THE INFLUENCE OF THE PREY COMMUNITY ON THE GROWTH AND LIFE HISTORY VARIATION OF AQUATIC APEX PREDATORS IN THE CANADIAN BOREAL SHIELD

by

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Abstract

Northern Pike (*Esox lucius* (Linnaeus, 1758)) and Lake Trout (*Salvelinus namaycush* (Walbaum, 1792)) are important apex predatory fish species that have ubiquitous distributions across Canada. While these species have been well studied due to their economic value, there remains considerable uncertainty around the influence of prey community dynamics on their growth and life history variation across the Canadian Boreal Shield. I investigated how changes and differences in prey community dynamics of Boreal Shield lakes influence the growth and life history traits expressed by these apex predators to further understand how their life history strategies have evolved, as well as how their life history strategies might shift in the face of environmental change. Broad geographic comparisons among Northern Pike populations revealed evidence for a widespread generalist foraging strategy, one that takes advantage of the availability of offshore Cisco (*Coregonus artedi* (Lesueur, 1818)). Similar to the offshore predator Lake Trout, Northern Pike reached larger asymptotic lengths in lakes with greater abundances of Cisco. Northern Pike additionally exhibited slower early growth rates and lower mortality rates in lakes with greater abundances of Cisco. In the absence of larger offshore prey fish, Lake Trout growth appears to be strongly influenced by the availability of nearshore prey fish in Boreal Shield lakes. Following an increase in the productivity of cyprinids in an experimental lake, the early growth rates of Lake Trout increased significantly, with the greatest amount of growth occurring after a switch to piscivory at age 2. With a variety of stressors threatening the health and stability of aquatic ecosystems, this research provides vital information pertaining to the influence of prey community dynamics on the growth potential and life history variation of aquatic apex predators in the Canadian Boreal Shield.

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Chapter One: General Introduction

Life history evolution has been a subject at the forefront of ecology and evolution for decades and continues to be a major focus of research today (Stearns 1977, Stearns 2000). Researchers remain interested in how natural selection has shaped variation in growth and life history strategies of organisms, and there has been an emphasis on how and why these strategies vary with respect to resource and habitat availability, reproduction, competition, mortality, and genetics (Beverton 1987, Charnov 1993, Charnov et al. 2013, Reznick 1985, Roff and Fairbairn 2012). Life history strategies of organisms reflect a series of trade-offs among traits to maximize overall fitness in a given environment (Stearns 1989, Stearns 2000). Traditional examples of life history trade-offs within organisms include faster early growth rates and earlier reproductive investment with greater adult mortality (Reznick et al. 1990, Williams 1957), slower early growth rates with greater juvenile mortality and lower adult mortality (Dmitriew 2011), and larger asymptotic sizes with larger sizes at maturity (Martin and Fry 1973, Shuter et al. 2016). Understanding what influences variation and trade-offs in life history strategies of organisms will continue to further our understanding of evolution and provide essential information for the conservation and preservation of species in changing environments.

In the Canadian Boreal Shield, research on growth and life history variation of many species has helped researchers and conservationists understand how species persistence might change with shifts in their environment. The Canadian Boreal Shield is home to over a million freshwater lakes that support a combination of subsistence, commercial, and recreational fisheries (Fisheries and Oceans Canada 2012), and aquatic apex predatory species (e.g. Lake Trout *Salvelinus namaycush*, Northern Pike *Esox lucius*) have been studied extensively because of their ecological importance and economic value. These aquatic ecosystems currently face a variety of threats to their ecological health and stability, including: nonnative species invasions (Vander Zanden et al. 1999); climate change (Chu et al. 2005, Schindler et al. 1996); pollution, such as mercury, endocrine disruptors, and excess nutrients (Fitzgerald et al. 1998, Kidd et al. 2014, Schindler 2006); and anthropogenic development (Søndergaard and Jepessen 2007). Thus, it is vital to fully understand constraints on the growth and life history variation of aquatic apex predatory species in the Canadian Boreal Shield to effectively manage populations in response to future environmental change.

A variety of environmental, physical, and biological factors influence the growth and life history of fish. While environmental factors such as climate can influence the growth of fish via changes in metabolic rates, habitat and resource accessibility (Gillooly et al. 2001, Venturelli et al. 2010), the growth of fish is also directly mediated by genetic constraints (Wilson et al. 2003). Throughout their lives, aquatic apex predators will encounter a wide array of prey sizes as they grow, and they typically undergo multiple ontogenetic diet shifts (Trippel and Beamish 1989, Vander Zanden and Rasmussen 1996). These ontogenetic diet shifts are accompanied by shifts in foraging behavior and habitat use as apex predators seek out larger, more energetically-favorable prey (Mittelbach and Persson 1998). Increased availability of larger-bodied prey results in a decrease in the ratio of predator-to-prey body size, which in turn allows aquatic apex predators to reach larger body sizes by maximizing differences between energy gained and energy spent foraging (Kaufman et al. 2006, Pyke et al. 1977, Shuter et al. 2016). In the absence of larger-bodied prey, aquatic apex predators are often stunted and exhibit smaller body sizes (Pazzia et al. 2002, Venturelli and Tonn 2006). However, larger body sizes can also be obtained when smaller-bodied prey are highly productive. Rapid growth of fish early in life can result from a trade-off between foraging effort and predation risk (Biro et al. 2004), where the rate of growth is limited by the amount of predation pressure that fish experience for aggressively foraging during their early life history. Despite this, the early growth rates of fish are often sub-maximal even in the absence of predation, suggesting that rapid early growth can influence fitness via trade-offs with other key biological traits (Dmitriew 2011). Indeed, the availability of prey appears to influence growth and other key life history traits of aquatic apex predators via both intrinsic and extrinsic factors.

In addition to influencing body size, the availability of larger-bodied prey can result in larger sizes at maturity of aquatic apex predators (Martin and Fry 1973, Shuter et al. 2016). As more energy is diverted to reproduction after the onset of maturity, less energy is available for growth, and thus aquatic apex predators may undergo selection to delay maturation to reach larger sizes and avoid gape-size limitations that prevent them from foraging upon larger-bodied prey (Martin and Fry 1973). Obtaining larger body sizes and greater condition by feeding upon high quality prey allows aquatic apex predators to maximize their fitness by increasing the quantity (because fecundity is strongly related to body size in female fishes; Kamler 2005) and quality of their eggs (Heinimaa and Heinimaa 2004), ultimately resulting in greater amounts of offspring and their survival (Roff 1992, Stearns 1992). When larger-bodied prey are absent, smaller prey are more abundant, and there are no additional constraints to early growth (i.e. risk of mortality), aquatic apex predators undergo selection to grow rapidly and reach maturity earlier in life. Each of these life history strategies allow aquatic apex predators to maximize their reproductive output over time in a given environment.

Mortality is another key trait that drives trade-offs with growth and reproduction through extrinsic factors. High extrinsic mortality rates of populations have been shown to result in faster growth and greater reproductive investment early in life (Reznick et al. 1990, Williams 1957). In contrast, when adult extrinsic mortality rates are low, organisms should exhibit slower early growth, reach sexual maturity later in life, and age more slowly (Stearns 2000, Williams 1957). These strategies are a means of bet-hedging so that organisms can maximize their lifetime reproductive success. The mortality rates of fish are influenced by a variety of mechanisms, including: habitat availability (Sogard 1997), climate (Beverton 1987), prey availability (Kaemingk et al. 2014), competition (Mehner et al. 1996), and predation and exploitation (Allen et al. 1998, Wasylenko et al. 2014). These factors feedback with each other and help shape the life history strategies that we observe in the natural world.

Theoretical work on life history evolution has provided a substantial, reliable framework used by researchers to understand how organisms have evolved to survive in their environments. In combination with behavioral and community ecology, life history theory can be used to investigate what ultimately drives trade-offs in life history traits observed both within and among populations. While a large amount of work has been published on the life history variation of aquatic apex predators in the Canadian Boreal Shield (Shuter et al. 1998, Venturelli et al. 2010), research has focused primarily on environmental drivers without considering the potential impact of the prey community in describing unexplained variation across the geographic range of the predators. There remains uncertainty in how changes and differences in community dynamics of aquatic ecosystems influences life history variation of aquatic apex predators, specifically that of Northern Pike and Lake Trout.

Northern Pike Biology

Northern Pike (*Esox lucius*) is a member of the Esocidae and is the only species in the genus *Esox* with a circumpolar distribution throughout the Holarctic (Craig 2008). While the evolutionary origin of Northern Pike is still debated, research suggests that the present day distribution of Northern Pike radiated from multiple glacial refugia (Skog et al. 2014). However, Skog et al. (2014) also found that one lineage of Northern Pike was found throughout the Holarctic, which suggests that the species originally dispersed from a common refugium. This refugium was most likely in Asia, as the overall genetic diversity of Northern Pike is greater in Eurasia than in North America (Skog et al. 2014). In North America, Northern Pike are widely dispersed and have a ubiquitous distribution across the Canadian Boreal Shield (Scott and Crossman 1973). Although they are mainly a freshwater species, Northern Pike can also inhabit coastal brackish water habitats of the Baltic Sea (Craig 2008, Engstedt et al. 2014) and the Arctic Ocean (Loewen, pers. comm.).

Northern Pike are prolific, spawning in the spring around ice-off, and they have a strong dependence on littoral vegetation for spawning and nursery habitat (Casselman and Lewis 1996, Pierce and Tomcko 2005). Northern Pike eggs are adhesive and stick to macrophytes, which helps protect eggs from predators (Scott and Crossman 1973). Furthermore, littoral vegetation helps both juvenile and adult Northern Pike avoid predation from competing species and cannibalistic Northern Pike (Eklöv 1997). Casselman and Lewis (1996) showed that the depth of nursery habitat was related to the size and age of Northern Pike. Thus, the amount of vegetation in an ecosystem has strong effects on both the survival and behavior of Northern Pike.

Northern Pike grow rapidly and typically reach sexual maturity around 2-5 years of age (Scott and Crossman 1973). They are efficient predators that are thought of as specialist piscivores due to their morphology and foraging behavior. Their elongated bodies, large and wide snout, depressed vomerine teeth, and sharp, regenerable teeth allow Northern Pike to capture, hold, and consume prey (Raat 1988). Northern Pike are visual predators that typically forage by ambush tactics, their strike success rates improve with experience and are as high as

95% (Raat 1988, Webb and Skadsen 1980). Young Northern Pike typically strike at their prey catching them crossways in their mounts and swallowing them head first (Raat 1988). Analogous with their foraging success, the introduction of Northern Pike into small Boreal Shield lakes at the IISD-Experimental Lakes Area led to the extirpation of prey fish communities (Findlay et al. 2005, Nicholson et al. 2015). Typically, Northern Pike are opportunistic, omnivorous predators that will subsist on anything from invertebrates to waterfowl (Solman 1945, Venturelli and Tonn 2006). However, Nilsson and Brönmark (2000) found Northern Pike to be size-selective predators that can eat larger prey than their gape-size would suggest.

Although they are thought of as specialist piscivores, Northern Pike can subsist as the only fish species in some lakes by feeding on benthic invertebrates and energy-rich leeches (Venturelli and Tonn 2006). However, Venturelli and Tonn (2006) found that while feeding on invertebrates was adequate to meet the energy requirements of juvenile Northern Pike, the growth of adults in these lakes was stunted. Margenau et al. (1998) found that small fusiform prey species like Yellow Perch compose an important contribution to the diet of Northern Pike, where as the availability of larger fusiform prey may be important to the growth of adult Northern Pike (Diana 1979, Jacobson 1992). Although Northern Pike are generally found in shallow, moderately productive, and vegetated waters (Harvey 2009), case studies show that larger Northern Pike may prefer colder, deeper water with larger offshore prey (Chapman and Mackay 1984, Jacobson 1992, Makowecki 1973). Furthermore, multiple studies have shown that Northern Pike take advantage of productive habitats and may distribute themselves in an ideal-free manner (Haugen et al. 2006, Kobler et al. 2009). However, there has to date been no widespread investigation of the influence of the prey community on growth and life history variation of Northern Pike. In addition to prey type, other abiotic and biotic factors, such as productivity, water temperature, water transparency, and density of competitors may influence their growth (Casselman and Lewis 1996, Margenau et al. 1998, Pierce et al. 2003).

Northern Pike population size and structure is influenced by a variety of factors. As discussed previously, the availability and size of their prey likely has a large impact on the population dynamics on Northern Pike (Diana 1979, Jacobson 1992, Margenau et al. 1998, Venturelli and Tonn 2006). Inter and intra-specific predation on Northern Pike has also been shown to structure Northern Pike populations. Juvenile Northern Pike abundance and growth increases when predator abundances are reduced (Grimm 1981). Furthermore, large, cannibalistic Northern Pike may reduce intra-specific competitive impacts by foraging on smaller juveniles (Grimm 1981). Pierce et al. (2003) highlighted potential negative effects of intra-specific competition by showing that Northern Pike size structure was negatively related to Northern Pike density in Minnesota and Wisconsin lakes. Finally, Northern Pike may exhibit a compensatory response to increased exploitation, which could lead to increased abundances of fast growing, early maturing individuals (Allen et al. 1998).

Lake Trout Biology

Lake Trout (*Salvelinus namaycush*) are a long-living, late-maturing member of the family Salmonidae that are indigenous to, and have a widespread distribution across, northern North America (Scott and Crossman 1973). Native Lake Trout populations can be found as far north as the brackish water lakes connected to the Arctic Ocean and as far south as the southern tip of Lake Michigan. They are thought of mainly as a freshwater species, but recent research has found evidence that Lake Trout can reproduce in brackish water (Kissinger et al. 2015). Due to the rapid decline of Lake Trout in the Laurentian Great Lakes during the 20th century and a resulting surge in stocking efforts, the genetic diversity of Lake Trout has been well studied

(Guinand et al. 2002, Selgeby et al. 1995). Guinand et al. (2002) highlighted that there has been a significant loss in the genetic diversity of Lake Trout in the Great Lakes over time. However, significantly less research has focused on the genetic diversity of Lake Trout in inland lakes (Piller et al. 2005). While specific details on their evolution remain unknown, Lake Trout are thought to have evolved in response to environmental change during the Pleistocene glaciations (Wilson and Mandrak 2004). The distribution of Lake Trout in North America has likely arisen from multiple glacial refugia, and it is thought that Lake Trout survived the most recent Wisconsinan glaciation in six or more different refugia (Gunn et al. 2004).

Lake Trout are stenothermic and need cold, well-oxygenated water (Evans 2007, Plumb and Blanchfield 2009). In their northern-most range, Lake Trout can be found in cold rivers and shallow lakes (Scott and Crossman 1973). However, in their southern range, Lake Trout are constricted to cold, deep lakes that remain from the Pleistocene glaciations. The preferred temperature of Lake Trout is around 10-12° C (Magnuson et al. 1990), and Lake Trout spend most of their time in deep water associated with these temperatures. However, Lake Trout may enter shallower habitats when water temperatures are in their desired range or when prey resources are limited (Dolson et al. 2009, Morbey et al. 2006).

Lake Trout spawn in autumn when water temperatures fall below 11°C (Scott and Crossman 1973). Females develop large eggs and scatter them over rocky shoals where they get displaced in the interstitial space within the rocky substrate. This substrate is typically made up of pebble, cobble, or broken rubble, and the size of the substrate has been found to be an important feature of Lake Trout spawning shoals (Sly 1988). The size of the substrate may be important to the survival of Lake Trout embryos because of shelter from predators and the exchange of oxygen (Gunn 1995). Wind has also been hypothesized to be an important factor in

Lake Trout reproduction, as currents induced by wind can remove fine sediments and circulate oxygen to the eggs (Gunn 1995, Sly 1988).

Lake Trout are pelagic predators that can sustain long periods of swimming. The metabolism of Lake Trout is adapted to cold water which allows them to move and forage at low temperatures (Gunn et al. 2004). Lake Trout are opportunistic predators that can endure extensive periods without feeding (Gunn et al. 2004). In the Canadian Boreal Shield, Lake Trout are productive in small lakes with simple prey fish communities (Shuter et al. 1998). As young-of-the-year, they primarily forage upon zooplankton and benthic invertebrates (Scott and Crossman 1973). When available, the macro-invertebrates *Mysis* and *Chaoborus* have been found to be important components in the diets of juvenile and adult Lake Trout (Ellis et al. 2011, Trippel and Beamish 1993). Though Lake Trout can subsist in lakes without any prey fish, prey fish are important for the growth efficiency of Lake Trout (Pazzia et al 2002). Lake Trout often forage on prey fish by making vertical dashes through the water column and attacking them from below (Dunlop et al. 2010). Cisco (*Coregonus artedi*) are common prey for adult Lake Trout, and the availability of Cisco may result in greater growth rates, larger sizes, older ages and larger sizes at maturity, and greater fecundity of Lake Trout (Martin 1970, Mason et al. 1998, Trippel and Beamish 1989). However, few studies have quantified the influence of Cisco and other offshore prey species on the growth and life history variation of Lake Trout across the Canadian Boreal Shield. Furthermore, there remains significant uncertainty around the constraints to the early growth and life history variation of Lake Trout.

