., 2006). As a result, only mature fish were examined to account for allometric growth effects on otolith shape (Campana and Casselman, 1993; Cardinale et al., 2004). Sex effects have been previously shown to not impact otolith shape in lake trout (Simoneau et al., 2000), however I conducted a multivariate analysis to test this (see below). Due to my small sample size (CW = 61, GL = 48, SCL = 36), comparing specific ages or

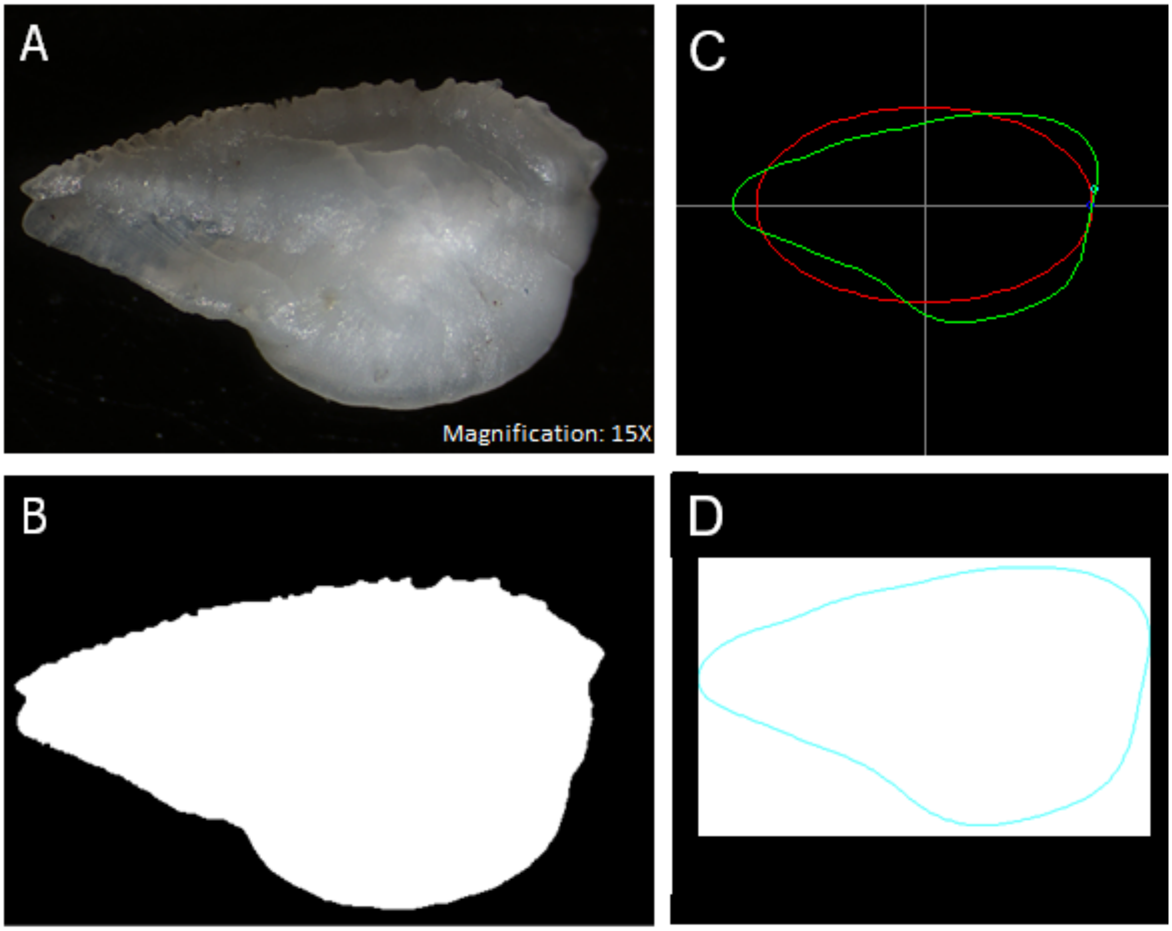

Figure 3.2. SHAPE flowchart from raw lake trout (*Salvelinus namaycush*) otolith to 2-D digitized contour. **A**: A photo of a left lake trout otolith. **B**: A white and black binarized version of photo A by the SHAPE program. **C**: 2-D otolith contour (green) (8th harmonic), which has been standardized to an ellipse (1st harmonic). **D**: The 8th harmonic of the digitized otolith.

ages ranges would reduce the statistical power associated with my study, and was not incorporated.

Statistical analysis

I first determined the appropriate number of nEFDs. Because I analyzed an initial 20 nEFDS, there were 80 coefficients to be analyzed. However, because the first EFD is used to normalize the remaining EFDs, I omitted the first EFD and its four coefficients from further analyses (Campana and Casselman, 1993; Iwata and Ukai, 2002; Lord et al., 2012). To determine the number of appropriate harmonics to analyze for the best reconstruction of the otolith shape, I used the Fourier Power (PF_n) equation:

$$PF_n = (A_n^2 + B_n^2 + C_n^2 + D_n^2)/2$$

, where A_n, B_n, C_n, and D_n are the nEFD coefficients to the *n*th nEFD (Crampton, 1995). From that, the cumulative Fourier power percentage (PF_c) was calculated:

$$PF_c = \sum_1^n PF_n\% = (\sum_1^n PF_n\%)^{-1} PF_n$$

. A threshold mean value of 99% cumulative Fourier power percentage was selected to determine the number of nEFDs required for this analysis (Crampton, 1995; Pavlov, 2016). To carry this out, I randomly selected a subset of 30 otoliths from the dataset. Once a threshold nEFD was identified, the remaining nEFDs were omitted from further analyses.

I then used a PCA to reduce the dimensionality of the dependent variables for all subsequent multivariate analyses. I removed univariate and multivariate extreme outliers to avoid bias in my statistical analyses by using the boxplot interquartile ranges and Mahalanobis distance procedures, respectively. Furthermore, to determine the appropriate number of principal components to keep for subsequent interpretation, I incorporated a broken stick model combined with a scree-plot (Jackson, 1993). I plotted PCA eigenvalues against the broken stick model to determine a sufficient number of principal components to use for subsequent multivariate analyses. Based on growth rate analyses also conducted in CW, there appears to be a split of individuals, whereby individuals greater than 650mm displayed elevated maximum sizes (Navarroli et al., Chapter 2, this thesis). This split in growth rates may be an indicator of different ecotypes, therefore lake trout were split into two groups based on their total length - >650mm or <650mm. Because my data did not conform to multivariate normality, I used a multivariate Kruskal-Wallis test (mKW) to identify potential otolith shape differences between sex, lakes, and suspected ecotypes in Clearwater Lake, respectively. This involved using the R package "*npmv*" to conduct a non-parametric analysis, while also providing a post-hoc test using a multiple algorithms procedure to identify significant pairwise combinations at the factor and dependent variable levels (Burchett et al., 2017). To account for multiple pairwise comparisons, I used Bonferroni adjusted *p*-values to ensure stronger statistical power (Burchett et al., 2017). Non-parametric relative effect sizes were also generated for each dependent variable (i.e., principal component) by the *npmv* package to display degree of differences between the independent variables (Burchett et al., 2017). I then used a secondary post hoc Linear Discriminant Analysis (LDA) to attempt to discriminate individuals from predefined groups (e.g., CW, GL, and SCL) into new groups by using the seven principal components identified by the broken stick model as the independent predictor variables (Cardinale et al., 2004). The predictor variables were all assessed concurrently. I used a jack-knife method as a cross-validation method, which omits a single individual, executes the LDA, reclassifies the omitted individual into one of the pre-defined groups and repeats this action for every individual (Curtis et al., 2014). This approach was also conducted ecotypes, however since there are only factors/independent variables, the two ecotype groups were only separated by a singular linear discriminant axis.

Results

Seven nEFDs (nEFD 2–9, 32 coefficients) were identified using the Fourier power spectrum analysis and described 99% of the otolith shape variation (Figure 3.3). The remaining nEFDs were omitted from further analyses. A PCA was conducted on the 32 remaining coefficients describing otolith shape, and seven principal components were identified by the broken stick model as the optimal number to explain variation (65.23% cumulative percentage of variance) (Figure 3.4). Sex across all lakes did not significantly alter otolith morphology ($F_{6.205, 847.193} = 1.065$, $P = 0.381$). Nor did sex significantly impact otolith shape in CW ($F_{5.676, 307.717} = 1.854$, $P = 0.087$). Therefore, because I cannot reject the null hypothesis that sexes altered otolith morphology, I can pool both male and female otoliths together for the remainder of my analyses across lakes. Significant otolith morphological differences existed across the principal components associated with CW, GL, and SCL ($F_{12.073, 816.806} = 2.813$, $P = 0.001$). The first two linear discriminant axes described 60% and 40% of the otolith morphology variation across lakes, respectively. The multiple algorithm post-hoc test identified that the pairwise combinations of CW-GL and GL-SCL were the primary contributors of significance in the mKW. Furthermore, the combination of principal components 2, 3, 4 and 6 were the primary drivers of otolith shape differences across Manitoban lakes. The principal component effect sizes indicate a medium degree of separation (Table 3.1). These differences were also supported by the post-hoc LDA, whereby the otoliths were successfully discriminated with an overall cross-validated classification of 55.86%. Additionally, the LDA correctly classified 78.6% of Clearwater otoliths, 54.17% of GL otoliths, and 19.44% of Second Cranberry otoliths (Table

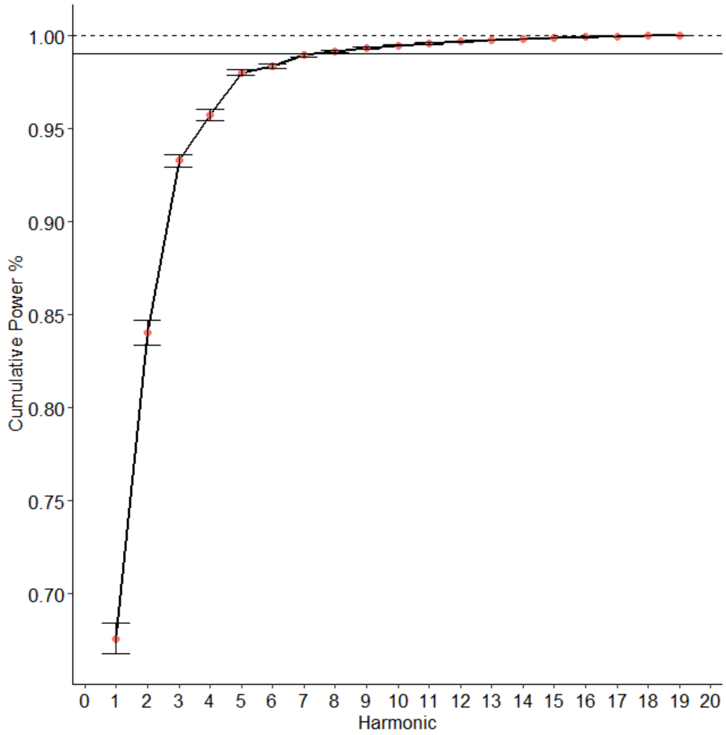

Figure 3.3. Mean cumulative Fourier power describing lake trout (*Salvelinus namaycush*) otolith morphological variation (n = 30). Vertical bars are error bars associated with mean variance explained. The horizontal bar indicates the 99% threshold of explained variation. Eight harmonics were sufficient to account for 99% of the variation of the otolith morphologies.

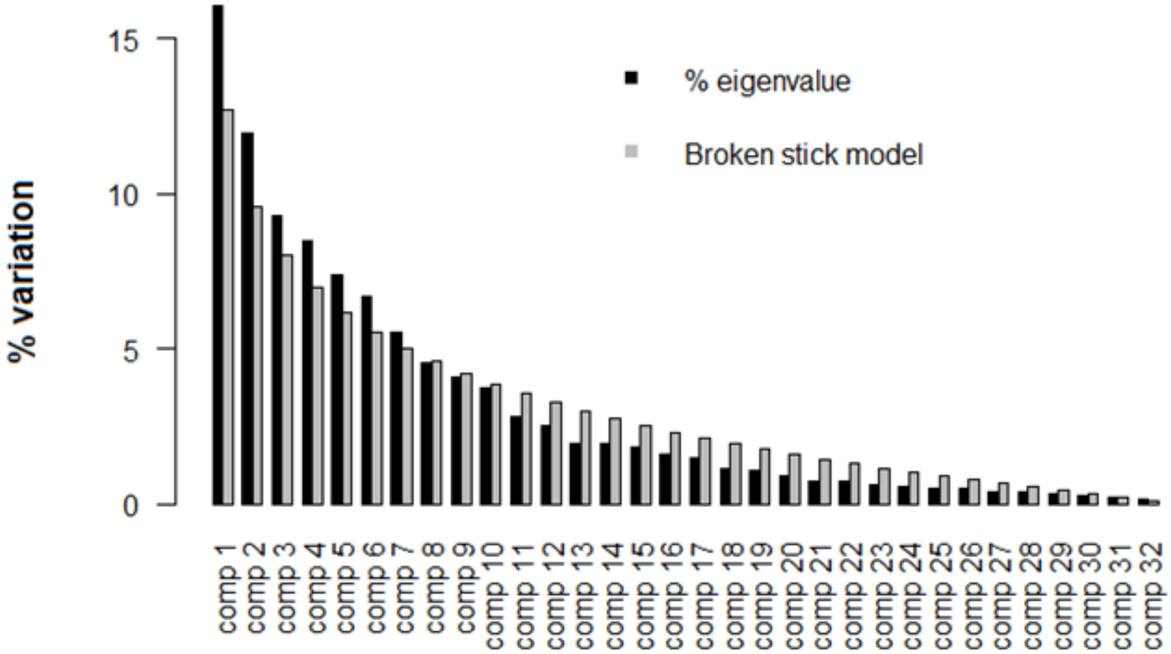

Figure 3.4. A scree plot displaying the percent variation explained by individual principal components (black bar), and the percent of expected variation explained by the broken stick model (grey bar). The sufficient number of principal components was identified once the percent variation explained by the broken stick model was higher than percent variation for a given principal component in the scree plot. Seven principal components were selected, which explain 65.23% of the variation within the dataset.

Table 3.1. Multivariate Kruskal-Wallis test (mKW) effect sizes of lake trout (*Salvelinus namaycush*) otolith principal components (PC) on lake identity.

Lake	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**
Clearwater	0.498	0.592	0.409	0.434	0.547	0.529	0.491
George	0.491	0.382	0.546	0.578	0.471	0.536	0.534
Second Cranberry	0.516	0.502	0.593	0.458	0.402	0.402	0.470

Table 3.2. Linear discriminant analysis (LDA) classification of lake trout (*Salvelinus namaycush*) otoliths in the Manitoban lakes (Clearwater, George, and Second Cranberry lakes). Bolded numbers represent the correct classification.

Lake	Clearwater	George	Second Cranberry	Sample size	Discrimination success
Clearwater	**48**	8	5	61	78.69%
George	19	**26**	3	48	54.17%
Second Cranberry	23	6	**7**	36	19.44%
LDA ID	90	40	15	145	**55.86%**

3.2). The first two discriminant functions of the LDA accounted for 99.99% of the variance. SCL had the lowest classification success, whereby 63.88% were incorrectly assigned to CW. When the linear discriminants were plotted, the first discriminant axis (LD1) showed separation among CW and GL otoliths, while the second discriminant (LD2) separated SCL otoliths from the other two lakes the most (Figure 3.5).

Significant otolith morphological differences were also identified between alleged ecotypes in CW ($F_{(5.225,\ 213.063)} = 2.626$, $P = 0.022$). The post-hoc test did not identify a singular variable associated with the differences in ecotype otolith shape, rather a combination of all principal components were responsible based on their effect sizes (Table 3.3). The post-hoc LDA results did not support the mKW, whereby despite the cross-validated success rate of 72.13%, only 7.14% (1/14) of the >650mm group was correctly classified as such (Table 3.4).

Discussion

Across Lakes

My multivariate Kruskal-Wallis analysis showed significant otolith morphology differences across the three allopatric lake trout lakes, specifically between CW and GL, and GL and SCL, which was consistent with my LDA. The principal component effect sizes generated by the mKW are deemed to be moderate (Cohen, 1988), which are consistent with the LDA jackknifed cross-validated discrimination success rate of ~55%. Despite this consistency, there are potential reasons that both support and contradict the observed discrimination success rate.

Historically, Fisheries Manitoba has extensively used stocking as a management tool (MBGOV, 2021). Furthermore, it is well-known that Fisheries Manitoba sources its lake trout gametes from Clearwater Lake, Manitoba (Butler, 1950). Between 1945 and 2001, GL was stocked 34 different occasions with lake trout, while SCL has only been stocked twice in 1948

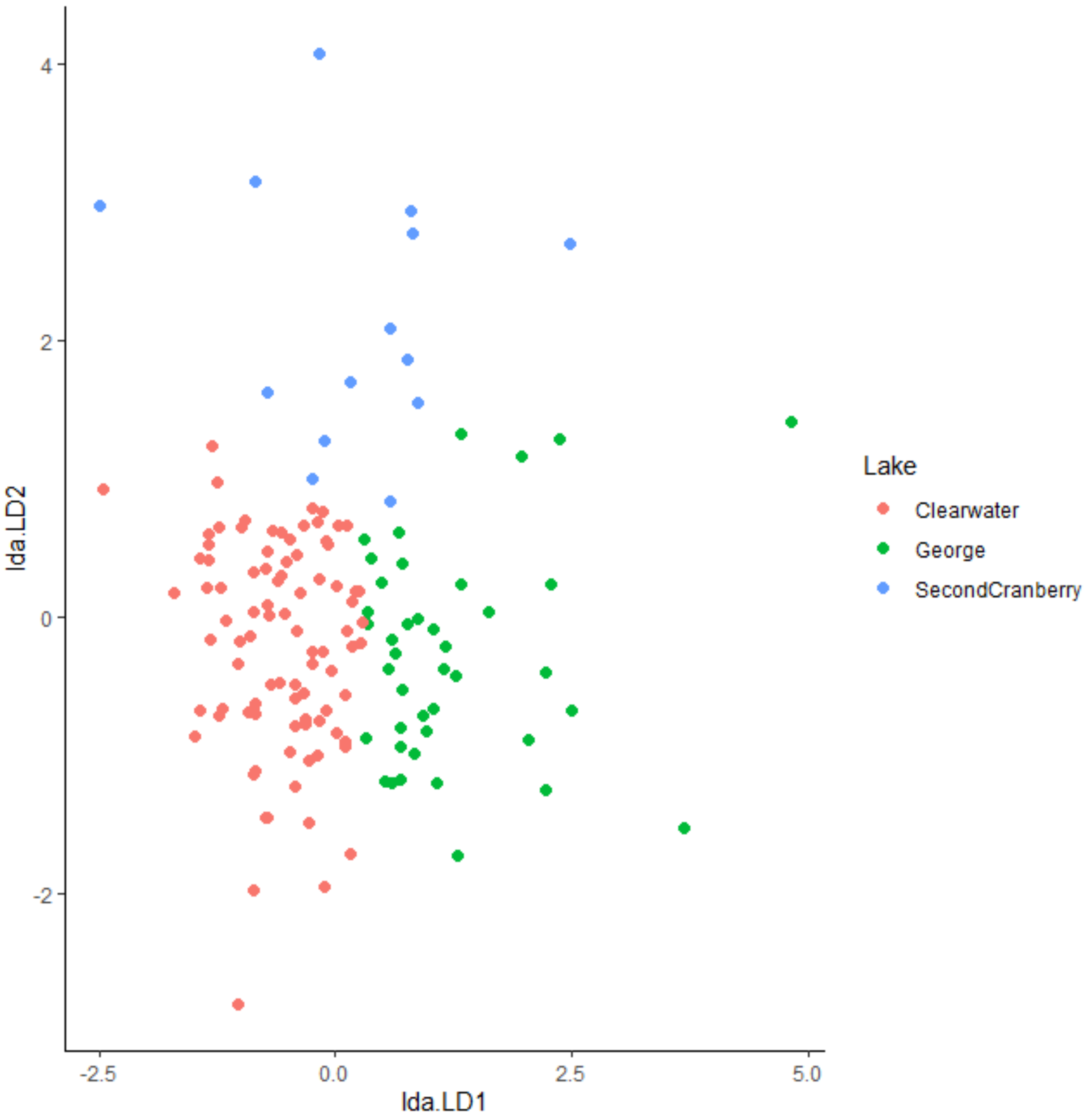

Figure 3.5. A linear discriminant analysis on principal components of left otoliths from mature lake trout (*Salvelinus namaycush*) originating from three lakes: Clearwater Lake (n = 61, discrimination success = 78.69% [red]), George Lake (n = 48, discrimination success = 54.17% [green]), and Second Cranberry lake (n = 36, discrimination success = 19.44% [blue]).