Thesis Objectives

This thesis investigates the influence of prey community composition and dynamics on the growth and life history variation of two aquatic apex predators in the Canadian Boreal Shield, Northern Pike and Lake Trout. I expect that the availability of different prey types during the ontogenetic stages of these predators will influence their life history traits and associated trade-offs. Specifically, in Chapter 2, I sought to evaluate the evidence for a generalist foraging strategy of Northern Pike— one that takes advantage of offshore prey— by quantifying the influence of offshore prey on growth and life history traits of Northern Pike across the Canadian Boreal Shield. The response of Northern Pike, generally regarded as a nearshore apex predator, was then compared with Lake Trout, a species traditionally viewed as an offshore apex predator, to determine if the life history strategies of the two species respond similarly to the availability of high quality offshore prey. In Chapter 3, I quantified changes in the early growth and condition of Lake Trout in one lake over time in response to shifts in the abundance of *Mysis diluviana* and forage fish following an increase in lake productivity. By examining the influence of prey community composition and dynamics on growth and life history traits of aquatic apex predators both across and within ecosystems in the Canadian Boreal Shield, I provide vital information for researchers and fisheries managers on the connection between community changes in aquatic ecosystems and the life history strategies of aquatic apex predator populations.

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Chapter Two: Northern Pike (*Esox lucius*) Life History Variation in the Canadian Boreal Shield: Specialist or Generalist Predator?

Abstract

Northern Pike (*Esox lucius*) are important aquatic apex predators in freshwater ecosystems across the Canadian Boreal Shield. Historically, Northern Pike have been described as nearshore, sit-and-wait predators that use the cover of littoral vegetation to ambush their prey. However, more recent literature suggests that many aquatic apex predatory species may act more as generalists and feed more opportunistically than previously thought. Here, I investigated the degree to which Northern Pike might be generalist apex predators by examining the influence of the offshore prey community on their growth and life history variation across a large portion of the Canadian Boreal Shield. I then compared these results to those of Lake Trout (*Salvelinus namaycush*), a well-known pelagic predator, to evaluate similarities between these two species with purportedly different foraging strategies. The life history analyses revealed that, like Lake Trout, Northern Pike reach significantly larger asymptotic lengths in lakes with greater abundances of the offshore prey fish, Cisco (*Coregonus artedi*). Additionally, Northern Pike have significantly slower early growth rates and lower mortality rates in lakes with greater abundances of Cisco. Nearshore species like Yellow Perch (*Perca flavescens*) are more strongly correlated with early growth rates of Northern Pike, while Northern Pike likely make an ontogenetic shift later in life to foraging on Cisco when they are available. Variation in the relative abundances of both Northern Pike and Lake Trout populations was best explained by physical lake characteristics and growing degree days. The results of this study revealed similar responses of both Northern Pike and Lake Trout life history strategies to the abundance of

offshore prey across the Canadian Boreal Shield, suggesting that Northern Pike behave more as generalists, rather than nearshore specialists, when offshore prey are readily available.

Introduction

Foraging strategies of animals are positively selected through natural selection as a means of maximizing fitness (Pyke et al. 1977). This selective pressure results in a variety of foraging strategies of animals, most of which can be sorted into two groups: generalist or specialist strategies. Generalist species are omnivorous and able to thrive in a broad range of environmental conditions. In contrast, specialist species have a limited diet and narrow range of environmental conditions in which they can thrive, as they have been selected to adapt to specialized ecological niches to obtain competitive advantages. However, specialization often comes with the trade-off of not being able to adapt as well to changing conditions (McKinney 1997). Generalists are typically better at responding to ecological change because of their wider ecological niche and ability forage across habitats where prey are abundant. Such foraging behavior may be beneficial for predators and can lead to different life history strategies depending on the quality and quantity of their prey. In the Canadian Boreal Shield, aquatic apex predators can integrate nearshore and offshore food webs (Dolson et al. 2009, Vander Zanden and Vadeboncoeur 2002), and this behavior may be beneficial to their growth and life history (Kaufman et al. 2009). As such, aquatic apex predators may exhibit more generalized and opportunistic foraging strategies than the historical literature would suggest (Bartley et al. 2015, McMeans et al. 2016).

Northern Pike (*Esox lucius*) are ecologically important aquatic apex predators that have a circumpolar distribution throughout the Holarctic and can be found in lakes, rivers, and streams across the Canadian Boreal Shield (Scott and Crossman 1973). Research on Northern Pike across their distribution has highlighted their behavioral plasticity and adaptability as a species (Craig 2008, Raat 1988). Despite this, Northern Pike have been mainly described as nearshore specialists that ambush their prey from the cover of littoral vegetation, woody debris, etc. (Raat 1988, Scott and Crossman 1973). This is likely because Northern Pike abundance is associated with the amount of littoral vegetation in aquatic ecosystems which serves as their spawning and nursery habitat (Casselman and Lewis 1996, Pierce and Tomcko 2005). However, Northern Pike display a large amount of plasticity in their ecology, growth, and life history traits (Craig 2008, Malette and Morgan 2005), and they integrate into offshore food webs on occasion, which may influence their growth and life history strategies (Colby et al. 1987, Makowecki 1973).

As life history strategies of organisms are under natural selection to maximize fitness, they vary across environmental gradients with respect to resource and habitat availability, competition, and mortality (Beverton 1987, Charnov 1993, Charnov et al. 2007, Charnov et al. 2013). To explain variation in life history strategies expressed by populations, life history traits (e.g. asymptotic length, early growth rate, size and age at maturation, mortality rate) have been compared within and among populations of one or more species (Beverton 1987, Kaufman et al. 2009, Pauly 1980, Shuter et al. 1998, Shuter et al. 2016). Variations in life history traits are often explained by trade-offs among growth, maturity, and longevity. For example, higher mortality rates are often associated with faster growth rates, earlier ages at maturity, smaller sizes at maturity, and smaller asymptotic sizes of fish populations (Charnov and Berrigan 1990, Pauly 1980). Moreover, smaller ratios of predator to prey size often results in larger sizes, older ages at maturity and larger asymptotic lengths of particulate feeding fish (Shuter et al. 2016).

Although many factors combine to influence the growth and life history traits of aquatic apex predators, a major determinant of these traits is both the quality and quantity of food (Kaufman et al. 2009, Margenau et al. 1998, Trippel and Beamish 1989). Fish exhibit indeterminate growth, with rapid growth during early life history and slower growth following sexual maturation due to the allocation of energy to gonadal development (Stearns 1992). Thus, surplus of energy intake over the cost of reproduction is required to grow post-maturation. According to optimal foraging theory, natural selection acts upon organisms to maximize their fitness by increasing the difference between energy obtained from prey and energy spent foraging (Charnov 1976, Pyke et al. 1977). Optimal foraging can be carried out by aquatic apex predators by foraging upon larger, more energy-dense prey as they grow to larger sizes and experience increased energetic costs of foraging. Since predator foraging costs increase as the ratio of their size to the size of their prey increases (Kerr 1971, Kerr and Ryder 1977), the availability of larger, energy-dense prey is needed for predators to avoid energetic bottlenecks and stunting (Kaufman et al. 2006, Pazzia et al. 2002).

In the Canadian Boreal Shield, offshore prey such as Cisco (*Coregonus artedi*) and Lake Whitefish (*Coregonus clupeaformis*) often reach larger body sizes and have higher energy densities than their nearshore counterparts, Yellow Perch (*Perca flavescens*) and White Sucker (*Catostomus commersonii*) (Bryan et al. 1996), which are common prey for Northern Pike (Beaudoin et al. 1999, Diana 1979, Margenau et al. 1998). Thus, foraging on large offshore prey may be more beneficial for Northern Pike than strictly foraging nearshore. Case studies have reported that large offshore prey can be important contributors to the diet and growth of Northern Pike (Colby et al. 1987, Jacobson 1992, Makowecki 1973) and other aquatic apex predators when they are available (Kaufman et al. 2009, Mason et al. 1998, Matuszek et al. 1990, Pazzia et al. 2002, Trippel and Beamish 1989). As such, the availability of offshore prey is likely to have a strong influence on the growth and life history variation of Northern Pike populations across the Canadian Boreal Shield.

The objective of this study was to evaluate evidence for a generalist foraging strategy of Northern Pike that takes advantage of large-bodied offshore prey fish when they are available. If Northern Pike are generalist predators, I predict that their growth and life history traits will respond positively to the availability of offshore prey and in a similar manner to that of Lake Trout (*Salvelinus namaycush*), a free-swimming offshore apex predator. The influence of the offshore prey fish community (i.e. Cisco, Lake Whitefish) was investigated relative to common nearshore prey species (i.e. Yellow Perch, White Sucker), physical lake characteristics (i.e. lake surface area, mean depth), and environmental variables (i.e. growing degree days) that have been hypothesized to affect the growth and life history variation of Northern Pike (Casselman and Lewis 1996, Chezik et al. 2014a, Chezik et al. 2014b, Pierce and Tomcko 2005). Based on limited published case studies that indicate Northern Pike may take advantage of offshore prey (Colby et al. 1987, Jacobson 1992, Makowecki 1973), I predict that Northern Pike and Lake Trout will reach larger asymptotic lengths, exhibit slower early growth rates, and exhibit lower mortality rates across a wide range of lakes characterized by greater offshore prey abundance.

Methods

Data Compilation

I used multiple standardized gillnetting datasets in this study to evaluate and compare Northern Pike and Lake Trout life history traits with prey community composition. The Ontario Ministry of Natural Resources and Forestry’s (OMNRF) Broad-scale Fish Community Monitoring (BsM) program (2008-2013) was used for Northern Pike and Lake Trout life history analyses, and the Fall Walleye Index Netting (FWIN) survey (1993-2002) was used for female and male Northern Pike life history analyses. The FWIN dataset did not contain sufficient data to investigate Lake Trout life history variation, and the BsM dataset did not contain sufficient data to investigate female and male Northern Pike life history traits separately. However, the use of both BsM and FWIN surveys allowed for a comparison to ensure that the results observed were not artifacts of differences in sampling methodologies.

Fish Sampling

FWIN

The FWIN sampling procedure utilized a stratified random sampling design that consisted of overnight sets of multi-mesh gillnets with eight sequential mesh panels of 25, 38, 51, 64, 76, 102, 127, and 152 mm (Morgan 2002). Gillnets were set for 24 hours perpendicular to shore at two different depth strata: 2-5 m and 5-10 m. Net sets alternated between the large or small mesh panels placed closest to the shore. The location and number of nets set were estimated from the surface area and depth of the lakes, and there were a minimum of eight nets set for each lake. Sampling occurred in the fall when surface water temperatures had cooled to 15° C and proceeded until surface temperatures cooled below 10° C. Fish captured were assigned a unique identification number, and the net number, mesh size, location, date, and length of time the net was set were recorded. The species identification, fork length, total length, round weight, sex, maturity, and age were recorded for all sportfish caught in the nets. Scales and cleithra were used by biologists and technicians from the provincial fisheries ageing lab located in Dryden, ON, to estimate the age of Northern Pike. Only the fork length and total length were measured for non-sport fish species. Catch-per-unit-effort (CPUE) estimates were calculated for all species of fish caught in at least 50 percent of the FWIN lakes sampled. Additional details can be found in Morgan (2002).

BsM

Fish were sampled according to the OMNRF BsM protocol, which incorporated two types of gillnets: the North American (NA1) large-mesh gillnet targeting fish larger than 20 cm in length, and the Ontario small-mesh gillnet, which targets smaller fish (Sandstrom et al. 2013). Only the large-mesh gillnet data were used in this study. Large-mesh gillnets were comprised of eight non-sequential panels with stretched mesh sizes of 38, 51, 64, 76, 89, 102, 114, and 127 mm. Nets were set during summer when the surface water temperature is greater than 18° C. Large-mesh gillnets were set for 16-22 hours. The large-mesh gillnets are 49.6 m long and 1.8 m tall, and they were set oriented perpendicular to oblique contours, depth stratified to up to 75 m, and spatially stratified to have effort equally distributed over the entirety of the lakes. All fish sampled using the large-mesh gillnets had their species identification, fork length, round weight, sex, and gonad condition recorded. Calcified ageing structures (i.e. scales, otoliths, cleithra, and fin rays) were also collected from each fish. Scales and cleithra were used for estimating the age of Northern Pike, while otoliths and scales were used for Lake Trout. All structures were aged by biologists and technicians from the provincial fisheries ageing lab located in Dryden, ON. Additional details can be found in Sandstrom et al. (2013).

Ecological variables

Abiotic and biotic predictor variables were included in this study (Table 2.1). Biotic variables included in the life history analyses were CPUE data for Northern Pike, Lake Trout, and putative prey species, including Cisco, Lake Whitefish, Yellow Perch, and White Sucker. CPUE was calculated as a lake-wide area-weighted CPUE, where CPUE and benthic area were calculated in each sampled depth stratum; CPUE was then estimated as an area weighted lake-wide mean. CPUE is proportional to the abundance of a stock present during the time fishing took place (Ricker 1975), therefore seasonal differences in fishing effort have the ability to influence the estimates. Northern Pike and Lake Trout CPUE were included as predictor variables in their respective life history models to investigate density dependent effects (Pierce et al. 2003, Rose et al. 2001). Cisco and Lake Whitefish CPUE were used as a measure of the abundance of offshore prey fish commonly found throughout the Boreal Shield. Yellow Perch and White Sucker CPUE were included as measures of the abundance of common nearshore prey species.

Abiotic predictor variables included growing degree days, lake surface area, and mean depth. Growing degree days were calculated as the cumulative number of degree days above 5° C and were used as an indicator of atmospheric temperature. Atmospheric temperatures are highly correlated with and drive lake water temperatures (Shuter et al. 1983), and growing degree days have been found to be correlated with fish distribution and life history traits (Chezik et al. 2014a, Chezik et al. 2014b, Chu et al. 2005, Venturelli et al. 2010). The surface area and mean depth of each lake were compiled from the OMNRF Aquatic Habitat Inventory (AHI) (Dodge et al. 1985).

All variables included in the analyses were tested for multicollinearity by examining Pearson's correlation coefficients (Appendix A) and variance inflation factors (VIFs) in statistical models. VIFs were calculated for all covariates, and those with the highest VIFs were removed sequentially until all VIF values were less than three (Zurr et al. 2010). The only variable to be removed from any of the models was percent littoral zone, an initial variable of interest for this study because Northern Pike depend on littoral vegetation for spawning habitat, cover from predators, and cover for ambushing prey (Casselman and Lewis 1996, Pierce and Tomcko 2005). Percent littoral zone was removed because it had a high variance inflation factor, large Pearson correlation coefficient (r = -0.88) and strong negative relationship with mean depth (r^2 = 0.80, Figure A6).

Life History Traits

Life history traits of Northern Pike and Lake Trout examined as response variables were asymptotic fork length, early growth rate, instantaneous total mortality rate, and relative abundance (CPUE). Male and female Lake Trout catch data within a lake were analyzed together to increase sample sizes; analyses of Ontario Lake Trout populations have shown minimal differences between male and female Lake Trout life history traits (McDermid et al. 2010). On the contrary, Northern Pike exhibit considerable sexual size dimorphism (SSD), where females mature later, reach larger asymptotic lengths, and reach older maximum ages than males (Craig 1996, Malette and Morgan 2005). Therefore, it is possible that conclusions drawn from the Northern Pike life history analyses would be different for combined sexes and separated sexes. To address this question, I used the FWIN dataset to investigate male and female Northern Pike life history variation with respect to the predictor variables of interest. Due to smaller sample sizes of Northern Pike in the BsM dataset, male and female catch data were combined to retain larger sample sizes for analyses. These patterns were compared to sex-specific patterns from the FWIN dataset for consistency in our life history results. The average Northern Pike sex ratio for the BsM dataset was 1.62 females per male, potentially biasing results towards females.

Asymptotic fork lengths (L_∞) of Northern Pike and Lake Trout populations were calculated by fitting the von Bertalanffy growth model (VBGM) to fork length-at-age data (Ricker 1975; Figure 2.1). The VBGM is described by the following equation:

$$L(t) = L_{\infty}(1 - e^{K(t-t0)}) \quad \textbf{(2.1)}$$

Where $L(t)$ is the fork length (mm) at age t (years), L_{∞} is the asymptotic fork length, K is Brody's growth coefficient, and t_0 is the theoretical age when the fish would have been zero length. The size of larval Northern Pike and Lake Trout at age 0 is often less than 10mm, thus t_0 was set to 0 for the VBGMs. A key assumption of the VBGM is that K is invariant (Ricker 1975). Early growth rates were described by the parameter omega (ω), which is useful for comparing von Bertalanffy growth curves, corresponds to the growth rate near time zero, and is the product of L_{∞} (mm) and K (per year) (Brody 1945, Charnov 2010, Gallucci and Quinn 1979).