Table 3.3. Multivariate Kruskal-Wallis test (mKW) effect sizes of otolith principal components (PC) on lake trout (*Salvelinus namaycush*) length group/suspected ecotype identity.

Lake	PC1	PC2	PC3	PC4	PC5	PC6	PC7
<650mm Ecotype	0.567	0.529	0.383	0.716	0.451	0.725	0.330
>650mm Ecotype	0.433	0.471	0.617	0.284	0.549	0.275	0.670

Table 3.4. Linear discriminant analysis (LDA) classification of lake trout (*Salvelinus namaycush*) length groups/suspected ecotypes in Clearwater Lake. Bolded numbers represent the correct classification.

Ecotype	<650mm	>650mm	Sample size	Discrimination success
<650mm	**43**	4	47	91.48%
>650mm	13	**1**	14	7.14%
LDA ID	56	5	61	**72.13%**

and 1951 (MBGOV, 2021c; Table A.3.1). My analysis suggest that GL and SCL otoliths were commonly and unsuccessfully classified as CW otoliths. Stocking and the potential genetic homogenization could be a likely reason why 33% of GL otoliths being incorrectly classified as CW otoliths. Furthermore, my sample sizes were different across lakes, but if they were more homogenous and I had a higher sample size, the discrimination rate might be higher. A similar hypothesis was suggested by Souza et al. (2020), whereby they attempted to identify native and hatchery-reared zander (*Sander lucioperca*) based on otolith morphology. Despite their relatively high discrimination rate of 78%, hatchery-origin zander were only successfully identified as such 32% of the time (Souza et al., 2020). While the hatchery-reared zander otoliths were bigger overall, displayed a rougher surface, and longer rostrum, the main reasons for the low success rate include a small sample size of hatchery-reared fish and variability of their multiple growing ponds (Souza et al., 2020).

Conversely, evidence against my stocking hypothesis exists as well. Linear discriminant analysis found differences between Lake Duval, Quebec, which was stocked several times with hatchery-reared lake trout from Lake Trente et un Milles, and the source Lake Trente et un Milles displayed significant otolith length/height allometry differences (Simoneau et al., 2000). While stocking did not appear to reduce the variation in otolith shape between the lakes, it was suggested that the unique hatchery temperature and feeding regimes were the primary reason for the shape differences (Simoneau et al., 2000). Similar results also exist in marine environments as well. Canonical variate analysis results comparing native and non-native common bluestripe snapper (*Lutjanus kasmira)* otolith morphologies hailing from two French Polynesian islands and Hawaii respectively, revealed strong separation between stocks (Vignon and Morat, 2010). Results indicated that stock lineage may not explain all the variation in otolith shape (Vignon and Morat, 2010). Furthermore, genetic lineage analyses indicated that the otolith shape differences between native and non-native snapper otoliths are mainly driven by environmental factors and are not genetics-based (Vignon and Morat, 2010). While evidence exists against my theory, it is still entirely possible that stocking has played an influential role on otolith morphology due to the long stocking history on George Lake and the fact that it is difficult to disentangle the relative impact between environmental and genetic factors. Due to the low stocking effort of lake trout in SCL, it is less likely that stocking greatly impacted the genetic makeup of SCL lake trout and in turn, otolith morphology. However, other reasons including geographical proximity and environmental homogeneity may help explain the low discrimination success between SCL and CW.

Geographical proximity between lakes may be a factor that influences otolith shape. Eight Arabian toothcarp (*Aphanius dispar)* populations varying in degrees of geographic isolation were examined near the Arabian Gulf (Reichenbacher et al., 2009). The two most inland populations that were isolated for over 4,000 years had the highest discrimination rate based on otolith shape characteristics (Reichenbacher et al., 2009). Thus, geographical isolation is likely the cause of suspected genetic differentiation between the most inland populations and the remainder of the sample sites (Reichenbacher et al., 2009). A similar study was conducted on differences in lake trout otolith shape in two watersheds in Quebec (Simoneau et al., 2000). Lakes that were geographically closer to one another displayed only subtle otolith shape differences, and distance between lakes was suggested as a potential cause for this as lake trout are more genetically similar (Simoneau et al., 2000). In terms of my findings, SCL and CW are closer geographically to each other than GL (CW-SCL distance = ~65 km apart, CW-GL distance = ~567 km apart). This may explain why 64% of SCL otoliths were misclassified as

CW otoliths. While GL's successful discrimination rate is only 54% obscures the validity of this hypothesis, the mKW results identified the pairwise combinations of CW-GL and GL-SCL as the most important drivers of significant differences. The omission of the CW-SCL combination supports the claim that geographic isolation and distance plays a role in dictating otolith shape. Geographic proximity influencing otolith shape is also supported by mitochondrial DNA diversity markers that identified CW and Athapapuskow Lake as sharing similar mitochondrial DNA distributions (Wilson and Hebert, 1998). Athapapuskow Lake and SCL are approximately 2 km apart from one another, therefore it is likely that SCL's mitochondrial lineage distribution is similar as a result of being remnant lakes from Lake Agassiz (Wilson and Hebert, 1998). Although evidence exists highlighting geographic distance as a potential influence on otolith shape due to genetic isolation, significant differences in common bluestripe snapper otolith shape was revealed despite sample sites being separated by only a few hundred metres in an estuary system in French Polynesia (Vignon, 2012). Different environmental conditions have been suggested as the leading cause of different otolith morphologies in adult snappers living the channel and the outer reef of the estuary (Vignon, 2012). While it difficult to quantify the relative importance of genetic and environmental influences on otolith shape (Vignon, 2012), it appears that the weight of importance for each factor is context-dependent.

Environmental factors can also contribute to otolith shape morphology (Cardinale et al., 2004; Vignon, 2012). A long-standing question has been how to disentangle the effects of genetics and environment on otolith shape (Simoneau et al., 2000; Cardinale et al., 2004). Atlantic cod (*Gadus morhua*) from two different genetic stocks were examined for such purpose (Cardinale et al., 2004). Hatchery-reared Atlantic cod from two separate spawning stocks were placed in pen cages placed at sea level, while a subset of them were released to their native habitat to test the role of different environmental conditions on otolith shape (Cardinale et al., 2004). Fish from the same stock lineage, but inhabiting different environmental conditions displayed different morphologies, whereby the centroid (centre of the mathematical shape), the otolith width, and higher order nEFDs responsible for the finer details of the otolith shape were the most contrasting variables (Cardinale et al., 2004). Conversely, Atlantic cod from different lineages exposed to similar environmental conditions also revealed significantly different otolith shape in regards to the finer details (higher order nEFDs), where both genetic and environmental factors in this species were revealed to be crucial in determining otolith shape (Cardinale et al., 2004). In the same vein, nuclear and mitochondrial DNA identified that non-native common bluestripe snapper in Hawaii belonged from the same lineage in French Polynesia (Vignon and Morat, 2012). Despite the genetic similarities, otolith shape differences were still observed, and were consequently attributed to different habitat characteristics (Vignon and Morat, 2012). Meanwhile, non-native snapper hailing from different genetic lineages residing on the same shoal, still presented otolith differences, therefore supporting the hypothesis that environment and genetics both modulate otolith shape (Vignon and Morat, 2010). This might help explain why despite GL and CW sharing some genetic history due to stocking, otolith shape still varies enough for the LDA to separate them, and the mKW post hoc test to identify the CW-GL combination as a major driver of significance. The same can be said regarding the GL-SCL combination, whereby different environments are the plausible cause of shape differences. Furthermore, in regard to the CW-SCL combination, due to both lakes experiencing similar climatic conditions and most likely becoming truly isolated from each other later on compared to GL, it is not surprising that I did not see significant shape differences between these two lakes.

Growth rate is inherently linked to environment; thus it is another factor to consider. Situated in the southeast portion of Manitoba, GL is exposed to different climatic norms compared to CW and SCL. Ice break-up is earlier, therefore influencing feeding and growth rates (Martin, 1970), which has also been noted as a possible contributor to otolith shape differences (Campana and Casselman, 1993; Hüssy, 2008; Kikuchi et al., 2021). Otolith shape analysis between multiple suspected stocks of Argentine croaker (*Umbrina canosai)* in the south Atlantic Ocean, revealed differences that are likely to be driven by different temperature regimes (Kikuchi et al., 2021). These temperature regimes in addition to oceanic currents influence prey availability, and ultimately growth rate (Kikuchi et al., 2021). This was corroborated by von Bertalanffy growth curves, whereby both growth curves and otolith analyses suggest that two populations exist in the southern Atlantic Ocean (Kikuchi et al., 2021). This supports the LDA and mKW post hoc test results, because growth rates between both lakes have been shown to be significantly different between CW and GL (This thesis, Chapter 2). Meanwhile, the geographical proximity of CW and SCL theoretically may limit the impact of temperature of on growth rate and otolith shape differences. However, CW and SCL growth rates and maturity schedules are significantly different, thus dampening the influencing effect of growth rate upon otolith morphology (This thesis, Chapter 2).

Within Clearwater Lake

The mKW results identified a significant difference between the two suspected ecotypes in Clearwater Lake. These results support the claims of Navarroli et al. (This thesis, Chapter 2), in which there appears to be a split in growth rates between lake trout individuals at the threshold length of 650 mm within CW, therefore indicating potential sympatric ecotypes. Lake trout ecotypes inhabit in separate areas of a lacustrine habitat, and predate on different food sources

(Chavarie et al., 2021), and as a result they will naturally have different growth rates from each other (Burnham-Curtis and Bronte, 1996). Furthermore, there could be a genetic basis for phenotypic expression of lake trout ecotypes (Goetz et al., 2010; Chavarie et al., 2021).

Despite all of this, the post-hoc LDA performed poorly when attempting to separate the two length groups. Sympatric ecotypes have been almost exclusively found in large lakes in Canada (e.g., the Laurentian Great Lakes; Eshenroder, 2008). Lake size might be an explanation for no sympatric ecotypes in CW; however, sympatric ecotypes have been observed in smaller lakes, such as Rush Lake, Michigan, which is a 1.3 km^2 lake with a max depth ~ 80m (Chavarie et al., 2016). Whether this differentiation occurred before or after the colonization of Rush Lake, the researchers suggested that differences in niche spaces could be sufficient to maintain the ecotypes (Chavarie et al., 2016). CW is much larger, but shallower than Rush Lake. My study provides some evidence that 2-D shape analyses of otoliths may carry enough power to identify such differences based on the mKW results, but do not based on the LDA results. Furthermore, the different niches that sympatric ecotypes inhabit may not be distinct enough to significantly alter otolith shape to be detected. To my knowledge, this is the first study attempting to use otolith shape analysis to identify potentially different ecotypes within a lake. Further studies are required to better disentangle potential effects of ecotypes on otolith shape, by examining lakes that have confirmed sympatric lake trout ecotypes (e.g. Lake Superior). Although this is just a singular study, genetic approaches appear to have greater potential than this approach despite the cost disparity.