Instantaneous total mortality rates (Z) were calculated for both datasets according to the Robson and Chapman method (Ricker 1975 pg. 31, Robson and Chapman 1961; Figure 2.2). The Robson and Chapman method assumes that all age classes are equally vulnerable to the sampling gear, survival is constant at all age classes, and all year classes recruited at the same abundance (Ricker 1975). Annual adult survival (S) was calculated as:

$$S = T/(\sum N + T - 1) \quad \textbf{(2.1)}$$

Where $T = N_x + 2N_{x+1} + 3N_{x+2}$, $\Sigma N = N_x + N_{x+1} + N_{x+2} + \ldots$, and N_x is equal to the number of fish whose age is equal to the modal age class plus 1 year (Smith et al. 2012). Instantaneous total mortality rates for the populations were then calculated as:

$$Z = -\log(S) \quad \textbf{(2.2)}$$

Relative abundance estimates of apex predators were represented by the CPUE of Lake Trout and Northern Pike, respectively. Relative abundance estimates were calculated and analyzed with males and females combined for both datasets. Life history traits were only calculated for populations of Northern Pike and Lake Trout with suitable sample sizes of at least 20 individuals per lake. For the FWIN dataset, this resulted in 155 and 109 lakes with suitable sample sizes for female and male Northern Pike life history analyses, respectively (Figure 2.3). For the BsM dataset, this criterion resulted in 130 and 96 lakes with suitable sample sizes for the Northern Pike and Lake Trout life history analyses, respectively (Figure 2.4). A summary of life history traits calculated for Northern Pike and Lake Trout populations are presented for both the FWIN (Table 2.2) and BsM (Table 2.3) datasets.

Statistical Analyses

Linear mixed models with a Gaussian error distribution were used to investigate which predictor variables (Table 2.1) accounted for the most observed variation in life history traits of Northern Pike and Lake Trout populations (Tables 2.2 and 2.3). Linear mixed models are extensions of linear models where the linear predictor contains both random effects and fixed effects, and they are useful for analyzing longitudinal data (Quinn and Keough 2002). Linear mixed models were developed and analyzed in R 3.1.2 (R Core Team 2014) using the packages "lme4" (Bates et al. 2015) and lmerTest (Kuznetsova et al. 2015). Significance of individual fixed effects in the models was estimated using a Satterthwaite approximation for denominator degrees of freedom (Kuznetsova et al. 2015). Random effects included in the analyses were the unique lake name and the year each lake was sampled. Fixed effects included the predictor variables discussed previously, with the exception that the CPUE of each study species was removed as a fixed effect when the CPUE of that species was the response variable being tested. CPUE data for each fish species, lake surface area, and mean depth were log-transformed ($\log_{10}$) in order to meet assumptions of normality. Growing degree days were scaled using the scale function in R 3.1.2 to convert growing degree days to a similar order of magnitude as other predictor variables. The summary function from the package "lmerTest" was used to calculate *p*-

values and degrees of freedom for *t*-tests based on a Satterthwaite approximation for denominator degrees of freedom (Kuznetsova et al. 2015).

To explicitly test the hypothesis that offshore prey abundance affects life history traits of aquatic apex predators, I used likelihood ratio tests to compare nested models with and without each offshore prey species abundance using the anova function in R 3.1.2. A statistically significant result ($p < 0.05$) indicated a significant effect of the abundance of that offshore prey species on the life history trait being tested. Marginal (including only fixed effects) and conditional (including fixed and random effects) pseudo-R-squared (R^2) values were calculated for the models. Pseudo-R^2 values were calculated for the linear mixed models according to methods developed by Nakagawa and Schielzeth (2013) and Johnson (2014). Marginal pseudo-R^2 values are calculated by gauging the variance explained by the fixed effects as a proportion of the sum of all the variance components, while conditional pseudo-R^2 values are calculated by additionally including the variance explained by random effects (Johnson 2014). Finally, variance partitioning was performed to estimate the independent explanatory power (R^2) of each of the fixed effects, which was used as a means of comparing the influence of different predictor variables. I calculated individual pseudo-R^2 values for the fixed effects by calculating the variance around the regression line explained by each fixed effect, calculating the total variance explained by all of the fixed effects, and then taking the product of the percentage of variance explained by each fixed effect and the marginal R^2 value for the full model.

Results

Both Northern Pike and Lake Trout life history traits investigated in this study were strongly influenced by the abundance of offshore prey (Figures 2.5-2.7; Tables 2.4-2.8). Though coregonid abundance generally appeared to have strong effects both Northern Pike and Lake

Trout populations, Cisco abundance consistently had the strongest influence on life history traits compared with Lake Whitefish (Tables 2.4-2.8). Additionally, similar patterns of the influence of Cisco abundance on Northern Pike growth and life history traits were observed for female, male, and combined sex Northern Pike data (Figures 2.5-2.7A-C; Tables 2.4-2.7).

Asymptotic Length

Predictive models explained 34-85% of variation in asymptotic length overall, primarily due to random effects; fixed effects explained 11-28% of variation (Tables 2.4, 2.5, 2.7, and 2.8). The asymptotic lengths of both female (Likelihood ratio test, $X^2 = 7.46$, df = 1, $p < 0.01$) and male (Likelihood ratio test, $X^2 = 9.14$, df = 1, $p < 0.01$) Northern Pike were significantly influenced by the abundance of Cisco. Both sexes exhibited significantly larger asymptotic lengths in lakes with greater abundances of Cisco (Figure 2.5A-B), and Cisco abundance accounted for 59% and 39% of the total variation explained by the fixed effects for female and male Northern Pike asymptotic lengths, respectively (Tables 2.4-2.5). When female and male Northern Pike data were combined in the BsM dataset, increases in Cisco abundances similarly resulted in significantly larger Northern Pike asymptotic lengths (Likelihood ratio test, $X^2 = 4.26$, df = 1, $p < 0.05$; Figure 2.5C). Contrary to my hypotheses, increases in Lake Whitefish abundance either did not have a significant effect or resulted in decreased asymptotic lengths of Northern Pike populations (Tables 2.4, 2.5, and 2.7). Neither female asymptotic lengths from the FWIN dataset (Likelihood ratio test, $X^2 = 0.08$, df = 1, $p > 0.05$) nor the combined male and female Northern Pike asymptotic lengths in the BsM dataset (Likelihood ratio test, $X^2 = 0.06$, df = 1, $p > 0.05$) were significantly influenced by Lake Whitefish abundance. However, male Northern Pike (FWIN dataset) exhibited smaller asymptotic lengths with greater abundances of Lake Whitefish (Likelihood ratio test, $X^2 = 5.28$, df = 1, $p < 0.05$). Of the other predictor variables included in the asymptotic length analyses, only the abundances of Northern Pike significantly influenced Northern Pike asymptotic lengths. Male Nothern Pike had significantly smaller asymptotic lengths in lakes with greater abundances of Northern Pike ($p < 0.05$; Table 2.5). Additionally, variance partitioning revealed that Cisco abundance (females, $R^2 = 0.063$; males $R^2 = 0.074$) explained more observed variation than all of the other predictor variables included in the asymptotic length analyses for female and male Northern Pike (Tables 2.4-2.5), while Yellow Perch abundance ($R^2 = 0.039$) explained the most variation for the combined sex Northern Pike analysis (Table 2.7).

In a similar fashion as Northern Pike, the asymptotic lengths of the more pelagic predator, Lake Trout (BsM dataset), were significantly larger in lakes with greater abundances of Cisco (Likelihood ratio test, $X^2 = 11.82$, df = 1, $p < 0.001$; Figure 2.5D) and were not significantly influenced by the abundance of Lake Whitefish (Likelihood ratio test, $X^2 = 1.83$, df = 1, $p > 0.05$). The model predicted 34% of the total variation in Lake Trout asymptotic length, mostly attributed to fixed effects (Table 2.8). The abundance of Cisco accounted for 45% of the variation explained by the fixed effects for the Lake Trout asymptotic length model (Table 2.8) compared to 39-59% for male and female Northern Pike, though the overall variance in asymptotic length explained by Cisco was higher for Lake Trout than for Northern Pike (12.9% vs. 6.3% for females, 7.4% for males and only 3% for both sexes; Tables 2.4, 2.5, 2.7, and 2.8). The abundance of Lake Trout was the only other predictor variable besides Cisco to have a significant effect and negatively influenced the asymptotic lengths of Lake Trout ($p = 0.01$). Variance partitioning results revealed that, like Northern Pike, Cisco abundance ($R^2 = 0.129$) accounted for more observed variation than any of the other predictor variables included in the asymptotic length analysis, followed by the abundance of Lake Trout ($R^2 = 0.103$; Table 2.8).

Early Growth Rate

Fixed and random effects in the predictive models explained 26-91% of variation in early growth rate overall, while fixed effects explained 16-24% of variation (Tables 2.4, 2.5, 2.7, and 2.8). The early growth rates of female (Likelihood ratio test, $X^2 = 7.45$, df = 1, $p < 0.01$), male (Likelihood ratio test, $X^2 = 12.31$, df = 1, $p < 0.001$), and combined female and male Northern Pike (Likelihood ratio test, $X^2 = 9.62$, df = 1, $p < 0.01$) were significantly slower in lakes with greater abundances of Cisco (Figure 2.6A-C). Cisco abundance accounted for 34% and 66% of the total variation explained by the fixed effects for female and male Northern Pike early growth rates, respectively (Tables 2.4-2.5). Additionally, analyses on both sexes combined (BsM dataset) indicated significantly faster early growth rates for Northern Pike with increased abundances of Yellow Perch ($p < 0.001$; Figure 2.6D). Lake Whitefish abundance did not significantly influence the early growth rates for Northern Pike females (Likelihood ratio test, $X^2 = 3.72$, df = 1, $p > 0.05$), males (Likelihood ratio test, $X^2 = 1.30$, df = 1, $p > 0.05$), or combined sexes (Likelihood ratio test, $X^2 = 0.84$, df = 1, $p > 0.05$). Similar to the asymptotic length analyses, variance partitioning revealed that Cisco abundance (females, $R^2 = 0.059$; males, $R^2 = 0.123$) accounted for more observed variation than all of the other predictor variables for the female and male early growth rate analyses (Tables 2.4-2.5), and Yellow Perch abundance ($R^2 = 0.126$) explained the most observed variation for the combined sex early growth rate analysis (Table 2.7).

In contrast with Northern Pike, Lake Trout early growth rates were not significantly influenced by the abundance of offshore prey (Cisco, likelihood ratio test, $X^2 = 1.75$, df = 1, $p > 0.05$; Lake Whitefish, likelihood ratio test, $X^2 = 2.00$, df = 1, $p > 0.05$), nor by any of the other predictor variables included in our models of Lake Trout early growth rates (Table 2.8).

Instantaneous Total Mortality

Fixed and random effects in the predictive models explained 32-72% of variation in instantaneous total mortality, while fixed effects explained 15-28% of variation (Tables 2.4, 2.5, 2.7, and 2.8). The influence of offshore prey on the instantaneous total mortality rates of Northern Pike varied depending on the dataset being analyzed. Increases in Cisco abundance resulted in significantly lower mortality rates of female Northern Pike (FWIN dataset, likelihood ratio test, $X^2 = 5.35$, df = 1, $p < 0.05$; Figure 2.7A) and combined female and male Northern Pike data from the BsM dataset (Likelihood ratio test, $X^2 = 5.29$, df = 1, $p < 0.05$; Figure 2.7C), but Cisco abundance did not significantly influence male Northern Pike mortality rates (Likelihood ratio test, $X^2 = 1.36$, df = 1, $p > 0.05$) (Tables 2.4, 2.5, and 2.7). By contrast, male Northern Pike had higher mortality rates in lakes with greater abundances of Lake Whitefish (Likelihood ratio test, $X^2 = 4.00$, df = 1, $p < 0.05$; Figure 2.7B), while Lake Whitefish abundance did not significantly affect the mortality rates of female (Likelihood ratio test, $X^2 = 0.21$, df = 1, $p > 0.05$) or combined sex data for Northern Pike (Likelihood ratio test, $X^2 = 1.96$, df = 1, $p > 0.05$). When both sexes were combined in the BsM dataset, greater Yellow Perch abundances resulted in significantly higher Northern Pike mortality rates ($p < 0.001$; Figure 2.7D; Table 2.7).

Environmental and physical lake variables also appeared to be important drivers of Northern Pike mortality rates. Female ($p < 0.05$) and male ($p < 0.01$) Northern Pike had significantly higher mortality rates in lakes that experienced greater growing degree days (Figure 2.8A,C), and combined male and female Northern Pike mortality rates were significantly lower in lakes with greater surface area ($p < 0.01$; Figure 2.8E; Tables 2.4, 2.5, and 2.7). Results from variance partitioning revealed that growing degree days (females, $R^2 = 0.048$; males, $R^2 = 0.095$) accounted for the most observed variation in the mortality rates of female and male Northern

Pike (Tables 2.4-2.5). However, the variance observed in the mortality rates of combined Northern Pike data was best explained by the abundance of Yellow Perch ($R^2 = 0.119$; Table 2.7).

Lake Trout instantaneous total mortality rates were not influenced by the abundance of offshore prey (Cisco, likelihood ratio test, $X^2 = 0.14$, df = 1, $p > 0.05$; Lake Whitefish, likelihood ratio test, $X^2 = 0.40$, df = 1, $p > 0.05$). However, similar to Northern Pike, the mortality rates of Lake Trout were significantly influenced by physical lake characteristics and environmental variables (Figure 2.8). Like Northern Pike from the BsM analyses, Lake Trout had significantly lower mortality rates in lakes with larger surface areas ($p < 0.01$; Figure 2.8D) and significantly higher mortality rates in lakes with greater growing degree days ($p < 0.01$; Figure 2.8B). Lake Trout also had lower mortality rates in lakes with greater mean depths ($p < 0.05$; Figure 2.8F). Variance partitioning revealed that lake surface area ($R^2 = 0.094$), growing degree days ($R^2 = 0.080$), and mean depth ($R^2 = 0.042$) explained more observed variation than biological predictor variables included in the Lake Trout instantaneous total mortality analysis (Table 2.8).

Relative Abundance

Fixed and random effects in the predictive models explained 51-87% of variation in relative abundance overall, while fixed effects explained 27-41% of variation (Tables 2.6-2.8). The effect of offshore prey fish abundance on Northern Pike abundance varied across datasets. Northern Pike in the FWIN dataset had increased abundances in lakes with greater abundances of both Cisco (Likelihood ratio test, $X^2 = 13.71$, df = 1, $p < 0.001$) and Lake Whitefish (Likelihood ratio test, $X^2 = 4.44$, df = 1, $p < 0.05$). However, the abundance of Cisco (Likelihood ratio test, $X^2 = 1.98$, df = 1, $p > 0.05$) and Lake Whitefish (Likelihood ratio test, $X^2 = 0.19$, df = 1, $p > 0.05$) did not significantly influence the abundance of Northern Pike in the BsM dataset. Instead, the abundance of Northern Pike was influenced more strongly by physical lake characteristics. Lake surface area and mean depth accounted for 67% and 80% of the observed variation in the abundance of Northern Pike explained by the fixed effects for the FWIN and BsM datasets, respectively (Tables 2.6-2.7). The abundance of Northern Pike was lower in lakes with larger surface areas and greater mean depths (Figures 2.9A-B). Additionally, Northern Pike abundance was positively influenced by the abundance of Yellow Perch ($p < 0.01$) in the FWIN dataset and White Sucker ($p < 0.05$) in the BsM dataset (Tables 2.6-2.7), but these variables explained less variation than physical lake characteristics. Variance partitioning revealed that lake surface area explained the majority of the observed variation in the abundance of Northern Pike in the FWIN dataset ($R^2 = 0.161$; Figure 2.9A; Table 2.6), while lake surface area ($R^2 = 0.150$) and mean depth ($R^2 = 0.177$) explained most of the observed variation in the abundance of Northern Pike in the BsM dataset (Figure 2.9A-B; Table 2.7).

Like Northern Pike in the BsM dataset, the abundance of Lake Trout was not influenced by the availability of offshore prey (Cisco, likelihood ratio test, $X^2 = 2.55$, df = 1, $p > 0.05$; Lake Whitefish, likelihood ratio test, $X^2 = 0.0001$, df = 1, $p > 0.05$), however, physical lake characteristics explained the majority of the variation observed in Lake Trout abundance (Table 2.8). Lake Trout abundance was significantly greater in lakes with greater mean depths ($p < 0.01$; Figure 2.9D), whereas this relationship was negative for Northern Pike. Similar to Northern Pike, the abundance of Lake Trout was significantly lower in lakes with larger surface areas ($p < 0.001$; Figure 2.9C), but was also lower with increasing growing degree days ($p < 0.01$; Table 2.8). Like Northern Pike, variance partitioning revealed that lake surface area ($R^2 = 0.204$) explained the majority of the observed variation in the Lake Trout abundance analysis (Table

2.8). Growing degree days ($R^2 = 0.072$) and mean depth ($R^2 = 0.065$) explained the second and third largest amounts of the observed variation for Lake Trout, respectively.

Discussion

Cisco abundance had a significant and similar influence on the growth and life history traits of Northern Pike and Lake Trout across a large portion of the Canadian Boreal Shield, suggesting strongly that Northern Pike behave as generalist predators that take advantage of the availability of large-bodied offshore prey. These results demonstrate that life history strategies of Northern Pike foraging on offshore prey are likely much more common than previously acknowledged. While there are accounts of Northern Pike foraging on offshore prey (Colby et al. 1987, Makowecki 1973), this study is the first to demonstrate the widespread influence of offshore prey on Northern Pike life history traits. Furthermore, the greater asymptotic lengths of both Northern Pike and Lake Trout in lakes with greater abundances of Cisco suggests similar impacts of offshore feeding on both species.

Larger asymptotic lengths of Northern Pike and Lake Trout in lakes with greater abundances of Cisco are consistent with previous case studies on the influence of offshore prey on Northern Pike and Lake Trout growth (Colby et al. 1987, Jacobson 1992, Makowecki 1973, Martin and Fry 1973, Mason et al. 1998, Pazzia et al. 2002, Trippel and Beamish 1989). As Cisco are soft-rayed fusiform species that are often larger and more energy-dense than nearshore prey species (Bryan et al. 1996), and they are ideal prey for large apex predatory species that have the physiological and trophic adaptability to take advantage of them. Bryan et al. (1996) reported Cisco (1,799-2,304 cal/ g) caloric densities were 1.5-2.7 times greater than other prey species investigated (e.g. Yellow Perch, ~1000-1,300 cal/ g; White Sucker, 857-884 cal/ g). Foraging upon large, energy-dense prey allows predators to maximize energy gained from prey, as foraging costs are lower and growth efficiency is higher as the ratio of predator to prey size decreases (Kaufman et al. 2006, Kerr 1971, Pazzia et al. 2002). Thus, integrating nearshore and offshore environments is likely profitable for Northern Pike, specifically larger individuals that can forage upon Cisco. For females, foraging upon Cisco is beneficial because body size is related to clutch size and thus reproductive fitness, as greater numbers of eggs results in greater offspring survival (Craig and Kipling 1983, Roff 1992, Stearns 1992). Furthermore, reaching larger body sizes by foraging upon Cisco may reduce predation pressure, as well as intra and interspecific competition; Northern Pike are cannibalistic and they exhibit competitive interactions with other apex predatory species (e.g. Walleye, Lake Trout; Scott and Crossman 1973). Reaching larger body sizes may allow Northern Pike to escape predation from coexisting predators and reduce their competitive interactions. In contrast with Cisco, Lake Whitefish do not seem to be common prey for Northern Pike. Although previous case studies reported that large Northern Pike occasionally feed on Lake Whitefish (Makowecki 1973), they may be less accessible for Northern Pike because they reach larger sizes than Cisco and are associated with benthic hypolimnetic habitats (Scott and Crossman 1973).

The data presented here suggests that the generalist foraging strategy of Northern Pike is ontogenetic. While Cisco abundance was positively related to Northern Pike asymptotic length, Cisco abundance was negatively related to Northern Pike early growth rates. Instead, Northern Pike early growth rates were positively related to the abundance of nearshore Yellow Perch, which agrees with previous studies that found Yellow Perch are important prey for juvenile Northern Pike (Heath and Roff 1996, Venturelli and Tonn 2006). Isotopic evidence from food web studies has demonstrated some evidence for generalist strategies in Northern Pike (Vander Zanden et al. 1997, Vander Zanden and Vadeboncoeur 2002). However, data presented here based strictly on life history patterns strongly suggests that the degree of generalist foraging is dependent on body size and/ or life stage of prey or predator. The slower early growth rates of Northern Pike in lakes with greater abundances of Cisco suggests that Cisco are not common prey for Northern Pike during their early growth and life history. Juvenile Northern Pike spend most of their time in nearshore environments limiting habitat overlap with Cisco (Casselman and Lewis 1996), and smaller Northern Pike are gape-limited from foraging upon larger prey (Nilsson and Brönmark 2000). This study suggests that Northern Pike are more reliant on nearshore species (i.e. Yellow Perch) during their early growth and development, and as they grow they make an ontogenetic shift to feeding upon Cisco, specifically when Cisco are in high abundance.

In contrast with Northern Pike, Lake Trout early growth rates were not significantly influenced by any of the predictor variables in the analysis. Lake Trout grow more slowly than Northern Pike and rely more heavily on invertebrates such as *M. diluviana* during their early growth and development (Trippel and Beamish 1993), so it is likely that a significant effect was not detected because prey at lower trophic levels were not included in these analyses. This highlights a broader challenge in evaluating early Lake Trout growth in that the information on the distribution of invertebrate predators like *M. diluvania* is limited and based on surveys conducted nearly half a century ago (Dadswell 1974). Further investigation into the factors influencing the early growth rates of Lake Trout is necessary to understand the constraints on their rapid early growth.

The results of this study additionally suggest that quality of prey influences the mortality rates of Northern Pike. The influence of food quality on the health and mortality rates of animals has previously been reported across a variety of aquatic and terrestrial taxa (Oedekoven and

Joern 2000, Sterner et al. 1993). In this study, Northern Pike exhibited lower instantaneous total mortality rates in lakes with greater abundances of Cisco. The availability of high quality Cisco may provide Northern Pike with a surplus of energy over the costs of growth and reproduction with which they can allocate to processes such as cellular maintenance to slow down the rate of senescence (Kirkwood and Rose 1991). Additionally, Northern Pike in the BsM dataset had significantly higher mortality rates in lakes with greater abundances of Yellow Perch. It is possible that the growth potential of Northern Pike may be limited by lake size and shape; larger lakes likely experience a shift between the proportion of littoral vs. offshore area with increasing size, which in turn suggests a tradeoff in the abundance of Yellow Perch and offshore prey (Dolson et al. 2009). If Northern Pike cannot gain enough energy from larger offshore prey (i.e. Cisco) to grow efficiently and reach larger body sizes, they may select for faster life history strategies in order to maximize their reproductive output. However, the data here do not support a tradeoff between Yellow Perch and Cisco abundance, rather that their abundances are either positively correlated or not correlated for each of the datasets (Appendix A).

Life history theory indicates that longer-lived organisms that reach larger body sizes often grow more slowly and mature later in life, a trade-off that occurs to maximize fitness (Charnov 2011, Charnov and Berrigan 1991, Pauly 1980). The results of this study support this theory, where Northern Pike reached larger asymptotic sizes, had slower early growth rates, and had lower mortality rates in lakes with greater abundances of Cisco. In lakes with fewer Cisco, Northern Pike had smaller asymptotic sizes, faster early growth rates, and greater mortality rates. Growing quickly and maturing early in life is costly, can cause damage to cellular structures (e.g. lipids, proteins, DNA), and can increase the rate of senescence in organisms (Lemaître et al. 2015). Moreover, mortality is inversely related to age at maturity (Charnov and Berrigan 1990, Lester et al. 2004). As such, natural selection has likely acted upon Northern Pike to grow slower and delay the onset of maturity in lakes with greater abundances of Cisco as a means of optimizing their reproductive output over time. However, it is also likely that Northern Pike undergo selection to grow fast early in life if nearshore resources are abundant, as evidenced by Northern Pike having significantly faster early growth rates in lakes with greater abundances of Yellow Perch (Diana 1979, Margenau et al. 1998). Thus, lakes that have a balance between nearshore and offshore prey abundance may provide the optimal environment for rapid growth of Northern Pike throughout their lifespan.

Similarities between Northern Pike and Lake Trout mortality rates in response to physical limnology and environmental variables further suggest that there are similarities in habitat use between these two species. Northern Pike (females and males) and Lake Trout mortality rates were significantly higher in lakes that experienced more growing degree days. As both Northern Pike and Lake Trout are adapted to northern latitudes, warmer climates may result in greater stress for both species through limitation of optimal thermal habitat (Chu et al. 2005, Mackenzie-Grieve and Post 2006). Warmer environments result in faster metabolisms for ectotherms, which can speed up and shorten their life cycles (Gillooly et al. 2001, Holt and Jørgensen 2015, Kelly et al. 2014). Additionally, it is likely that the influence of growing degree days on Northern Pike mortality rates was observed in the FWIN dataset but not the BsM dataset because of differences in the latitudes of the lakes sampled, where the FWIN dataset included more Northern Pike lakes at lower latitudes. Lakes at lower latitudes are also closer in proximity to the large urban centers of southern Ontario, and they likely experience greater fishing pressure. In addition to growing degree days, the mortality rates of Northern Pike and Lake Trout in the BsM dataset were significantly lower in lakes with larger surface areas. Larger lakes may provide more opportunities for cool water refuge for Northern Pike and Lake Trout. An analysis of the correlation among the predictor variables revealed that lake surface area and mean depth were positively correlated (Appendix A). Furthermore, lake surface area was positively correlated with the abundance of Cisco in the lakes. Thus, larger lakes may provide a combination of both cool water refuge and high quality prey, which in turn may result in lower mortality rates of adult Northern Pike and Lake Trout.

Physical lake characteristics were the most important variables in explaining the relative abundances of Northern Pike and Lake Trout, and they appear to best describe conditions these species are adapted to in their early life history. Lake surface area and mean depth together accounted for greater than 60% of the variation explained by the fixed effects in the relative abundance models, and both Northern Pike and Lake Trout had lower abundances in lakes with larger surface areas. Larger lakes may support a greater diversity of predators that prey on these species during their early development, as well as more competitors for resources, both of which could lead to lower abundances. Mean depth had contrasting effects on Northern Pike and Lake Trout. Greater mean depths were related to lower abundances of Northern Pike and higher abundances of Lake Trout. Lake Trout is an obligate cold-water species that has been shown to be productive in deep Boreal Shield lakes (Gunn 2004, Scott and Crossman 1973), whereas Northern Pike is a cool-water species whose abundance has been associated with the amount of littoral vegetation (Casselman and Lewis 1976, Pierce and Tomcko 2005, Scott and Crossman 1973). Investigations into multicollinearity among variables revealed a high Pearson's correlation coefficient (r = -0.88) and strong negative relationship (r^2 = 0.80, n = 255) between mean depth and percent littoral zone for the FWIN lakes. Thus, the influence of mean depth may more so reflect the importance of littoral vegetation to Northern Pike prolificacy. In addition to physical lake characteristics, growing degree days negatively impacted Lake Trout abundance, further highlighting the sensitivity of this species to warmer climates (Chu et al. 2005, Mackenzie-Grieve and Post 2006).

Although the effects were not as strong as physical lake characteristics, the availability of different prey types influenced Northern Pike abundances. Northern Pike in the FWIN dataset had greater abundances in lakes with more Cisco, but Cisco abundance was not significantly related to Northern Pike abundance in the BsM dataset. Greater availability of Cisco was related to larger asymptotic lengths of Northern Pike, thus allowing for greater fecundity which may lead to greater numbers of offspring survival (Craig and Kipling 1983). Additionally, greater Cisco availability may allow Northern Pike to widen their ecological niche and reduce intraspecific competition.

Due to the large number of statistical tests performed, it is possible that some significant results reported here are false positives obtained purely by chance. However, it cannot explain the weight of evidence observed; of 117 statistical tests, with an $\boldsymbol{\alpha} = 0.05$, only 6 out of 33 significant tests are expected to be spurious, just 18% of all significant observations. The observed importance of Cisco abundance across a range of life history traits in both species speaks to the importance of this variable in my findings. Additionally, the relatively small minimum sample size for calculating growth and life history traits may have influenced the results, and greater sample sizes would surely increase the precision of estimates. Acknowledging this, it is unlikely that numbers required for ‘stable’ estimates in the literature can be obtained from freshwater lake surveys for these species (Coggins et al. 2013), therefore some degree of error is assumed in this estimation. This study covered a broad range of lakes across the Canadian Boreal Shield, and there are undoubtedly additional factors that influence the growth and life history of Northern Pike and Lake Trout across this range (e.g. fishing pressure). However, the abundance of Cisco consistently had some of the greatest explanatory power for growth and life history traits investigated here, adding confidence to the inference that Cisco abundance influences growth and life history variation of Northern Pike and Lake Trout in the Canadian Boreal Shield.

In conclusion, the investigations of the influence of the offshore prey community on growth and life history traits of Northern Pike and Lake Trout revealed some striking similarities between the two species. Although both species are adapted to different environmental conditions, their asymptotic lengths were similarly influenced by the abundance of Cisco. This corresponds with theories that indicate that there are basic physiological principles influencing the ability of predatory fish to obtain larger body sizes (Kerr 1971). Additionally, the response of Northern Pike to the abundance of Cisco was similar between the different datasets analyzed in this study, highlighting the reproducibility of this research and that the results are not likely due to biases in one sampling design vs. the other. These results demonstrate a widespread reliance on Cisco for Northern Pike and suggest that adult Northern Pike may act as generalist predators in Boreal Shield lakes when Cisco are abundant. This generalist strategy is likely ontogenetic and develops with increasing body size, with juvenile Northern Pike behaving strictly as nearshore predators. An analysis of Northern Pike dietary reliance on different prey types across their life cycle using stable isotopes and direct diet analysis is needed to help test these conclusions.

The comprehensive life history investigations of this study provide an abundance of information that is useful for the management of Northern Pike and Lake Trout populations across the Canadian Boreal Shield, and they display some clear and interesting general patterns across a broad range of lakes. This research demonstrates the importance of prey availability on apex predator life histories, and future management decisions should incorporate the availability of both prey and habitat into their assessments of predatory fishes. The differences observed between life history traits of male and female Northern Pike suggest that management strategies need to adapt to recognize the differential importance of offshore prey and other variables on female and male life histories. Northern Pike exhibit sexual size dimorphism, and although the data suggest that the two share important similarities, the factors influencing their growth and life history variation can be different. I recommend analyzing female and male life history parameters separately to obtain greater precision on the state of Northern Pike populations. Furthermore, slot size harvest regulations should be adjusted based on these analyses so that neither sex is more vulnerable to overfishing. Further assessment of the behavior of the different sexes should be done to understand their habitat and vulnerability to fishing efforts. Finally, these results provide further context on how differences in prey community composition and abiotic variables have shaped the evolution of life history strategies expressed by Northern Pike and Lake Trout across the Canadian Boreal Shield.

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Table 2.1 Ecological predictor variables included in the study.

Variable	Abbreviation	Data Type	Description
Fixed Effects			
Cisco Relative Abundance	log93	Numeric	Log_{10} Cisco CPUE + 1
Whitefish Relative Abundance	log91	Numeric	Log_{10} Whitefish CPUE + 1
White Sucker Relative Abundance	log163	Numeric	Log_{10} White Sucker CPUE + 1
Yellow Perch Relative Abundance	log331	Numeric	Log_{10} Yellow Perch CPUE + 1
Apex Predator Relative Abundance	log131/ log81	Numeric	Log_{10} CPUE of Northern Pike or Lake Trout + 1
GDD	GDD	Numeric	Cumulative growing degree days above 5°C
Lake Surface Area	LG_AREA	Numeric	Log_{10} lake surface area (ha)
Mean Depth	logMD	Numeric	Log_{10} mean depth of the lake (m)
Random Effects			
Lake Name	Lake.Name	Factor	Unique lake identifier
Year	Year	Factor	Year in which the sampling occurred

Table 2.2 Descriptive statistics of the response variables calculated for female and male Northern Pike in the FWIN dataset.

	N	*Mean*	*Min*	*Max*	*Std. Deviation*	*Std. Error*
Females						
Asymptotic Fork Length (L_∞)	155	866.36	509.64	1330.70	165.79	13.32
Omega (ω)	155	220.13	119.20	417.61	51.84	4.16
Instantaneous Total Mortality Rate (Z)	155	0.41	0.17	1.24	0.20	0.02
Males						
Asymptotic Fork Length (L_∞)	109	646.36	480.58	911.60	86.98	8.33
Early Growth Rate (ω)	109	255.71	147.93	430.19	53.05	5.08
Instantaneous Total Mortality Rate (Z)	109	0.53	0.25	1.79	0.25	0.02
Females and Males						
Relative Abundance (Log_{10} CPUE)	264	3.63	0.62	11.00	1.98	0.12

Table 2.3 Descriptive statistics of the response variables calculated for Northern Pike and Lake Trout populations in the BsM dataset.

	N	*Mean*	*Min*	*Max*	*Std. Deviation*	*Std. Error*
Northern Pike						
Asymptotic Fork Length (L_∞)	130	725.79	511.64	1596.97	144.74	12.69
Early Growth Rate (ω)	130	258.14	119.92	562.59	78.22	6.86
Instantaneous Total Mortality Rate (Z)	130	0.35	0.18	0.97	0.14	0.01
Relative Abundance (Log_{10} CPUE)	130	1.46	0.31	4.58	0.85	0.07
Lake Trout						
Asymptotic Fork Length (L_∞)	96	609.73	355.30	1090.81	115.92	11.83
Early Growth Rate (ω)	96	95.27	51.01	173.26	24.96	2.55
Instantaneous Total Mortality Rate (Z)	96	0.16	0.06	0.45	0.09	0.01
Relative Abundance (Log_{10} CPUE)	96	1.11	0.24	4.43	0.73	0.07

Table 2.4 Model outputs from the FWIN female Northern Pike life history analyses. *P*-values reported are based on Satterthwaite approximations for denominator degrees of freedom. Individual variables that were found to be significant in the models are in bold. Marginal R^2 (*R2m*) values are the amount of variation explained by all of the fixed effects for each response variable. Conditional R^2 (*R2c*) values are the amount of variation by explained by both the fixed and random effects for each response variable. R^2 values are the pseudo-R^2 values derived from the variance partitioning for each predictor variable.