Further studies should try to incorporate genetics to complement the morphological analysis to better understand its efficacy in discriminating distinct lake trout populations from one another. Otolith shape analysis is intended to be a quick method to acquire data on populations without requiring more expensive alternatives like genetics. It remains relatively unused in Canadian contemporary freshwater stock assessments despite its success in previous studies (Casselman et al., 1981; Campana and Casselman, 1993; Simoneau et al., 2000). As genetic studies are quite expensive, 2-D otolith morphology still might be a worthwhile investigation in larger lakes with confirmed ecotypes such as Great Slave, Great Bear and the Laurentian Great Lakes. This would surely be worthwhile due to the lack of implementation of otolith morphological studies in freshwater environments.

Other otolith shape influencers

While genetic and environmental factors influence otolith shape, there are several other confounding factors that have not been addressed. The effect of sex has been noted as a potential confounding factor on otolith shape (Campana and Casselman, 1993). However, in my study, mKW results did not reveal such differences across lakes, nor within Clearwater Lake. My results are consistent with the only other lake trout otolith shape analysis study conducted in Quebec lakes that did not observe sexual dimorphic otoliths (see Simoneau et al., 2000). It is therefore unlikely that the pooling of both sexes affected my multivariate analyses. Age has also been attributed to altering otolith morphology (Castonguay et al., 1999; Cardinale et al., 2004). Castonguay et al. (1999) investigated otolith shape differences between two stocks of Atlantic mackerel (*Scomber scombrus*) and determined that age had a significant effect on otolith shape. Although I do have age estimate data for the different lake trout stocks, my sample size limits my statistical power from examining an effect of age. That said, removing all immature fish and only analyzing mature lake trout was an attempt to somewhat dampen this effect. By only examining mature fish I reduced the impact of ontogenetic effects like maturity and age on my results (see Hüssy, 2008; Vignon, 2012; Khemiri et al., 2018). Another point to consider are otolith deformations, in the form of translucent vateritic otoliths, because they have been observed to occur quite often in hatchery-reared lake trout (Bowen et al., 1999). Although GL has had a long stocking history, I did not observe many vateritic otoliths, therefore I do not believe this facet of otolith morphology applies to my dataset. Lastly, there are a variety of methods to extract shape data from otoliths (i.e. Elliptical Fourier Analysis, Fast-Fourier Transformation, shape indices, and landmark-based approaches); however, elliptical Fourier analysis appears to be the most common and strongest approach as harmonics are independent from each other, are unrelated to otolith size, and are less prone to measurement bias and errors (Crampton, 1995; Iwata and Ukai, 2002). Consequently, I believe the methods I chose to use are valid for such an experiment.

Fisheries Management

My otolith morphological analyses offer evidence that is relevant to fisheries management. The main result that can directly apply to management is the potential for sympatric ecotypes to exist within CW. Currently, Manitoba's lake trout hatchery programs involves collecting gametes from lake trout situated on the western side of CW. If multiple ecotypes exist, then it should be important to investigate further, because of the stocking ramifications on recipient lakes. This potential mismatch of lake trout ecotype stocking has been observed in small boreal lakes in Ontario and Quebec, which poses several risks such as reduction in body condition and growth of stocked individuals (Morissette et al., 2018). Furthermore, without genetic studies, it is impossible to determine the level of genetic differentiation between suspected ecotypes. This becomes important when regarding if CW lake trout home to their natal spawning reef, or randomly select one. If the spawning reefs that are targeted by hatchery initiatives are more heavily weighted by one ecotype than another, then this may not be an optimal program to obtain the highest genetic variation across stocked lakes due to genetic bottleneck effects thus reducing stocking success (Agostinho et al., 2010). Recreational fishing may also be impacted by the discovery of sympatric ecotypes. If the slower growing and greater maximum size reaching ecotype matures later, and is randomly targeted more heavily than the faster growing and presumed earlier maturing lake trout, then this poses a risk to reducing genetic variability, which has been shown to reduce the capacity of a population to withstand a suite of stressors (e.g. anthropogenic – invasive species, environmental – season climate extremes; see Elton, 1958). If this is the case, reducing daily bag limits to zero may be a management strategy worth considering. Another benefit from my analyses are my LDA results. If otolith shape in the context of my project is at least moderately regulated by genetic factors, then GL's genetic makeup is moderately influenced by the stocking of CW individuals. Furthermore, because it had the second highest CPUE and estimated biomass density values (This thesis, Chapter 2), then an argument can be made regarding the successful stocking in GL. While otolith morphological research is a tool with interesting potential, it should be used a complementary technique to supplement the traditional stock assessment tools. More research is needed to support the usefulness and accuracy of otolith morphology studies, namely in the form of genetic studies. The SHAPE package is a relative easy program to learn, and can produce results rather quickly. It is a free program, and the labour associated with processing the otolith samples would be at a fraction of the cost that genetic studies demand. There is genuine promise that this method can be used in Canadian waters as a stock identification tool.

Chapter 4: General Discussion

Lake trout remain an understudied species in Manitoba. Economically, lake trout fishing stimulates the Manitoban economy, and it is important to keep monitoring and learning about their most important fisheries. To my knowledge, there are no routine lake trout monitoring programs, other than the biennial disease control and collection of lake trout gametes at CW. Rather, the province has mainly focused on rearing juvenile lake trout for stocking purposes. Stocking success is not a guaranteed venture (Zimmerman and Krueger, 2009; Morissette et al., 2018). I have seen this firsthand with Davidson Lake. Only ever using a singular strain of lake trout to stock lakes throughout the province may have inhibited lakes such as DL to rebound due to the reduced life-history and ecological diversity of the stocked fish (Zimmerman and Krueger, 2009). Even if CW does hold two forms of lake trout, the province currently has no idea what proportion of each they acquire during their gamete collection. Genetic studies are an avenue Fisheries Manitoba may want to pursue for CW lake trout, because of their importance to stocking.

Stocking is an expensive management effort that could be replaced by more viable management options such as monitoring programs. While stocking create new tourism avenues for stakeholders, being able to consistently conduct population surveys might be a better strategy to understand population dynamic of a fishery in relation to angling regulations. Fisheries Manitoba appears to hold on to legacy traditions of put and take fisheries and continue to stock lakes with a wide variety of species that are both native and non-native to the region (stocking records). While stock assessments provide vital information in data-limited fisheries, Manitoba lacks the financial and personnel resources to conduct such programs on top of their current projects.

The sustainability model created by Lester et al. (2021) is an invaluable tool for managers who strive for the long-term success of lake trout fisheries. By using lake morphometry, air temperature, lake trout life-history and density data from SPIN (Lester et al., 2021), fisheries managers have an effective framework to better manage their lake trout populations. Combing SPIN's rapid assessment and simplicity of the sustainability model, it may be feasible, economically and timewise, to incorporate lake trout monitoring programs into the current rotation of management programs Manitoba.

Another avenue that the Fisheries Branch of Manitoba should consider is to continue investigating catch-and release (C&R) impacts upon lake trout. C&R is aimed at conserving a fish population by opting to release a fish back to the water instead of harvesting it (Arlinghaus et al., 2007). Unfortunately, angling of lake trout in Manitoba does lead to death and/or sub-lethal physiological responses, and behavioural impairment of fishes (Howell et al., 2023) and due to its life history strategies that are geared toward slow growth and maturation, this species is especially vulnerable to this activity (Shuter et al., 1998). This year, Fisheries Manitoba has set daily bag limits to one across the province, therefore C&R events are almost inevitable for lake trout anglers. While recent research highlights behavioural and physiological impairments of C&R upon lake trout (Howell et al., 2023), many questions are still left unanswered; particularly, how to best deal with barotrauma-stricken lake trout. The most recent angling regulations had an excerpt about the utility of descending devices, which are designed to alleviate barotrauma by sinking the fish back to an appropriate depth (MBGOV, 2023). While this is a good approach, an accompanying video on how to use such tools is crucial, because anglers are more likely to use something in that has been shown to work on camera. Lake trout experiencing barotrauma is something I encountered quite often while gillnetting and angling throughout the summer. In lakes like CW and SCL that receive a lot of angler traffic, it stands to reason that anglers can negatively impact a fish populations sustainability if inappropriate handling and release measures are used. In spite of my observations, stock assessments do not have the capacity to better understand this phenomenon. Consequently, future organismal centric research should investigate whether descending devices are suitable for lake trout.

Other research avenues exist regarding lake trout aging structures. While otoliths are currently the most common age structure to use, recent studies have provided evidence that using the maxillae performed better than otoliths in terms of time spent prepping the samples, percent agreement, and lower bias (see Wellenkamp et al., 2015; Murphy et al., 2018). The method is so successful that the Great Lakes Fish Monitoring and Surveillance Program has now shifted their focus to collecting maxilla as the primary age structure for lake trout (Murphy et al., 2018). While there is a learning curve to aging this structure, it may be a worthwhile shift it can be validated for old lake trout individuals. Another avenue of research that has been rarely investigated is the relationship of otolith weight and age, maturity and other life-history metrics for lake trout. As a lake trout gets older, more calcium carbonate deposits on the otolith, therefore there is reason to believe that there is merit to this analysis. Hansen et al. (2022) investigated this and concluded that otolith weight was not a good indirect measure to estimate lake trout age. However, otolith weight was accurate to estimate age-at-maturity and survival rates (Hansen et al., 2022). While this provides evidence that scientists are able to find innovative techniques to infer some information about some life-history metrics, its applicability is limited.