Response Variable	*Fixed Effects*	*Parameter Estimate*	*Standard Error*	*T value*	*P value*	R^2	*R2m*	*R2c*
Asymptotic Length (L_∞)	Log$_{10}$ Lake Whitefish CPUE	-13.282	47.708	-0.278	0.781	< 0.001		
	Log$_{10}$ Cisco CPUE	**92.896**	**34.696**	**2.677**	**0.008**	**0.063**		
	Log$_{10}$ Northern Pike CPUE	-121.584	95.341	-1.275	0.204	0.015		
	Log$_{10}$ White Sucker CPUE	11.488	59.910	0.192	0.848	< 0.001		
	Log$_{10}$ Yellow Perch CPUE	-19.767	38.857	-0.509	0.612	0.002		
	Log$_{10}$ Lake Surface Area	12.807	24.532	0.522	0.602	0.004		
	Log$_{10}$ Mean Depth	-80.492	52.598	-1.530	0.128	0.017		
	Growing Degree Days	-13.234	18.022	-0.734	0.464	0.005		
							0.107	**0.514**
Early Growth Rate (ω)	Log$_{10}$ Lake Whitefish CPUE	-26.688	13.841	-1.928	0.056	0.025		
	Log$_{10}$ Cisco CPUE	**-26.694**	**9.981**	**-2.675**	**0.008**	**0.059**		
	Log$_{10}$ Northern Pike CPUE	-8.375	27.531	-0.304	0.761	< 0.001		
	Log$_{10}$ White Sucker CPUE	4.072	17.280	0.236	0.814	< 0.001		
	Log$_{10}$ Yellow Perch CPUE	21.593	11.221	1.924	0.056	0.027		
	Log$_{10}$ Lake Surface Area	-8.386	6.971	-1.203	0.232	0.018		
	Log$_{10}$ Mean Depth	**32.175**	**15.043**	**2.139**	**0.034**	**0.032**		
	Growing Degree Days	6.164	5.206	1.184	0.239	0.012		
							0.174	**0.472**

Table 2.4, continued

Instantaneous Total Mortality (Z)	Log$_{10}$ Lake Whitefish CPUE	0.023	0.051	0.447	0.656	0.001		
	Log$_{10}$ Cisco CPUE	**-0.083**	**0.037**	**-2.253**	**0.026**	**0.045**		
	Log$_{10}$ Northern Pike CPUE	-0.005	0.102	-0.047	0.963	< 0.001		
	Log$_{10}$ White Sucker CPUE	0.107	0.064	1.679	0.095	0.020		
	Log$_{10}$ Yellow Perch CPUE	-0.011	0.042	-0.256	0.798	< 0.001		
	Log$_{10}$ Lake Surface Area	-0.040	0.026	-1.563	0.121	0.032		
	Log$_{10}$ Mean Depth	0.007	0.056	0.118	0.906	< 0.001		
	Growing Degree Days	**0.044**	**0.019**	**2.278**	**0.024**	**0.048**		
							0.146	**0.455**

Table 2.5 Model outputs from the FWIN male Northern Pike life history analyses. *P*-values reported are based on Satterthwaite approximations for denominator degrees of freedom. Individual variables that were found to be significant in the models are in bold. Marginal R^2 (*R2m*) values are the amount of variation explained by all of the fixed effects for each response variable. Conditional R^2 (*R2c*) values are the amount of variation by explained by both the fixed and random effects for each response variable. R^2 values are the pseudo-R^2 values derived from the variance partitioning for each predictor variable.

Response Variable	*Fixed Effects*	*Parameter Estimate*	*Standard Error*	*T value*	*P value*	R^2	*R2m*	*R2c*
Asymptotic Length (L_∞)	**Log$_{10}$ Lake Whitefish CPUE**	**-70.219**	**30.373**	**-2.312**	**0.023**	**0.046**		
	Log$_{10}$ Cisco CPUE	**59.870**	**19.184**	**3.121**	**0.002**	**0.074**		
	Log$_{10}$ Northern Pike CPUE	**-140.529**	**62.219**	**-2.259**	**0.027**	**0.047**		
	Log$_{10}$ White Sucker CPUE	31.171	34.418	0.906	0.367	0.006		
	Log$_{10}$ Yellow Perch CPUE	10.934	23.505	0.465	0.643	0.002		
	Log$_{10}$ Lake Surface Area	-10.616	14.298	-0.742	0.460	0.008		
	Log$_{10}$ Mean Depth	18.246	28.587	0.638	0.525	0.004		
	Growing Degree Days	-7.742	12.566	-0.616	0.539	0.004		
							0.191	**0.847**
Early Growth Rate (ω)	Log$_{10}$ Lake Whitefish CPUE	20.545	18.861	1.089	0.279	0.013		
	Log$_{10}$ Cisco CPUE	**-42.180**	**11.789**	**-3.578**	**< 0.001**	**0.123**		
	Log$_{10}$ Northern Pike CPUE	49.250	32.921	1.496	0.145	0.020		
	Log$_{10}$ White Sucker CPUE	-5.043	21.273	-0.237	0.813	< 0.001		
	Log$_{10}$ Yellow Perch CPUE	17.741	14.308	1.240	0.219	0.015		
	Log$_{10}$ Lake Surface Area	-2.851	8.481	-0.336	0.737	0.002		
	Log$_{10}$ Mean Depth	1.761	17.970	0.098	0.922	< 0.001		
	Growing Degree Days	7.518	7.888	0.953	0.343	0.012		
							0.186	**0.889**

Table 2.5, continued

Instantaneous Total Mortality (Z)	Log_{10} Lake Whitefish CPUE	0.164	0.086	1.910	0.059	0.033		
	Log_{10} Cisco CPUE	-0.064	0.057	-1.123	0.264	0.011		
	Log_{10} Northern Pike CPUE	-0.183	0.189	-0.968	0.336	0.010		
	Log_{10} White Sucker CPUE	0.082	0.099	0.831	0.408	0.005		
	Log_{10} Yellow Perch CPUE	0.006	0.070	0.093	0.926	< 0.001		
	Log_{10} Lake Surface Area	-0.067	0.041	-1.644	0.104	0.041		
	Log_{10} Mean Depth	-0.102	0.080	-1.282	0.203	0.015		
	Growing Degree Days	**0.105**	**0.035**	**2.984**	**0.004**	**0.095**		
							0.210	**0.315**

Table 2.6 Model output for the FWIN Northern Pike relative abundance analysis. *P*-values reported are based on Satterthwaite approximations for denominator degrees of freedom. Individual variables that were found to be significant in the model are in bold. Marginal R^2 (*R2m*) values are the amount of variation explained by all of the fixed effects for each response variable. Conditional R^2 (*R2c*) values are the amount of variation by explained by both the fixed and random effects for each response variable. R^2 values are the pseudo-R^2 values derived from the variance partitioning for each predictor variable.

Response Variable	*Fixed Effects*	*Parameter Estimate*	*Standard Error*	*T value*	*P value*	R^2	*R2m*	*R2c*
Relative Abundance ($\log_{10}$ CPUE)	**$\log_{10}$ Lake Whitefish CPUE**	**0.069**	**0.033**	**2.096**	**0.037**	**0.013**		
	$\log_{10}$ Cisco CPUE	**0.087**	**0.024**	**3.708**	**< 0.001**	**0.043**		
	$\log_{10}$ White Sucker CPUE	0.064	0.042	1.547	0.123	0.007		
	$\log_{10}$ Yellow Perch CPUE	**0.074**	**0.027**	**2.714**	**0.007**	**0.023**		
	$\log_{10}$ Lake Surface Area	**-0.094**	**0.015**	**-6.159**	**< 0.001**	**0.161**		
	$\log_{10}$ Mean Depth	**-0.090**	**0.036**	**-2.510**	**0.013**	**0.022**		
	Growing Degree Days	-0.014	0.012	-1.169	0.244	0.005		
							0.274	**0.507**

Table 2.7 Model outputs for the BsM Northern Pike life history analyses. *P*-values reported are based on Satterthwaite approximations for denominator degrees of freedom. Individual variables that were found to be significant in the models are in bold. Marginal R^2 (*R2m*) values are the amount of variation explained by all of the fixed effects for each response variable. Conditional R^2 (*R2c*) values are the amount of variation by explained by both the fixed and random effects for each response variable. R^2 values are the pseudo-R^2 values derived from the variance partitioning for each predictor variable.

Response Variable	*Fixed Effects*	*Parameter Estimate*	*Standard Error*	*T value*	*P value*	R^2	*R2m*	*R2c*
Asymptotic Length (L_∞)	Log$_{10}$ Lake Whitefish CPUE	-16.185	56.438	-0.287	0.775	< 0.001		
	Log$_{10}$ Cisco CPUE	**91.640**	**46.110**	**1.987**	**0.049**	**0.030**		
	Log$_{10}$ Northern Pike CPUE	-88.240	110.293	-0.800	0.425	0.007		
	Log$_{10}$ White Sucker CPUE	12.302	70.980	0.173	0.863	< 0.001		
	Log$_{10}$ Yellow Perch CPUE	-114.613	59.263	-1.934	0.056	0.039		
	Log$_{10}$ Lake Surface Area	44.054	24.655	1.787	0.077	0.031		
	Log$_{10}$ Mean Depth	-2.614	56.352	-0.046	0.963	< 0.001		
	Growing Degree Days	23.180	24.142	0.960	0.343	0.017		
							0.125	**0.687**
Early Growth Rate (ω)	Log$_{10}$ Lake Whitefish CPUE	26.751	29.916	0.894	0.373	0.003		
	Log$_{10}$ Cisco CPUE	**-73.602**	**24.410**	**-3.015**	**0.003**	**0.034**		
	Log$_{10}$ Northern Pike CPUE	12.256	58.176	0.211	0.833	< 0.001		
	Log$_{10}$ White Sucker CPUE	-35.533	37.615	-0.945	0.347	0.004		
	Log$_{10}$ Yellow Perch CPUE	**156.272**	**31.198**	**5.009**	**< 0.001**	**0.126**		
	Log$_{10}$ Lake Surface Area	-22.879	12.812	-1.786	0.077	0.015		
	Log$_{10}$ Mean Depth	35.183	29.852	1.179	0.241	0.010		
	Growing Degree Days	**-28.459**	**10.921**	**-2.606**	**0.016**	**0.044**		
							0.236	**0.263**

Table 2.7, continued

Instantaneous Total Mortality (Z)								
	Log$_{10}$ Lake Whitefish CPUE	0.077	0.057	1.352	0.179	0.010		
	Log$_{10}$ Cisco CPUE	**-0.102**	**0.046**	**-2.195**	**0.030**	**0.026**		
	Log$_{10}$ Northern Pike CPUE	-0.083	0.110	-0.755	0.452	0.004		
	Log$_{10}$ White Sucker CPUE	0.001	0.071	0.016	0.987	< 0.001		
	Log$_{10}$ Yellow Perch CPUE	**0.239**	**0.059**	**4.037**	**< 0.001**	**0.119**		
	Log$_{10}$ Lake Surface Area	**-0.072**	**0.024**	**-2.951**	**0.004**	**0.058**		
	Log$_{10}$ Mean Depth	-0.019	0.057	-0.342	0.732	0.001		
	Growing Degree Days	-0.003	0.021	-0.165	0.873	< 0.001		
							0.220	**0.719**
Relative Abundance (Log$_{10}$ CPUE)	Log$_{10}$ Lake Whitefish CPUE	0.021	0.046	0.461	0.645	0.002		
	Log$_{10}$ Cisco CPUE	0.048	0.038	1.270	0.207	0.013		
	Log$_{10}$ White Sucker CPUE	**0.137**	**0.057**	**2.397**	**0.018**	**0.059**		
	Log$_{10}$ Yellow Perch CPUE	0.035	0.048	0.724	0.470	0.006		
	Log$_{10}$ Lake Surface Area	**-0.076**	**0.019**	**-4.059**	**< 0.001**	**0.150**		
	Log$_{10}$ Mean Depth	**-0.157**	**0.044**	**-3.555**	**< 0.001**	**0.177**		
	Growing Degree Days	-0.006	0.017	-0.368	0.718	0.002		
							0.408	**0.618**

Table 2.8 Model outputs for the BsM Lake Trout life history analyses. *P*-values reported are based on Satterthwaite approximations for denominator degrees of freedom. Individual variables that were found to be significant in the models are in bold. Marginal R^2 (*R2m*) values are the amount of variation explained by all of the fixed effects for each response variable. Conditional R^2 (*R2c*) values are the amount of variation by explained by both the fixed and random effects for each response variable. *R*^{2} values are the pseudo-R^2 values derived from the variance partitioning for each predictor variable.

Response Variable	*Fixed Effects*	*Parameter Estimate*	*Standard Error*	*T value*	*P value*	*R*^{2}	*R2m*	*R2c*
Asymptotic Length (L_∞)	Log$_{10}$ Lake Whitefish CPUE	63.376	49.761	1.274	0.206	0.022		
	Log$_{10}$ Cisco CPUE	**232.917**	**68.901**	**3.380**	**0.001**	**0.129**		
	Log$_{10}$ Lake Trout CPUE	**-266.125**	**100.970**	**-2.636**	**0.010**	**0.103**		
	Log$_{10}$ White Sucker CPUE	-4.612	66.971	-0.069	0.945	< 0.001		
	Log$_{10}$ Yellow Perch CPUE	-51.849	79.081	-0.656	0.514	0.006		
	Log$_{10}$ Lake Surface Area	21.369	27.009	0.791	0.431	0.014		
	Log$_{10}$ Mean Depth	-48.621	72.737	-0.663	0.509	0.008		
	Growing Degree Days	3.773	19.259	0.196	0.845	< 0.001		
							0.284	**0.335**
Early Growth Rate (ω)	Log$_{10}$ Lake Whitefish CPUE	18.064	11.914	1.516	0.135	0.029		
	Log$_{10}$ Cisco CPUE	-23.590	17.136	-1.377	0.172	0.022		
	Log$_{10}$ Lake Trout CPUE	-1.874	24.909	-0.075	0.940	< 0.001		
	Log$_{10}$ White Sucker CPUE	19.141	16.645	1.150	0.253	0.027		
	Log$_{10}$ Yellow Perch CPUE	18.834	19.292	0.976	0.332	0.014		
	Log$_{10}$ Lake Surface Area	7.784	6.308	1.234	0.226	0.030		
	Log$_{10}$ Mean Depth	16.174	17.892	0.904	0.369	0.016		
	Growing Degree Days	-4.363	4.244	-1.028	0.313	0.018		
							0.156	**0.914**

Table 2.8, continued

Instantaneous Total Mortality (Z)	Log$_{10}$ Lake Whitefish CPUE	0.021	0.036	0.597	0.552	0.002		
	Log$_{10}$ Cisco CPUE	-0.018	0.049	-0.370	0.711	0.001		
	Log$_{10}$ Lake Trout CPUE	-0.091	0.072	-1.261	0.211	0.011		
	Log$_{10}$ White Sucker CPUE	-0.095	0.048	-1.984	0.051	0.037		
	Log$_{10}$ Yellow Perch CPUE	-0.082	0.057	-1.442	0.153	0.015		
	Log$_{10}$ Lake Surface Area	**-0.058**	**0.019**	**-2.990**	**0.004**	**0.094**		
	Log$_{10}$ Mean Depth	**-0.112**	**0.052**	**-2.151**	**0.034**	**0.042**		
	Growing Degree Days	**0.039**	**0.014**	**2.713**	**0.008**	**0.080**		
							0.282	**0.413**
Relative Abundance (Log$_{10}$ CPUE)	Log$_{10}$ Lake Whitefish CPUE	0.007	0.052	0.135	0.893	< 0.001		
	Log$_{10}$ Cisco CPUE	0.110	0.072	1.521	0.132	0.011		
	Log$_{10}$ White Sucker CPUE	0.011	0.071	0.161	0.873	< 0.001		
	Log$_{10}$ Yellow Perch CPUE	0.086	0.082	1.044	0.300	0.007		
	Log$_{10}$ Lake Surface Area	**-0.135**	**0.024**	**-5.741**	**< 0.001**	**0.204**		
	Log$_{10}$ Mean Depth	**0.220**	**0.073**	**3.014**	**0.003**	**0.065**		
	Growing Degree Days	**-0.059**	**0.018**	**-3.344**	**0.002**	**0.072**		
							0.358	**0.873**