Three-dimensional (3D) otolith shape analysis is another stock identification analysis technique. While much newer than 2D otolith shape analysis, it does remove the inherent bias of only analyzing a singular plane of an otolith when conducting a 2D shape analysis (Andrialovanirina et al., 2023). When comparing the efficacy between both methods to identify different stocks of red mullet (*Mullus barbatus*), both methods revealed geographic differences between known Mediterranean stocks of red mullet (Andrialovanirina et al., 2023). However, only the 3D shape analysis were able to reveal asymmetrical differences between right and left otoliths, which is important because of the significant interaction between geography and otolith asymmetry throughout the study (Andrialovanirina et al., 2023). Evidence suggests that 2D shape analyses can influence the assignment of an individual to stock origin due to possible otolith asymmetries (Andrialovanirina et al., 2023). Despite this, it is only a singular study that has only examined a single species, therefore otolith asymmetries must be analysed at a species-specific level. Furthermore, 3D scanners are expensive and require longer processing times (Afanasyev et al., 2017; Andrialovanirina et al., 2023). Consequently, 2D shape analysis will probably used more frequently than 3D options at this point.

Manitoba has a plethora of recreational lake trout fisheries, and although each lake trout fishery has their own life-history strategies, each historically exposed to varying degrees of recreational fishing pressure. Recreational lake trout fisheries stimulate the Manitoban economy; thus, they are important ecologically and economically, and must be managed appropriately. Consequently, based on my findings, each examined lake trout fishery should have their own independent management regulations to best suit their needs. The collaboration between Fisheries Manitoba and The University of Winnipeg is great initiative to better understand lake trout fisheries in the province, but more programs within Fisheries Manitoba should be implemented to best manage this species. While it is important to acknowledge the limited time, effort, and money that Fisheries Manitoba has to monitor each lake each year, prioritizing lakes that stimulate the local economies may be a sensible avenue for managers.

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Appendix

Table A.2.1. Summary of pairwise comparisons between total length, following a Dunn test across seven lake trout (*Salvelinus namaycush*) populations. Statistical significance is accepted at a threshold of α < 0.05. Significant differences are in bold.

Group 1	Group 2	Sample Size 1	Sample size 2	Test statistic	P-value	Bonferroni adjusted p-value
Clearwater	Davidson	248	1	-0.769	0.442	1
Clearwater	George	248	86	-0.847	0.397	1
Clearwater	High	248	20	-0.283	0.777	1
Clearwater	Mantario	248	29	0.418	0.678	1
Clearwater	Second Cranberry	248	47	7.147	**<0.0001**	**<0.0001**
Clearwater	West Hawk	248	13	0.336	0.738	1
Davidson	George	1	86	0.660	0.509	1
Davidson	High	1	20	0.687	0.493	1
Davidson	Mantario	1	29	0.837	0.403	1
Davidson	Second Cranberry	1	47	1.888	0.591	1
Davidson	West Hawk	1	13	0.833	0.405	1
George	High	86	20	-0.163	0.871	1
George	Mantario	86	29	0.874	0.382	1
George	Second Cranberry	86	47	6.85	**<0.0001**	**<0.0001**
George	West Hawk	86	13	0.676	0.499	1
High	Mantario	20	29	0.506	0.612	1
High	Second Cranberry	20	47	4.510	**<0.0001**	**0.000136**
High	West Hawk	20	13	0.451	0.652	1
Mantario	Second Cranberry	29	47	4.475	**<0.0001**	**0.000160**
Mantario	West Hawk	29	13	0.0405	0.968	1
Second Cranberry	West Hawk	47	13	-3.329	**0.000871**	**0.0183**

Table A.2.2. Summary of pairwise comparisons between weight, following a Dunn test across seven lake trout (*Salvelinus namaycush*) populations. Statistical significance is accepted at a threshold of α < 0.05. Significant differences are in bold.

Group 1	Group 2	Sample Size 1	Sample size 2	Test statistic	P-value	Bonferroni adjusted p-value
Clearwater	George	117	85	-0.340	0.734	1
Clearwater	High	117	21	0.158	0.875	1
Clearwater	Mantario	117	29	-0.309	0.757	1
Clearwater	Second Cranberry	117	47	6.265	**<0.0001**	**<0.0001**
Clearwater	West Hawk	117	13	0.224	0.823	1
George	High	85	21	0.352	0.725	1
George	Mantario	85	29	-0.0725	0.942	1
George	Second Cranberry	85	47	6.219	**<0.0001**	**<0.0001**
George	West Hawk	85	13	0.383	0.702	1
High	Mantario	21	29	-0.354	0.723	1
High	Second Cranberry	21	47	3.980	**<0.0001**	**0.00104**
High	West Hawk	21	13	0.0796	0.937	1
Mantario	Second Cranberry	29	47	4.853	**<0.0001**	**<0.0001**
Mantario	West Hawk	29	13	0.389	0.698	1
Second Cranberry	West Hawk	47	13	-3.243	**0.00118**	**0.0179**

Table A.2.3. Summary of pairwise comparisons between relative weight, following a Dunn test across seven lake trout (*Salvelinus namaycush*) populations. Statistical significance is accepted at a threshold of $\alpha < 0.05$. Significant differences are in bold.

Group 1	Group 2	Sample Size 1	Sample size 2	Test statistic	P-value	Bonferroni adjusted p-value
Clearwater	George	117	85	0.891	0.373	1
Clearwater	High	117	19	-1.924	0.0544	0.815
Clearwater	Mantario	117	29	-3.355	**0.000793**	**0.0119**
Clearwater	Second Cranberry	117	47	-0.628	0.530	1
Clearwater	West Hawk	117	13	-0.561	0.579	1
George	High	85	19	-2.376	0.0175	0.263
George	Mantario	85	29	-3.827	**0.000129**	**0.00193**
George	Second Cranberry	85	47	-1.296	0.195	1
George	West Hawk	85	13	-0.976	0.331	1
High	Mantario	19	29	-0.746	0.456	1
High	Second Cranberry	19	47	1.351	0.177	1
High	West Hawk	19	13	0.867	0.386	1
Mantario	Second Cranberry	29	47	2.487	0.0128	0.192
Mantario	West Hawk	29	13	1.594	0.110	1
Second Cranberry	West Hawk	47	13	-0.172	0.863	1

Table A.2.4. Summary one-sample t-test for age differences of thin-sectioned lake trout (*Salvelinus namaycush*) otoliths across observer #1 and #2. Statistical significance is accepted at a threshold of $\alpha < 0.05$. Significant differences are in bold.

Observer #1 Final Age	Sample Size	Minimum difference (R2 age -R1 age)	Maximum difference (R2 age -R1 age)	Mean	Test statistic (t)	Bonferroni adjusted p-value
4	26	0	2	0.385	2.813	0.207
5	25	-1	4	0.560	2.498	0.415
6	28	-2	4	0.000	0.000	1.000
7	27	-2	2	-0.0741	-0.420	1.000
8	19	-2	2	0.263	1.316	1.000
9	17	-2	4	0.118	0.382	1.000
10	7	-2	0	-0.571	-1.921	1.000
11	21	-1	1	0.143	0.999	1.000
12	25	-2	5	0.0800	0.283	1.000
13	15	-3	2	0.000	0.000	1.000
14	7	-1	6	0.857	0.969	1.000
15	7	-5	3	0.143	0.152	1.000
16	11	-2	6	0.909	1.392	1.000
17	8	-1	1	0.125	0.424	1.000
18	4	-2	1	-0.250	-0.397	1.000
19	9	0	6	1.333	2.138	1.000
20	1	3	3	3.000	NA	NA
21	2	1	1	1.000	NA	NA
22	3	0	1	0.667	2.000	1.000
23	7	-2	4	0.286	0.400	1.000
24	3	-2	1	-0.667	-0.756	1.000
25	4	0	9	2.750	1.287	1.000
26	3	-1	0	-0.667	-2.000	1.000
27	1	2	2	2.000	NA	NA
28	3	-2	1	-0.667	-0.756	1.000
29	1	-2	-2	-2.000	NA	NA
30	1	-1	-1	-1.000	NA	NA
31	1	-1	-1	-1.000	NA	NA
32	1	-1	-1	-1.000	NA	NA
35	1	4	4	4.000	NA	NA
36	1	6	6	6.000	NA	NA
38	1	3	3	3.000	NA	NA
40	1	3	3	3.000	NA	NA
44	1	-3	-3	-3.000	NA	NA

Table A.2.5. Percent age differences of thin-sectioned lake trout (*Salvelinus namaycush*) otoliths between the final ages of observer #1 and observer #2.

-9	**-8**	**-7**	**-6**	**-5**	**-4**	**-3**	**-2**	**-1**	**0**	**1**	**2**	**3**	**4**	**5**
0.343	0.0	0.0	1.37	0.343	1.71	1.71	5.14	21.58	47.26	14.38	5.14	0.68	0.0	0.343

Table A.2.6. Summary of pairwise comparisons between age estimations, following a Dunn test across seven lake trout (*Salvelinus namaycush*) populations. Statistical significance is accepted at a threshold of α < 0.05. Significant differences are in bold.

Group 1	Group 2	Sample Size 1	Sample size 2	Test statistic	P-value	Bonferroni adjusted p-value
Clearwater	Davidson	118	1	-0.474	0.636	1
Clearwater	George	118	64	4.999	5.74E-7	0.00815
Clearwater	High	118	19	1.022	0.307	1
Clearwater	Mantario	118	29	3.357	0.000788	0.223
Clearwater	Second Cranberry	118	47	7.512	**<0.0001**	**<0.0001**
Clearwater	West Hawk	118	13	0.988	0.323	1
Davidson	George	1	64	1.242	0.214	1
Davidson	High	1	19	0.710	0.477	1
Davidson	Mantario	1	29	1.152	0.249	1
Davidson	Second Cranberry	1	47	1.753	0.0796	1
Davidson	West Hawk	1	13	0.737	0.461	1
George	High	64	19	-2.004	0.0450	0.947
George	Mantario	64	29	-0.359	0.720	1
George	Second Cranberry	64	47	2.705	0.00683	0.143
George	West Hawk	64	13	-1.602	0.109	1
High	Mantario	19	29	1.501	0.133	1
High	Second Cranberry	19	47	3.836	**0.000125**	**0.00262**
High	West Hawk	19	13	0.100	0.920	1
Mantario	Second Cranberry	29	47	2.541	0.011	0.232
Mantario	West Hawk	29	13	-1.219	0.223	1
Second Cranberry	West Hawk	47	13	-3.213	**0.00131**	**0.0275**

Table A.2.7. Summary of pairwise comparisons between the asymptotic length parametre (L_∞), following a Dunn test across seven lake trout (*Salvelinus namaycush*) populations. Statistical significance is accepted at a threshold of $\alpha < 0.05$. Significant differences are in bold.

Group 1	Group 2	Sample Size 1	Sample size 2	Test statistic	P-value	Bonferroni adjusted p-value
Clearwater	George	117	64	0.319	7.50e-1	1
Clearwater	High	117	18	2.252	2.43e-2	1
Clearwater	Mantario	117	29	0.583	5.60e-1	1
Clearwater	Second Cranberry	117	47	8.196	**<0.0001**	**<0.0001**
Clearwater	West Hawk	117	13	3.091	1.99e-3	0.405
George	High	64	18	1.951	5.11e-2	1
George	Mantario	64	29	0.319	7.49e-1	1
George	Second Cranberry	64	47	7.111	**<0.0001**	**<0.0001**
George	West Hawk	64	13	2.801	4.99e-3	1
High	Mantario	18	29	-1.497	1.34e-1	1
High	Second Cranberry	18	47	3.050	2.29e-3	0.464
High	West Hawk	18	13	0.917	3.59e-1	1
Mantario	Second Cranberry	29	47	5.482	**<0.0001**	**0.00573**
Mantario	West Hawk	29	13	2.345	1.90e-2	1
Second Cranberry	West Hawk	47	13	-1.633	1.02e-1	1

Table A.2.8. Summary of pairwise comparisons between the early growth rate parametre (*w*), following a Dunn test across seven lake trout (*Salvelinus namaycush*) populations. Statistical significance is accepted at a threshold of α < 0.05. Significant differences are in bold.

Group 1	Group 2	Sample Size 1	Sample size 2	Test statistic	P-value	Bonferroni adjusted p-value
Clearwater	George	117	64	-10.0152	**<0.0001**	**<0.0001**
Clearwater	High	117	18	-3.488	0.0885	0.363
Clearwater	Mantario	117	29	-4.934	0.00735	0.00815
Clearwater	Second Cranberry	117	47	-9.269	**<0.0001**	**<0.0001**
Clearwater	West Hawk	117	13	-3.657	0.0467	0.191
George	High	64	18	2.526	0.156	0.636
George	Mantario	64	29	2.384	0.231	0.945
George	Second Cranberry	64	47	-0.227	0.397	1
George	West Hawk	64	13	1.604	0.611	1
High	Mantario	18	29	-0.468	1	1
High	Second Cranberry	18	47	-2.589	0.479	0.530
High	West Hawk	18	13	-0.511	1	1
Mantario	Second Cranberry	29	47	-2.445	0.196	0.798
Mantario	West Hawk	29	13	-0.137	1	1
Second Cranberry	West Hawk	47	13	1.696	1	1

Table A.2.9. Summary of pairwise comparisons between the growth coefficient parametre (*K*), following a Dunn test across seven lake trout (*Salvelinus namaycush*) populations. Statistical significance is accepted at a threshold of α < 0.05. Significant differences are in bold.

Group 1	Group 2	Sample Size 1	Sample size 2	Test statistic	P-value	Bonferroni adjusted p-value
Clearwater	George	117	64	-7.539	**<0.0001**	**<0.0001**
Clearwater	High	117	18	-3.276	1.05e-3	0.0158
Clearwater	Mantario	117	29	-3.999	**<0.0001**	**0.000955**
Clearwater	Second Cranberry	117	47	-2.745	**<0.0001**	**<0.0001**
Clearwater	West Hawk	117	13	-3.771	**<0.0001**	**<0.0001**
George	High	64	18	1.285	1.99e-1	1.000
George	Mantario	64	29	1.531	1.26e-1	1.000
George	Second Cranberry	64	47	-2.993	**2.76e-3**	**0.0414**
George	West Hawk	64	13	0.842	8.19e-1	1.000
High	Mantario	18	29	-0.0516	9.99e-1	1.000
High	Second Cranberry	18	47	-3.311	**9.31e-4**	**0.0140**
High	West Hawk	18	13	-0.0516	4.53e-1	1.000
Mantario	Second Cranberry	29	47	-3.886	**1.02e-4**	**0.00153**
Mantario	West Hawk	29	13	-3.005	4.13e-1	1.000
Second Cranberry	West Hawk	47	13	2.057	3.97e-2	0.595

Table A.2.10. Summary of pairwise comparisons between the age-at-length 0 mm parametre (t_0), following a Dunn test across seven lake trout (*Salvelinus namaycush*) populations. Statistical significance is accepted at a threshold of $\alpha < 0.05$. Significant differences are in bold.

Group 1	Group 2	Sample Size 1	Sample size 2	Test statistic	P-value	Bonferroni adjusted p-value
Clearwater	George	117	64	-6.756	**<0.0001**	**<0.0001**
Clearwater	High	117	18	-3.043	**0.00234**	**0.0351**
Clearwater	Mantario	117	29	-2.648	0.00810	0.121
Clearwater	Second Cranberry	117	47	-9.621	**<0.0001**	**<0.0001**
Clearwater	West Hawk	117	13	-3.063	**0.00219**	**0.0328**
George	High	64	18	1.049	0.294	1
George	Mantario	64	29	2.238	0.0252	0.378
George	Second Cranberry	64	47	-3.182	**0.00146**	**0.0220**
George	West Hawk	64	13	0.509	0.611	1
High	Mantario	18	29	0.737	0.461	1
High	Second Cranberry	18	47	-3.214	**0.00130**	**0.0196**
High	West Hawk	18	13	-0.343	0.731	1
Mantario	Second Cranberry	29	47	-4.710	**<0.0001**	**<0.0001**
Mantario	West Hawk	29	13	-1.037	0.299	1
Second Cranberry	West Hawk	47	13	2.444	0.0145	0.218

Table A.2.11. Summary of pairwise comparisons between the expected 50% maturity threshold (A_{50}) from the age-at-maturity logistic regressions, following a Dunn test across three lake trout (*Salvelinus namaycush*) populations. Statistical significance is accepted at a threshold of $\alpha < 0.05$. Significant differences are in bold.

Group 1	Group 2	Sample Size 1	Sample size 2	Test statistic	P-value	Bonferroni adjusted p-value
Clearwater	George	1000	1000	24.774	**<0.0001**	**<0.0001**
Clearwater	Second Cranberry	1000	1000	50.717	**<0.0001**	**<0.0001**
George	Second Cranberry	1000	1000	25.944	**<0.0001**	**<0.0001**

Table A.2.12. Summary of pairwise comparisons between the slopes from the age-at-maturity logistic regressions, following a Dunn test across three lake trout (*Salvelinus namaycush*) populations. Statistical significance is accepted at a threshold of α < 0.05. Significant differences are in bold.

Group 1	Group 2	Sample Size 1	Sample size 2	Test statistic	P-value	Bonferroni adjusted p-value
Clearwater	George	1000	1000	-19.856	**<0.0001**	**<0.0001**
Clearwater	Second Cranberry	1000	1000	-22.609	**<0.0001**	**<0.0001**
George	Second Cranberry	1000	1000	-2.753	**5.90E-3**	**0.0177**

Table A.2.13. Summary of pairwise comparisons between the intercepts from the age-at-maturity logistic regressions, following a Dunn test across three lake trout (*Salvelinus namaycush*) populations. Statistical significance is accepted at a threshold of α < 0.05. Significant differences are in bold.

Group 1	Group 2	Sample Size 1	Sample size 2	Test statistic	P-value	Bonferroni adjusted p-value
Clearwater	George	1000	1000	13.941	**<0.0001**	**<0.0001**
Clearwater	Second Cranberry	1000	1000	1.350	0.177	0.531
George	Second Cranberry	1000	1000	-12.591	**<0.0001**	**<0.0001**

Table A.2.14. Summary of pairwise comparisons between the expected 50% maturity thresholds (L_{50}) from the length-at-maturity logistic regressions, following a Dunn test across three lake trout (*Salvelinus namaycush*) populations. Statistical significance is accepted at a threshold of $\alpha < 0.05$. Significant differences are in bold.

Group 1	Group 2	Sample Size 1	Sample size 2	Test statistic	P-value	Bonferroni adjusted p-value
Clearwater	George	1000	1000	-25.655	**<0.0001**	**<0.0001**
Clearwater	Second Cranberry	1000	1000	25.894	**<0.0001**	**<0.0001**
George	Second Cranberry	1000	1000	51.55	**<0.0001**	**<0.0001**

Table A.2.15. Summary of pairwise comparisons between the slopes from the length-at-maturity logistic regressions, following a Dunn test across three lake trout (*Salvelinus namaycush*) populations. Statistical significance is accepted at a threshold of α < 0.05. Significant differences are in bold.

Group 1	Group 2	Sample Size 1	Sample size 2	Test statistic	P-value	Bonferroni adjusted p-value
Clearwater	George	1000	1000	5.865	**<0.0001**	**<0.0001**
Clearwater	Second Cranberry	1000	1000	13.682	**<0.0001**	**<0.0001**
George	Second Cranberry	1000	1000	7.817	**<0.0001**	**<0.0001**

Table A.2.16. Summary of pairwise comparisons between the intercepts from the length-at-maturity logistic regressions, following a Dunn test across three lake trout (*Salvelinus namaycush*) populations. Statistical significance is accepted at a threshold of α < 0.05. Significant differences are in bold.

Group 1	Group 2	Sample Size 1	Sample size 2	Test statistic	P-value	Bonferroni adjusted p-value
Clearwater	George	1000	1000	5.382	**<0.0001**	**<0.0001**
Clearwater	Second Cranberry	1000	1000	-23.942	**<0.0001**	**<0.0001**
George	Second Cranberry	1000	1000	-29.324	**<0.0001**	**<0.0001**

Table A.3.1. List of lake trout (*Salvelinus namaycush*) stocked across the years in Clearwater Lake, George Lake and Second Cranberry Lake (Adapted from MBGOV (2021c)).