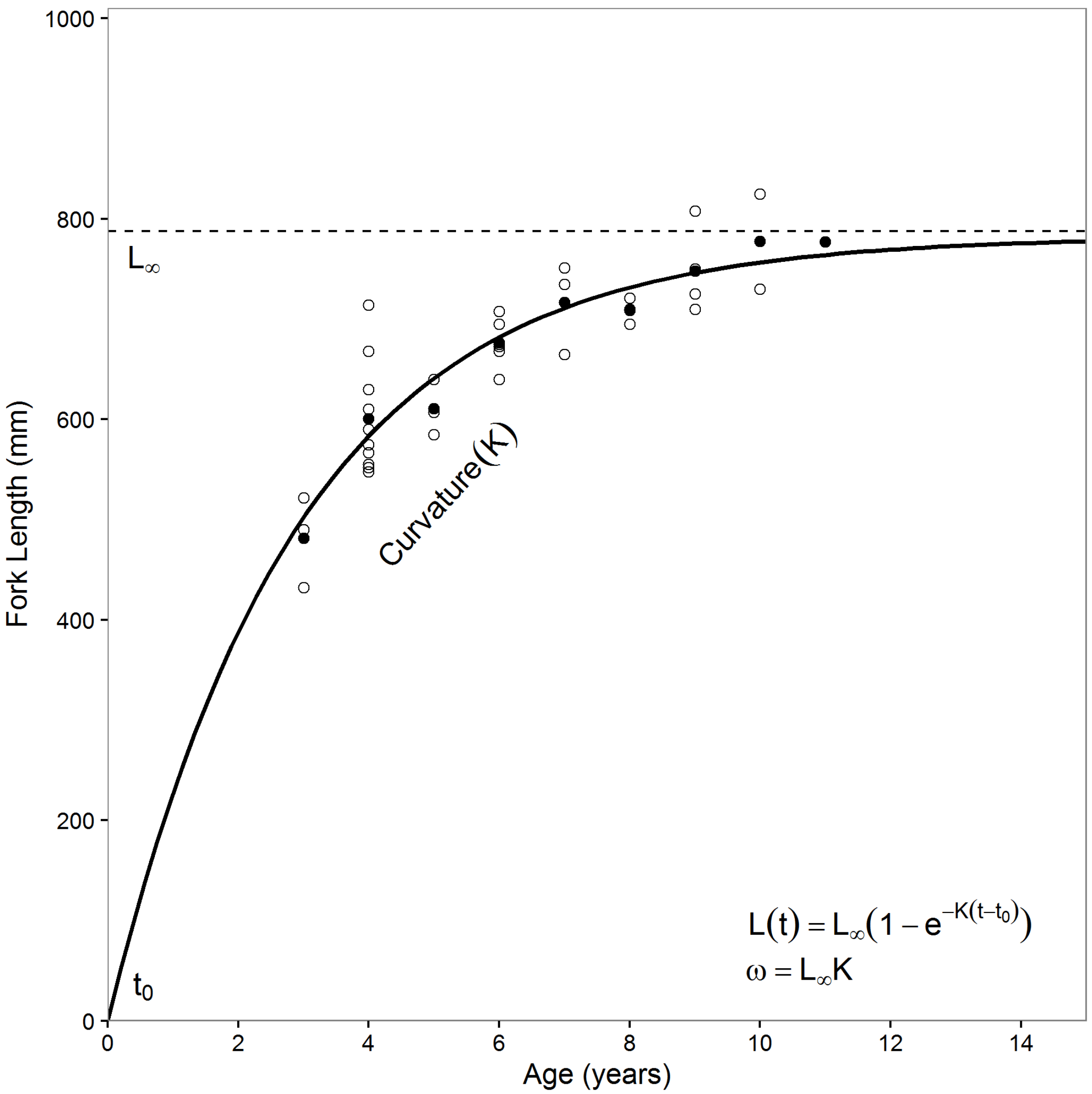

Figure 2.1 Example of a von Bertalanffy growth model fit through fork length (mm) at age (years) data for female Northern Pike sampled using the FWIN protocol in Makokibatan Lake, ON (*n*= 35). The von Bertalannfy growth equation and the equation for calculating the early growth rate (ω) of the population are displayed. Open circles represent length-at-age data for individuals and filled circles are the average length at each age.

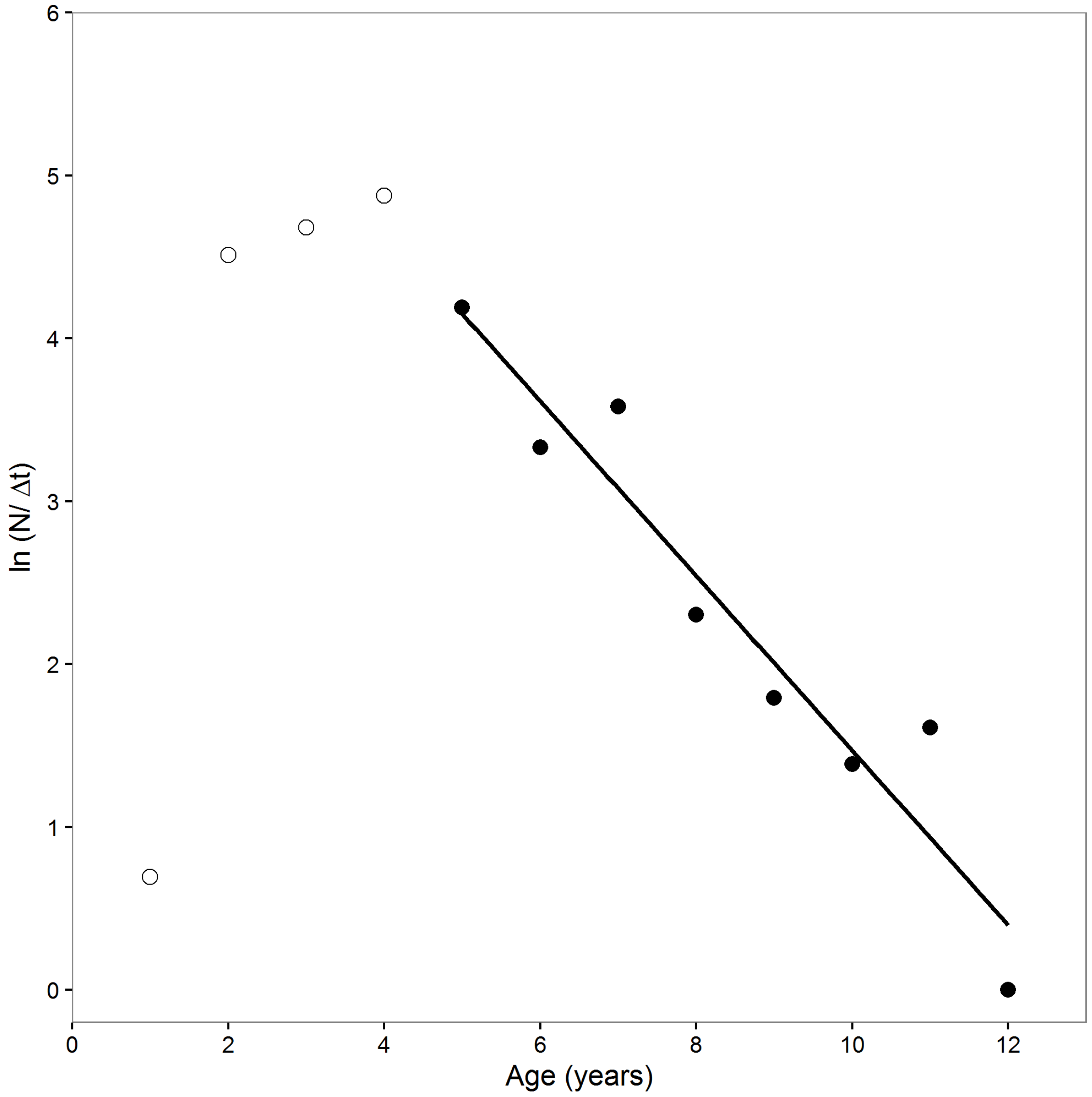

Figure 2.2 Example of the Robson and Chapman method for calculating annual survivorship and instantaneous total mortality rates for female Northern Pike sampled using the FWIN protocol in Lake Nipissing, ON. Closed circles represent the log number of individuals caught in each age class used in the regression analysis.

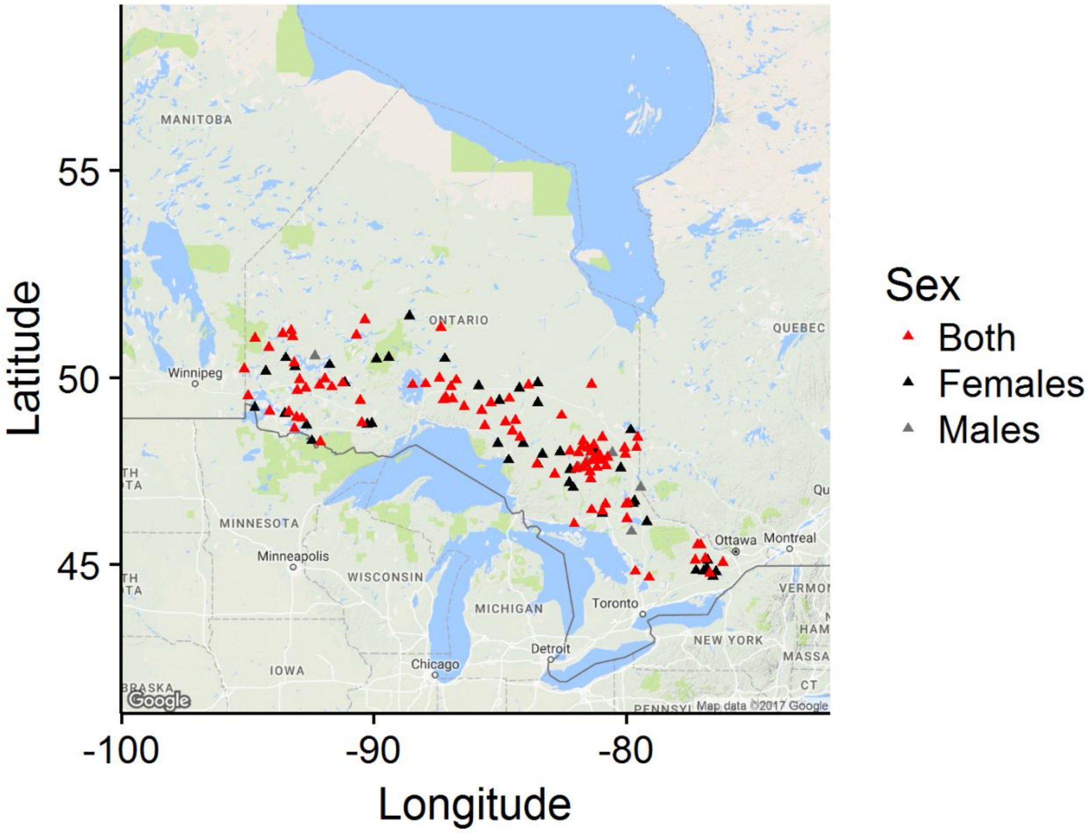

Figure 2.3 Map of FWIN lakes with suitable sample sizes for female Northern Pike, male Northern Pike, or both life history analyses.

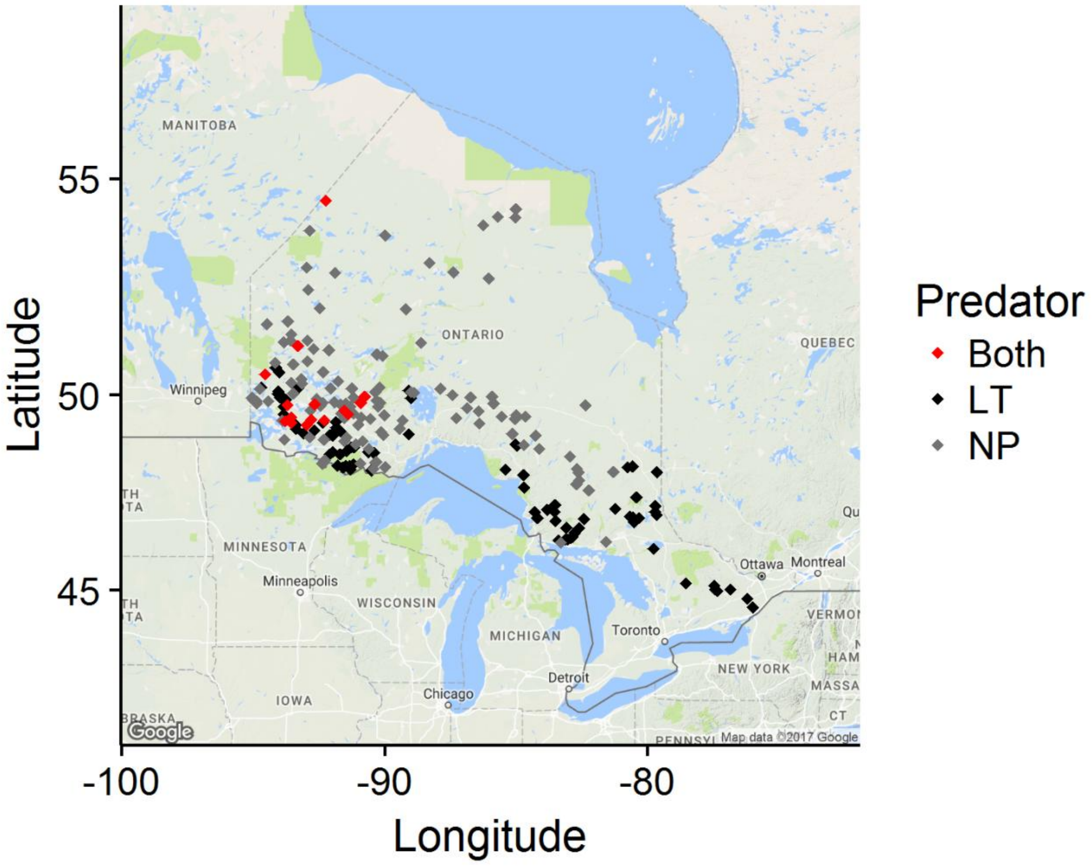

Figure 2.4 Map of BsM lakes with suitable sample sizes for Northern Pike (NP), Lake Trout (LT), or both life history analyses.

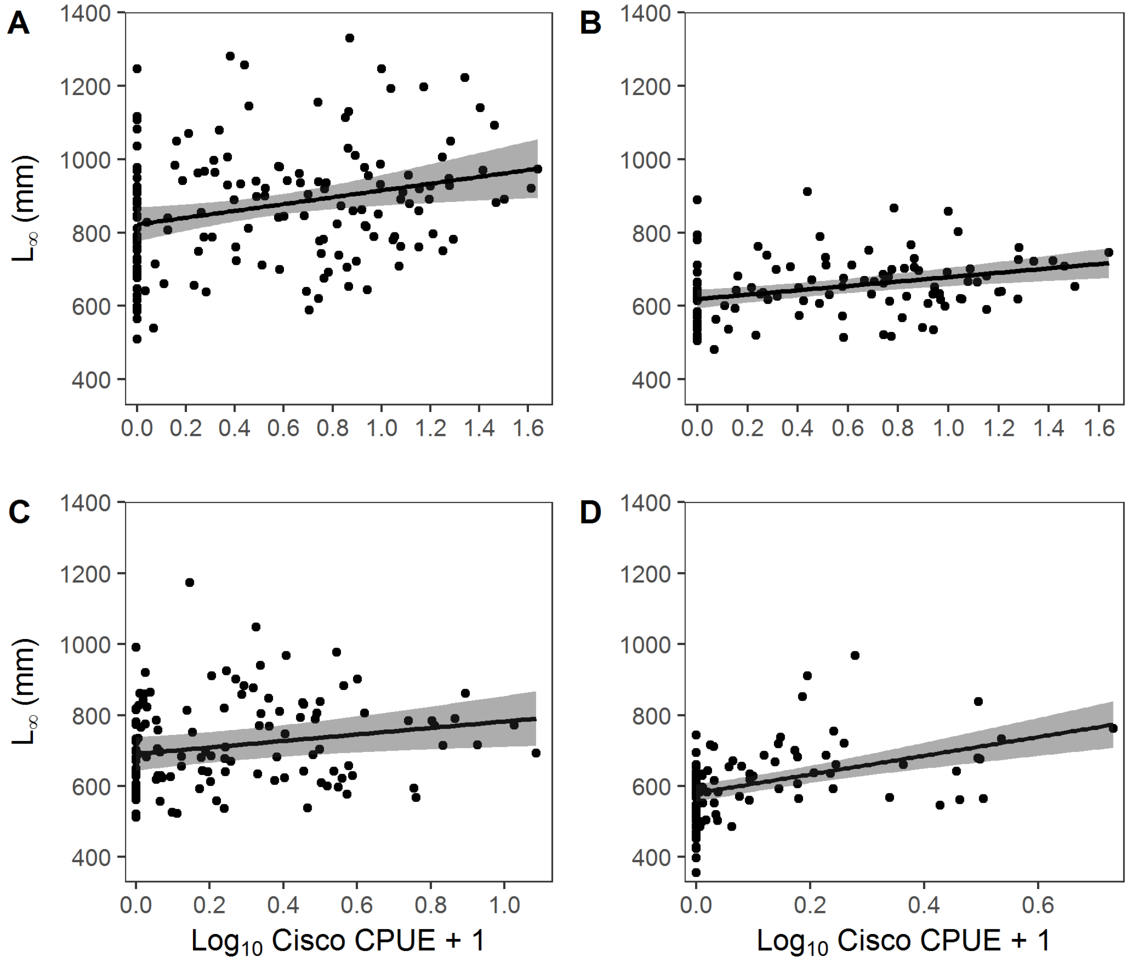

Figure 2.5 Relationships among Cisco relative abundance and (A) the asymptotic fork lengths (L_∞) of female Northern Pike ($p < 0.01$, $R^2 = 0.063$), (B) male Northern Pike ($p < 0.01$, $R^2 = 0.074$), (C) combined female and male Northern Pike ($p < 0.05$, $R^2 = 0.030$), and (D) Lake Trout ($p = 0.001$, $R^2 = 0.129$) populations. The solid lines represent the relationships and the shaded areas represent the 95% confidence intervals.