Lake	Year	Date	Size	Quantity
Clearwater	2001	2001-10-01	Egg	115,000
Clearwater	1996	1996-10-06	Egg	76,000
Clearwater	1995	1995-09-26	Egg	290,000
Clearwater	1992	-	Egg	270,000
Clearwater	1991	-	Egg	190,000
Clearwater	1990	-	Egg	300,000
Clearwater	1989	-	Egg	280,000
Clearwater	1985	-	Egg	357,000
Clearwater	1984	1984-10-28	Egg	1,157,640
Clearwater	1983	1983-10-25	Egg	269,000
Clearwater	1982	-	Egg	843,000
Clearwater	1981	1981-06-04	>1 year	15,000
Clearwater	1981	1981-11-04	Egg	688,000
Clearwater	1980	1980-05-28	>1 year	15,000
Clearwater	1979	1979-06-06	>1 year	15,000
Clearwater	1973	1973-05-30	>2 years	1,500
Clearwater	1972	1972-05-29	>1 year	10,000
Clearwater	1971	1971-05-15	>1 year	10,000
Clearwater	1970	1970-05-25	>1 year	15,000

Clearwater	1968	1968-05-22	>1 year	10,000
Clearwater	1967	1967-06-19	>1 year	3,000
Clearwater	1966	1966-06-08	>1 year	5,000
Clearwater	1966	1966-06-21	Fingerling	30,000
Clearwater	1965	1965-07-13	Fry	20,000
Clearwater	1965	1965-06-21	Fingerling	8,000
Clearwater	1954	-	Fingerling	6,000
Clearwater	1953	-	Fingerling	5,000
Clearwater	1952	-	Fingerling	12,000
Clearwater	1951	-	Fingerling	4,000
Clearwater	1950	-	Fingerling	3,000
George	2001	2001-06-04	Fingerling	25,000
George	2000	2000-05-23	12-15cm	25,000
George	1999	1999-06-02	12-15cm	27,300
George	1998	1998-05-07	Fingerling	25,000
George	1997	1997-05-29	Fingerling	38,000
George	1995	1995-05-17	Fingerling	27,000
George	1992	-	>1 year	26,000
George	1986	-	>1 year	81,658
George	1984	1984-04-17	>1 year	27,000
George	1983	1983-05-18	>1 year	32,000
George	1981	1981-05-11	>1 year	10,000
George	1980	1980-05-13	>1 year	6,000

George	1979	1979-05-24	>1 year	6,000
George	1978	1978-05-18	>1 year	6,800
George	1975	1975-05-26	>2 years	2,000
George	1975	1975-05-26	>1 year	4,000
George	1974	1974-05-22	>1 year	10,000
George	1968	1968-05-21	>1 year	5,000
George	1967	1967-05-24	>1 year	5,000
George	1962	1962-06-11	Fingerling	50,000
George	1961	1961-06-13	Fingerling	28,000
George	1960	1960-05-30	Fingerling	50,000
George	1959	1959-05-25	Fingerling	50,000
George	1958	1958-05-09	Fingerling	80,000
George	1957	1957-05-09	Fingerling	80,000
George	1956	-	Fingerling	80,000
George	1955	-	Fingerling	45,000
George	1954	-	Fingerling	64,000
George	1953	-	Fry	115,000
George	1952	-	Fry	186,660
George	1950	-	Fingerling	88,000
George	1949	-	Fingerling	24,000
George	1947	-	Fingerling	55,000
George	1946	-	Fry	52,000
George	1945	-	Fingerling	20,000

Second Cranberry	1951	-	Fingerling	3,000
Second Cranberry	1948	-	Adult (>30cm)	1,000

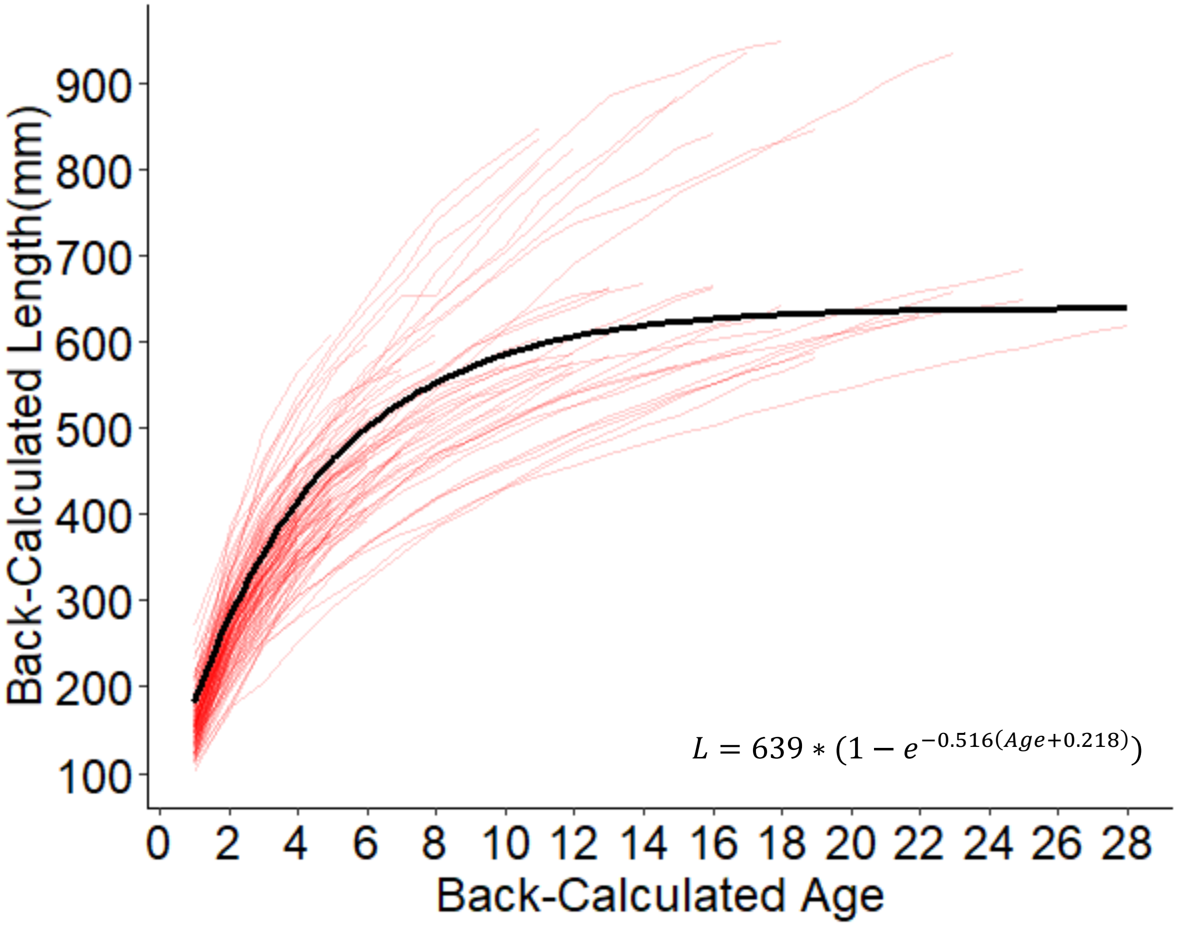

Figure A.2.1. Clearwater Lake lake trout (*Salvelinus namaycush*) von Bertalanffy growth function (n = 117). Main curve is depicted as the black line, while the individual back-calculated growth curves are in red (*L* = TL in mm). A split in growth occurs around the 650mm mark, which may indicate two different life-history strategies.

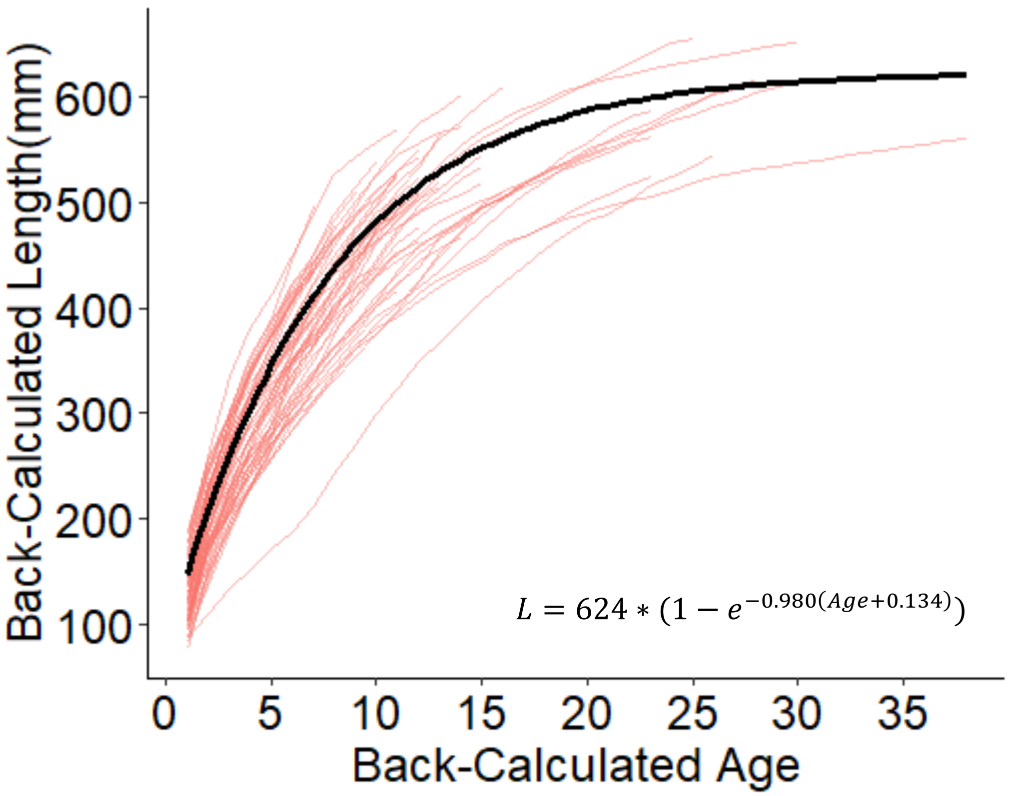

Figure A.2.2. George Lake lake trout (*Salvelinus namaycush*) von Bertalanffy growth function (n = 64). Main curve is depicted as the black line, while the individual back-calculated growth curves are in red (*L* = TL in mm).