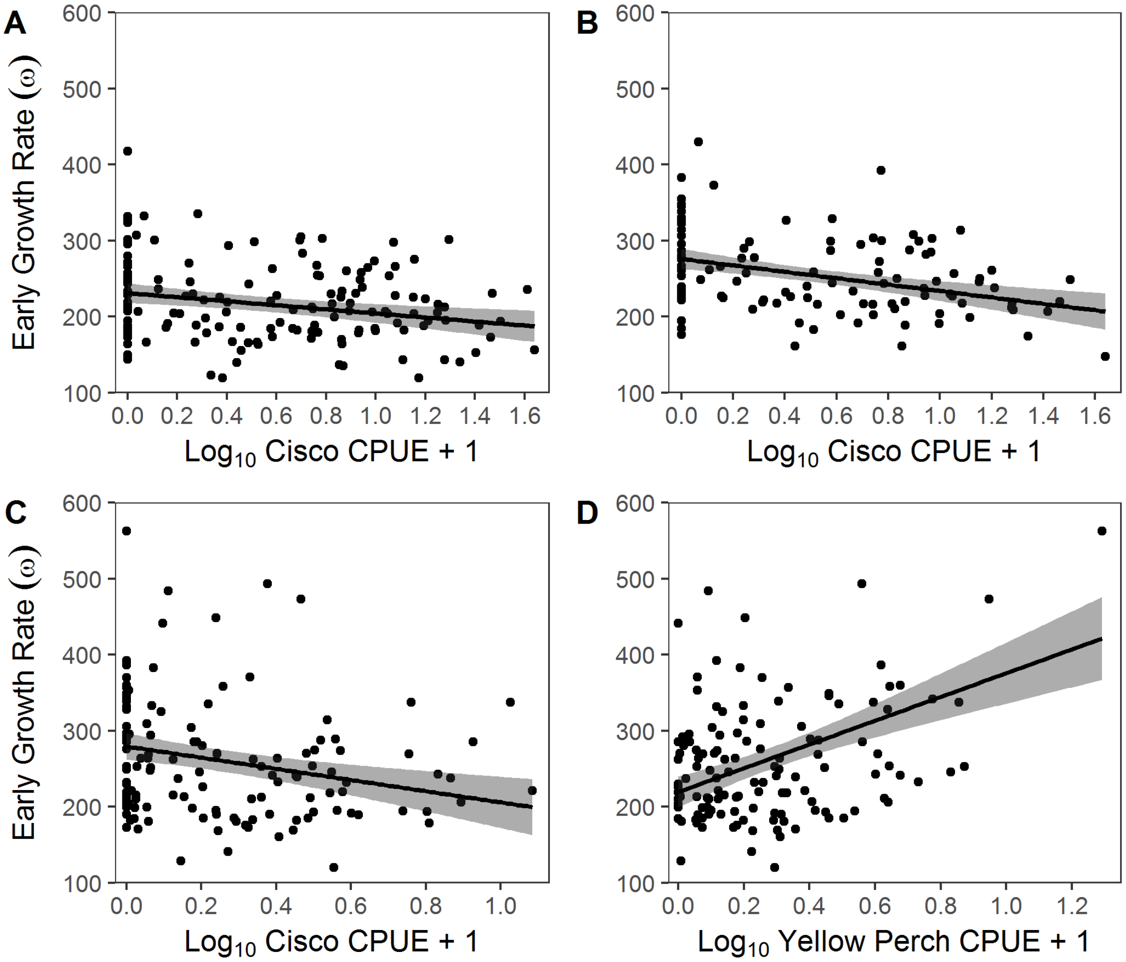

Figure 2.6 Relationships among Northern Pike early growth rates (ω) and prey abundance. (A), negative relationship between female Northern Pike early growth rates and Cisco abundance ($p < 0.01$, $R^2 = 0.059$); (B), negative relationship between male Northern Pike early growth rates and Cisco abundance ($p < 0.001$, $R^2 = 0.123$); (C), negative relationship between combined sex Northern Pike early growth rates and Cisco abundance ($p < 0.01$, $R^2 = 0.034$); and (D), positive relationship between combined sex Northern Pike early growth rates and Yellow Perch abundance ($p < 0.001$, $R^2 = 0.126$). The solid lines represent the relationships and the shaded areas represent the 95% confidence intervals.

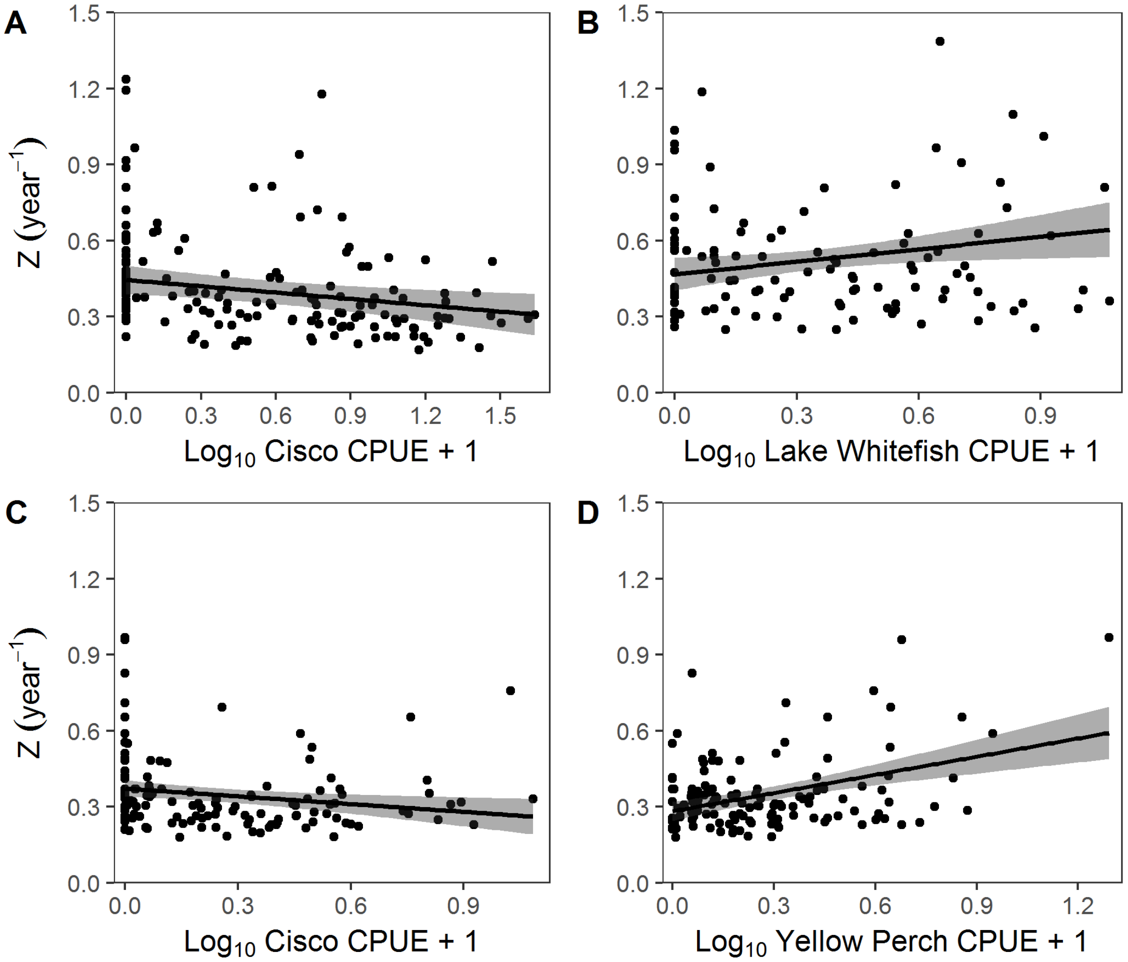

Figure 2.7 Relationships among Northern Pike instantaneous total mortality rates (Z) and prey abundance. (A), negative relationship between female Northern Pike Z and Cisco abundance ($p < 0.05$, $R^2 = 0.045$); (B), positive relationship between male Northern Pike Z and Lake Whitefish abundance ($p < 0.05$, $R^2 = 0.033$); (C), negative relationship between combined sex Northern Pike Z and Cisco abundance ($p < 0.05$, $R^2 = 0.026$); and (D), positive relationship between combined sex Northern Pike Z and Yellow Perch abundance ($p < 0.001$, $R^2 = 0.119$). The solid lines represent the relationships and the shaded areas represent the 95% confidence intervals.

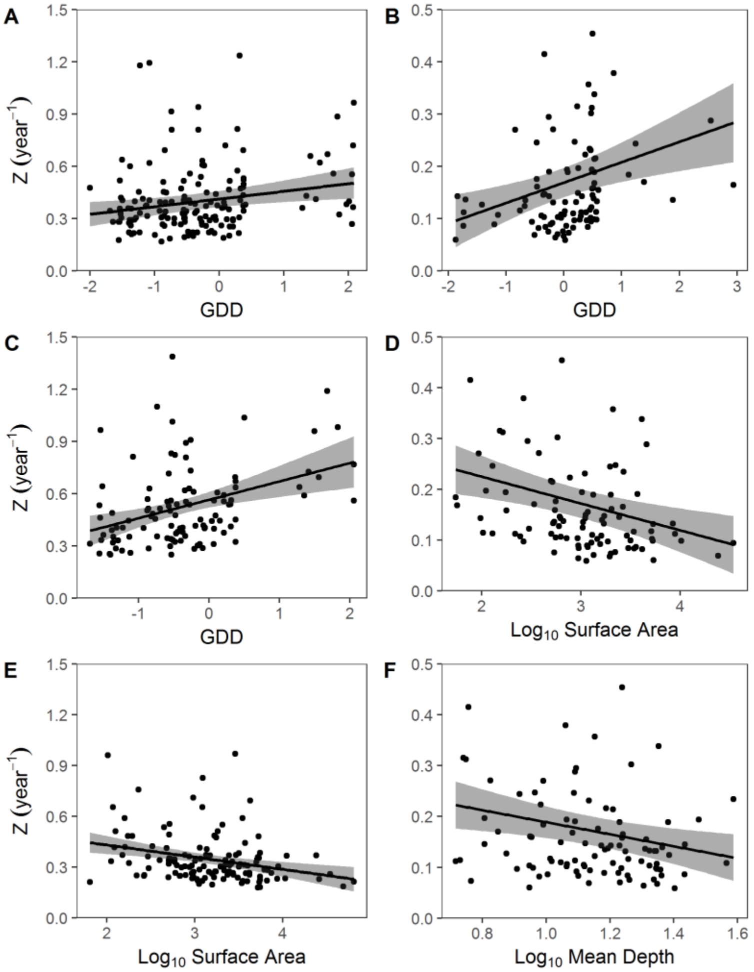

Figure 2.8 Relationships among Northern Pike and Lake Trout instantaneous total mortality rates (Z) and abiotic variables. (**A**), positive relationship between female Northern Pike Z and growing degree days (scaled) ($p < 0.05$, $R^2 = 0.048$); (**B**) positive relationship between Lake Trout Z and growing degree days (scaled) ($p < 0.01$, $R^2 = 0.080$); (**C**), positive relationship between male Northern Pike Z and growing degree days (scaled) ($p < 0.01$, $R^2 = 0.095$); (**D**) negative relationship between Lake Trout Z and lake surface area ($p < 0.01$, $R^2 = 0.094$); (**E**) negative relationship between combined sex Northern Pike Z and lake surface area ($p < 0.01$, $R^2 = 0.058$); and (**F**), negative relationship between Lake Trout Z and mean depth of the lakes ($p < 0.05$, $R^2 = 0.042$). The solid lines represent the relationships and the shaded areas represent the 95% confidence intervals. Note differences in scaling between left and right hand panels.

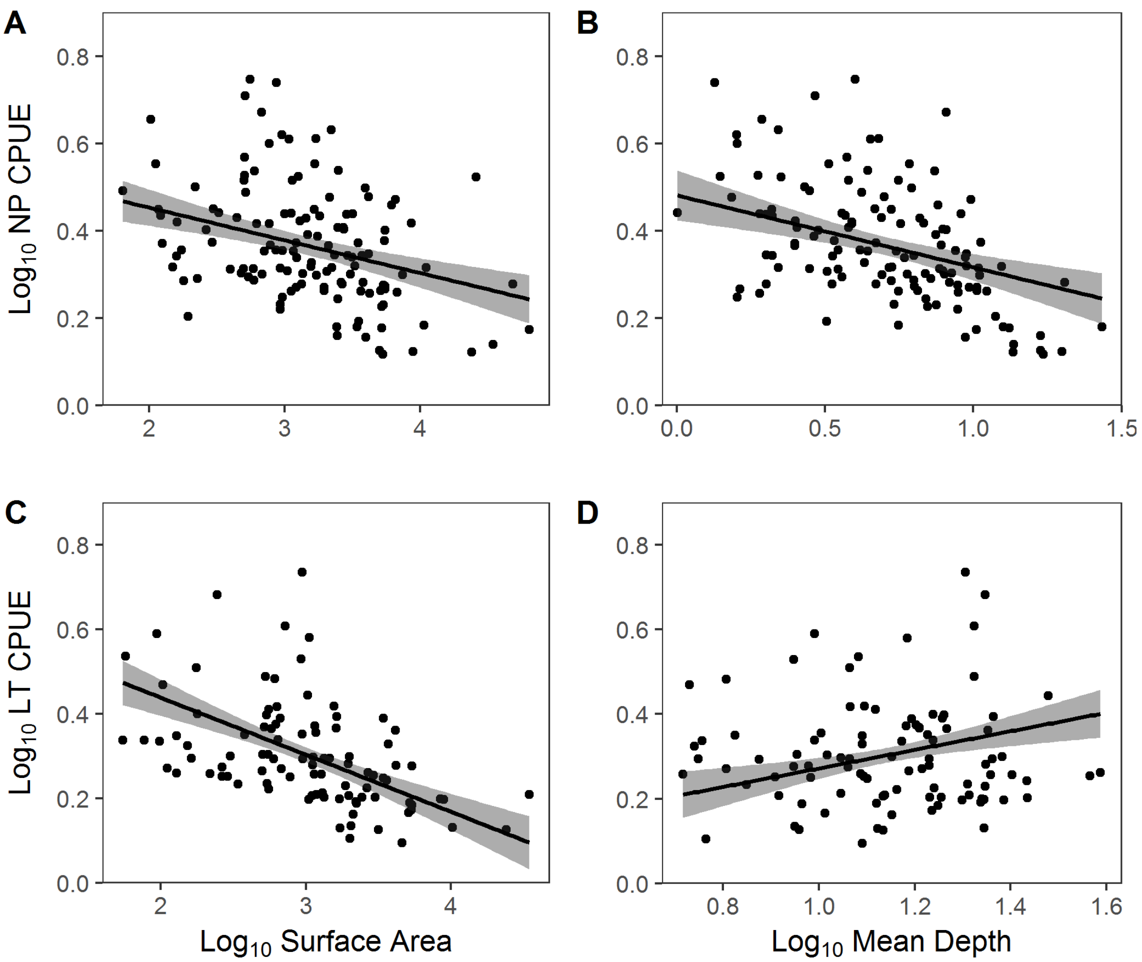

Figure 2.9 Factors influencing the relative abundance (CPUE) of Northern Pike and Lake Trout in Ontario Boreal Shield lakes. (A), relationship between Northern Pike CPUE (BsM) and lake surface area ($p < 0.001$, $R^2 = 0.150$); (B), relationship between Northern Pike CPUE (BsM) and the mean depth of lakes ($p < 0.001$, $R^2 = 0.177$); (C), relationship between Lake Trout CPUE and lake surface area ($p < 0.001$, $R^2 = 0.204$); (D), relationship between Lake Trout CPUE and the mean depth of lakes ($p < 0.01$, $R^2 = 0.065$). The solid lines represent the relationships and the shaded areas represent the 95% confidence intervals.

Chapter Three: Changes in the early growth and condition of Lake Trout (*Salvelinus namaycush*) in response to temporal shifts in prey community dynamics

Abstract

Lake Trout are a widespread and well-studied aquatic apex predatory species found throughout the Canadian Boreal Shield. However, there exists considerable uncertainty around constraints on their early growth and life history. I analyzed changes in the early growth and condition of Lake Trout from a small lake (23.2 ha) at the IISD-Experimental Lakes Area in response to temporal shifts in their prey community dynamics. The introduction of an experimental aquaculture operation resulted in a 3.74-fold increase in the abundance of cyprinid species, a 6.93-fold increase in the abundance of Slimy Sculpin (*Cottus cognatus*), and a 93% decrease in the density (number·m^{-2}) of *M. diluviana*. I predicted that early growth and condition of piscivorous Lake Trout would increase following increased prey fish availability during the aquaculture operation, but non-piscivorous juvenile Lake Trout growth and condition would decline following the decrease in *M. diluviana* density. During the experiment, the growth and condition of both juvenile and mature Lake Trout increased, and the early growth and condition of juvenile Lake Trout remained elevated for years after the aquaculture operation despite prey fish abundances declining near pre-experiment levels. The results of this experiment suggest that moderate nutrient enrichment may benefit the early growth and condition of Lake Trout in oligotrophic Boreal Shield lakes, and *M. diluviana* are potentially less important to the early growth and condition of Lake Trout in the presence of abundant prey fish in this lake, despite prey fish occupying thermally suboptimal Lake Trout habitat.