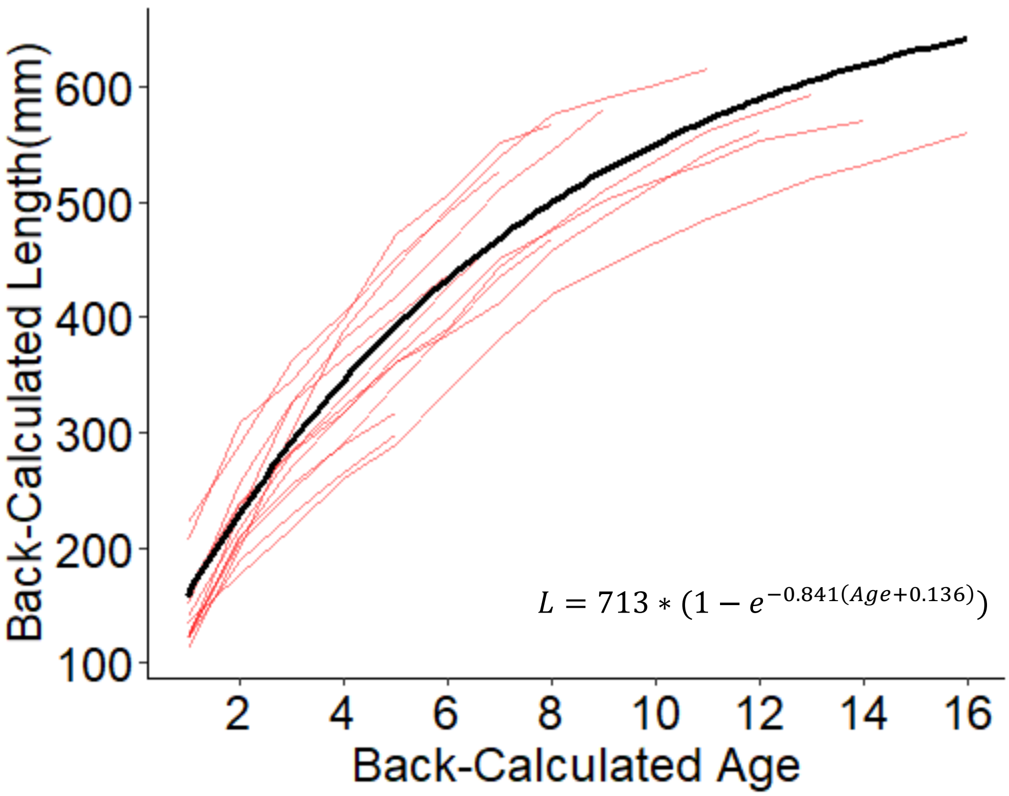

Figure A.2.3. West Hawk Lake lake trout (*Salvelinus namaycush*) von Bertalanffy growth function (n = 13). Main curve is depicted as the black line, while the individual back-calculated growth curves are in red (*L* = TL in mm).

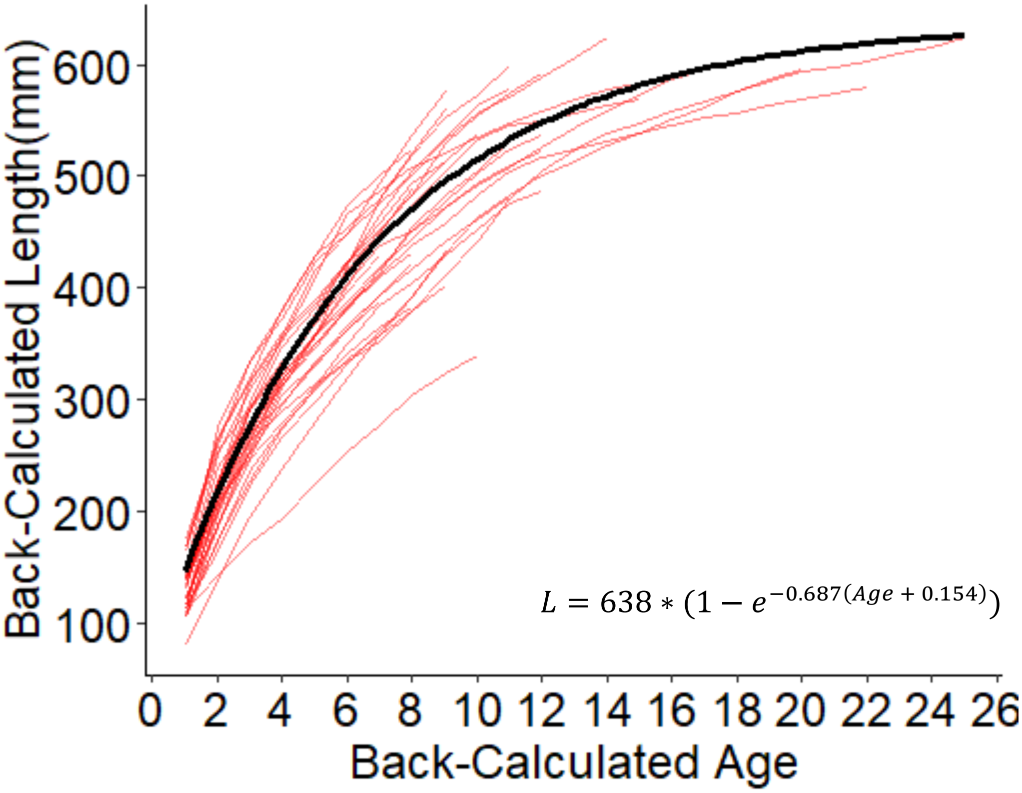

Figure A.2.4. Mantario Lake lake trout (*Salvelinus namaycush*) von Bertalanffy growth function (n = 29). Main curve is depicted as the black line, while the individual back-calculated growth curves are in red (*L* = TL in mm).

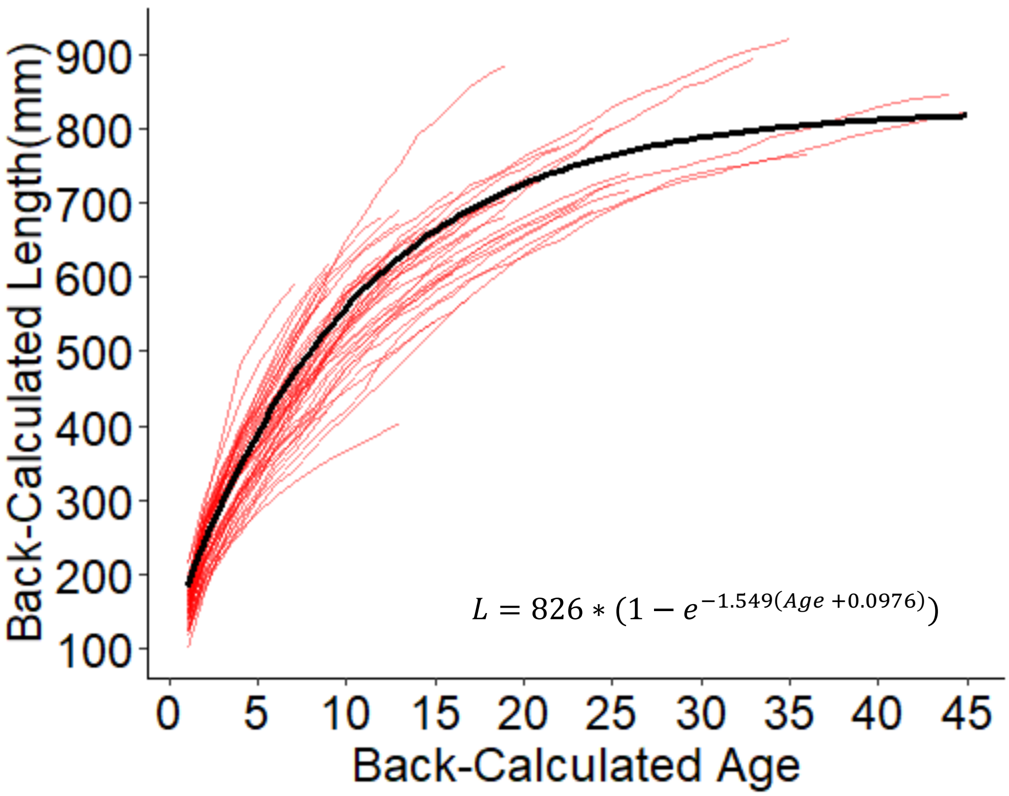

Figure A.2.5. Second Cranberry Lake lake trout (*Salvelinus namaycush*) von Bertalanffy growth function (n = 47). Main curve is depicted as the black line, while the individual back-calculated growth curves are in red (L = TL in mm).

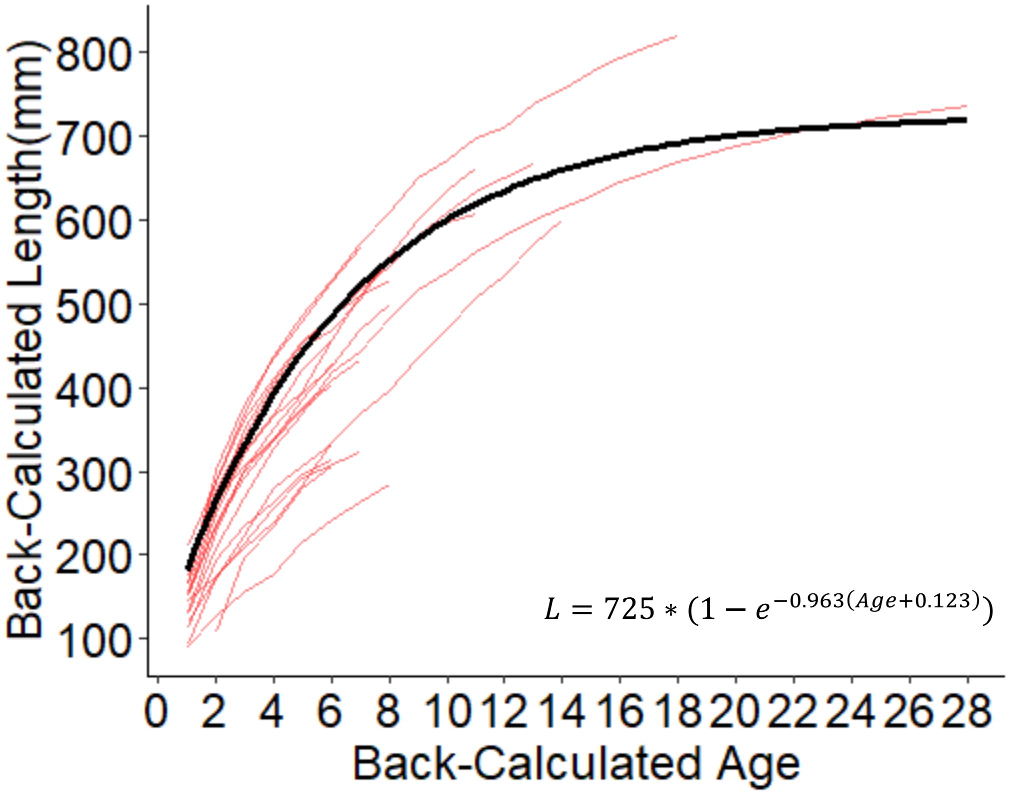

Figure A.2.6. High Lake lake trout (*Salvelinus namaycush*) von Bertalanffy growth function (n = 18). Main curve is depicted as the black line, while the individual back-calculated growth curves are in red (*L* = TL in mm).