Introduction

Canada's Boreal Shield lakes face a variety of stressors from the direct and indirect effects of anthropogenic development. In particular, eutrophication has a drastic impact on their physical, chemical, and biological states. Deforestation, agriculture, aquaculture, and habitation have altered habitats and increased nutrient inputs to freshwater ecosystems (Bristow et al. 2008, Carpenter et al. 1998). Additionally, anthropogenic-induced climate change may cause increases in algal biomass through leaching of nutrients trapped in permafrost (Hobbie et al. 1999), as well as increases in water residency times via extreme weather events (Findlay et al. 2001, Schindler 2006). These changes often lead to eutrophication which can have a variety of effects on Boreal Shield lake ecosystems.

Nutrient enrichment typically leads to increases in primary production, algal biomass, and changes in the species composition of algae and bacteria in aquatic ecosystems (Anderson et al. 2002, Schindler and Fee 1974, Sinkko et al. 2013). Algae eventually die and sink to the bottom of a water body where they are decomposed by bacteria. Bacterial decomposition can recycle nutrients through the ecosystem while using up dissolved oxygen, resulting in decreased hypolimnetic dissolved oxygen levels (Hecky et al. 1994). Decreases in hypolimnetic dissolved oxygen can be detrimental for stenothermic organisms that require cold, well-oxygenated water, such as *Mysis diluviana* (*M. diluviana*) and Lake Trout (*Salvelinus namaycush*; Evans 2005, Paterson et al. 2011, Plumb and Blanchfield 2009). As the hypolimnion becomes more hypoxic, the optimal habitat for these species becomes constricted, which in turn may impact their growth, distribution, recruitment, and abundance (Lienesch et al. 2005, Paterson et al. 2011). However, low-level fertilization and nutrient enrichment can also stimulate the productivity of freshwater ecosystems and enhance the growth, condition, and survivorship of many aquatic organisms (Ashley et al. 1997, Johnston et al. 1990), including top predators (Hyatt et al. 2004).

Lake Trout are a wide-spread aquatic apex predatory species found across the Canadian Boreal Shield (Scott and Crossman 1973). As they thrive in deep, well-oxygenated lakes, Lake Trout are thought to be especially vulnerable to the effects of eutrophication and resultant shifts in the community structure of lake ecosystems (Evans et al. 1996, Evans 2007, Gunn et al. 2004). Previous fertilization experiments have shown that Lake Trout growth and recruitment initially increased following nutrient enrichment, but prolonged eutrophication-induced hypoxia may cause declines in Lake Trout recruitment over time (Lienesch et al. 2005). Due to the difficulty in capturing Lake Trout at younger ages and smaller size classes, it has proven difficult to determine how changes in the community dynamics of lake ecosystems with eutrophication influences the growth rates of immature Lake Trout. Trippel and Beamish (1993) found *M. diluviana* to be an important contribution to the diet of immature Lake Trout, whereas Cisco (*Coregonus artedi*), Slimy Sculpin (*Cottus cognatus*), and Yellow Perch (*Perca flavescens*) dominated the diets of larger individuals. Additionally, the invasion of *M. diluviana* into Flathead Lake, Montana, led to increases in recruitment of invasive Lake Trout and declines in the abundance of the native salmonid Bull Trout (*Salvelinus confluentus*; Ellis et al. 2011). Thus, mysids may be a critical contributor to the growth and recruitment of juvenile Lake Trout.

From 2003-2008, an experimental aquaculture operation was conducted at the IISD-Experimental Lakes Area (IISD-ELA) in northwestern Ontario, Canada, to examine the effects of freshwater fish aquaculture on a whole-lake ecosystem. The aquaculture operation resulted in a variety of ecosystem effects including increases in nutrient input (e.g. total phosphorus, ammonium, suspended carbon; Bristow et al. 2008), increases in planktonic chlorophyll a and primary production (Findlay et al. 2009), decreases in hypolimnetic dissolved oxygen (Bristow et al. 2008, Paterson et al. 2011), decreases in the abundance of *M. diluviana* (Paterson et al. 2011), small shifts in the community structure of zooplankton (Paterson et al. 2010), and increases in the abundances of cyprinids and Slimy Sculpin (Mills et al. 2008). Initial measurements of Lake Trout revealed increases in their growth and condition (Mills et al. 2008). However, Mills et al. (2008) only reported data on the first two years of the experiment, three years before the completion of the experiment and before dramatic declines in dissolved oxygen content and the abundance of *M. diluviana* were detected (Paterson et al. 2011). Thus, there remains considerable uncertainty around the longer-term impacts of the aquaculture operation on the early growth and life history of Lake Trout.

In this study, I used archived ageing structures and historical data to retrospectively analyze changes in the early growth rates and condition of Lake Trout before, during, and after the experimental aquaculture operation. I predicted that the growth rates and condition of piscivorous Lake Trout would increase following the start of the aquaculture operation, and their increased growth and condition would mirror the increased abundances of prey fish in the lake. I also predicted that the decline in *M. diluviana* would negatively impact the early growth rates and condition of juvenile Lake Trout that had not yet shifted to piscivory.

Methods

Study Site and Aquaculture Operation

The IISD-ELA is a research station located in northwestern Ontario, Canada, and consists of 58 Precambrian shield lakes that are designated for whole-ecosystem research and long-term monitoring (Cleugh and Hauser 1971). Lake 375 (49°44'40"N, 93°47'20"W) is a small (23.2 ha), oligotrophic, dimictic lake that has maximum depths of 17 and 26 m in the north and south basins, respectively. An experimental aquaculture operation was initiated in the lake in the spring of 2003, and operations were conducted every year through the autumn of 2007. A 10 x 10 x 10 m steel frame cage was placed in the lake over 15 m of water in the north basin of the lake, and 10,000 fingerlings of female Rainbow Trout (*Oncorhynchus mykiss*) were stocked in the cage each spring. Rainbow Trout were fed pellets of Martin Mills Profishent© twice daily. Caged trout were harvested in late autumn each year when they weighed about a kilogram each (~10,000 tonnes harvested annually). Additional details can be found in Blanchfield et al. (2009), Paterson et al. (2011), and Rooney et al. (2009).

Fish Collection and Processing

The native fish community of Lake 375 consists of the cyprinids Finescale Dace (*Phoxinus neogaeus*), Northern Redbelly Dace (*Chrosomus eos*), Pearl Dace (*Margariscus margarita*), and Fathead Minnow (*Pimephales promelas*), as well as Slimy Sculpin (*Cottus cognatus*), White Sucker (*Catostomus commersoni*), and Lake Trout (*Salvelinus namaycush*). Fish were sampled in the spring and fall of each study year using small-mesh trap nets (7 mm) at fixed locations. Two types of trap nets were used for sampling fish: nets containing central leads that were set perpendicular to shore, and nets without central leads, where one of the wings was extended and tied to shore to capture fish moving in one direction (Guzzo et al. 2014, Mills et al. 1987). Both trap net designs contained holding pots with volumes of 2.2-6.1 m^2 that were framed with wood, anchored in place, and set in ~ 3-4 m of water (Beamish 1973, Mills et al. 1987). In the fall, short sets of small-mesh gillnets (38 mm) were used to sample Lake Trout on their spawning shoals via mandibular entanglement (Mills et al. 2002). Captured Lake Trout were anaesthetized (using Trimethane sulfonate), measured for their total and fork lengths (mm), weighed (g), and marked for the season by dorsal fin-ray scarring. Lake Trout fin rays were also clipped for age estimation. Additional details can be found in Beamish 1973, Guzzo et al. 2014, Mills et al. 1987, and Mills et al. (2002).

Prey Relative Abundance and Density

Relative abundance estimates (CPUE) for the cyprinid species and Slimy Sculpin were estimated as the number of fish caught per 24 hours for each trap net set. CPUE estimates for the cyprinids and Slimy Sculpin across each season were then averaged for each year. Percent change in the relative abundance of cyprinids and Slimy Sculpin were calculated between each experiment period (i.e. before, during, after). Lake-wide *M. diluviana* densities (number·m^{-2}) from vertical net hauls were calculated as a weighted average using the mean *M. diluviana* densities at each depth interval and the proportion of the lake area that each depth interval represented (Paterson et al. 2011). *M. diluviana* densities for the open-water season were averaged for each year and percent changes determined between years sampled before and during the experiment. Additional details on *M. diluviana* sampling can be found in Paterson et al. (2011).

Lake Trout Ageing Structure Preparation and Comparison

To estimate early growth of Lake Trout, I used archived ageing structures to back-calculate changes in growth over time. IISD-ELA researchers use non-lethal mark-recapture methods to investigate the growth, life history, and ecology of fish populations. Thus, researchers at the station have traditionally used fin rays (typically either pectoral or pelvic) for estimating the age of fish because they are non-lethal alternatives to sagittal otoliths (Mills and Chalanchuk 2004). Previous studies have shown that the precision of using otoliths and fin rays for estimating the age of long-lived salmonid species is similar and that both structures provide more accurate estimates than scales (Howland et al. 2004, Zymonas and McMahon 2009).

Otoliths have been found to have higher precision between readers compared to fin rays, and they provide older age estimates for slow-growing salmonids (Gallagher et al. 2015, Zhu et al. 2015). Since Lake Trout are a slow-growing, long-living fish species that can live to be greater than 30 years old in Boreal Shield lakes (Mills et al. 2002, Scott and Crossman 1973), I compared the precision and bias of estimating the age of IISD-ELA Lake Trout using paired fin rays (pectoral and pelvic) and otoliths to support using fin rays as the primary structures for estimating the age and early growth of Lake Trout. Paired fin ray and otolith samples were obtained from incidental fish mortalities from multiple IISD-ELA lakes over a 40-year time period. Final age estimates for the two structures were compared to determine the relationship between the two structures and designate a "cut off" age below which fin rays provide an accurate age estimate, and therefore can be used for back-calculations.

Fin rays were dried, mounted in epoxy, cut into 1 mm thick cross-sections using a Beuhler Isomet low-speed saw, and mounted on slides in sequential order for ageing. The first section was from the most proximal portion of the fin ray. Slides were aged under a Leica M125 stereo microscope using a combination of reflected and transmitted light. Ages were estimated by counting the number of annuli. Annuli were identified as the non-growth hyaline bands (dark under reflected light, translucent under transmitted light), while growth was identified as the opaque bands (light under reflected light, dark under transmitted light; DeVries and Frie 1996). Fin rays were typically aged using the larger, ventral hemisegment because these annuli were clearer than those on the dorsal hemisegments (Figure B1).

Otoliths were mounted in epoxy and processed by applying a cross-sectioning technique. Once the epoxy had dried, the nucleus of the otolith and the sectioning plane were marked using an ultra-fine tip Sharpie® marker. Otoliths were thinly sectioned (0.50 mm) through the nucleus along the marked plane using a Buehler Isomet low-speed saw, polished gently with sand paper to clarify annuli, and aged under a dissecting microscope using reflected light. All samples were interpreted blindly without any information about the fish size, capture location or date to minimize bias (Casselman 1983).

Ageing precision, defined as the agreement between first and second readings for the same structures, and the agreement of the estimated ages of 119 paired fin rays (either pectoral or pelvic) and otoliths were compared to assess the validity of using fin rays for back-calculations. The order of the ageing structures was randomized between readings. Precision for each structure and agreement between structures was assessed by calculating percent agreement and the coefficient of variation (CV; Campana et al. 1995, Chang 1982). The mean CVs of the first and second reads for each structure were compared using a paired *t*-test to compare ageing precision for each structure.

Annual Growth-at-Age Determinations

Pectoral fin ray sections from Lake 375 Lake Trout were aged and visualized under 100x magnification using a Leica M125 stereo microscope. Images of the samples were captured and digitized using a Leica DFC490 digital camera and Leica Application Suite software. As multiple rays from fins were sectioned and the quality of annuli varied, I used multiple rays from the pectoral fins of the same individuals for back-calculations. Images were taken of the clearest section and ray for each sample. Three distinct "shapes" of the fin ray sections were observed on individual sections (Figures C1-2). Relative to shape one, shape two was ventrally expanded while shape three was ventrally compressed (Figure B1). Because of the possible influence of shape on back-calculation procedures, the shape was noted for each sample and included as a categorical variable for statistical analyses. Back-calculations on the fin ray sections were performed by measuring distances using the image processing program ImageJ (Schneider et al. 2012). Anterior regions of the fin ray sections were measured for back-calculations because of their consistency among the sections, and the axes of measurement were perpendicular to the annuli (Figure B1). The consistency of growth during the first growing year was inconsistent. To minimize error, origins of measurements for the back-calculations were set to the first identified annuli. Fork lengths-at-age of Lake Trout were back-calculated using the Fraser-Lee intercept correction procedure (Campana 1990, DeVries and Frie 1996, Pierce et al. 1996):

$$L_a = d + (L_c + d)F_c^{-1}F_a \tag{3.1}$$

where L_a is the estimated fish fork length (L) at a given age (a), d is the intercept correction factor, L_c is the fork length (L) of the fish at capture (c), F_c is the size of the fin ray section (F) at capture (c), and F_a is the measured size of the fin ray section (F) at a given age (a). The intercept correction factor was calculated using the relationship between the fork length (mm) of the Lake Trout and the radius of each fin ray section (pixels·mm). Intercept-correction factors were calculated and applied to the equation for each of the three fin ray shapes (Figure B2).

The accuracy of this method was assessed by comparing back-calculated fork lengths-at-age of recaptured Lake Trout to their observed fork lengths-at-age when they were initially captured and tagged. This was performed using recaptured Lake 375 Lake Trout that were caught at the end of their growing season in autumn, and thus their observed fork lengths should be close to what they were at the formation of the next annuli. A combination of pectoral and pelvic fin rays was used for this comparison, as I was dependent upon the available archived fin rays from recaptured fish. Due to the small number of samples (n = 17) and different types of recaptured fin rays available, an accurate intercept correction factor for the back-calculations using the subset of recaptured fins could not be determined. Thus, the intercept correction factor for the back-calculation formula using the recaptured fin rays was calculated by taking the average of the three intercept correction factors from Figure B2 ($L_c = 154.36$) to represent the average size of Lake Trout at the start of age one. A paired *t*-test was used to evaluate differences between the observed (mean ± SE, 358.24 ± 6.14 mm) and back-calculated fork lengths (356.17 ± 10.17 mm; $p = 0.80$, $n = 17$), and a linear regression of observed vs. back-calculated fork lengths was performed to assess the strength and bias of the relationship (Figure B3).

Annual growth ($\text{mm}\cdot\text{year}^{-1}$) for individual Lake Trout in age classes 1-5 in a given year (1999-2013) was calculated by taking the difference between the back-calculated length-at-age of the Lake Trout and their back-calculated length-at-age from the previous year. As I was unable to back-calculate the length-at-age 1 due to the first annuli being used as the origins for the measurements, the annual growth-at-age 1 for individual Lake Trout was calculated by taking the difference between their back-calculated length-at-age 2 and their associated intercept correction factor (which represents the first annulus, as there is no origin point on fin rays; Figure B1). Average annual growth for ages 1-5 was compared among the periods before (1999-2002), during (2003-2007), and after (2008-2013) the experiment using R 3.1.2 (R Core Team 2014) and a mixed-effects analysis of variance (ANOVA) approach, followed by Tukey HSD post hoc tests. The mixed-effects model was run using the package "nlme" (Pinheiro et al. 2017), and Tukey HSD post hoc tests were run using the package "lsmeans" (Lenth 2016). The model included fixed effects (i.e. age of annual growth, experiment period) with an interaction between them and random effects (i.e. year the growth took place, individual fish ID).

In addition to the back-calculated annual growth measurements, growth-at-age ($\text{pixels}\cdot\text{mm}\cdot\text{year}^{-1}$) was also calculated using annual fin ray increment widths and the mixed-effects model approach described in Weisberg (2010) for Lake Trout (ages 1-5) before, during, and after the experiment. This approach differs from the back-calculation approach in that it directly compares the annual increment widths (pixels·mm) instead of comparing the converted back-calculation measurements. The mixed-effects ANOVA was run using the package "nlme" in R 3.1.2. The model included fixed effects (i.e. age of growth increment, experiment period) with an interaction term between them and random effects (i.e. fin ray shape, year the growth took place, individual fish ID). The model can be described by the following formula:

$$Y_{cka} = i_a + X_{ck} + (iX)_{a,ck} + S_{cka} + T_{cka} + U_{cka} + e_{cka} \tag{3.2}$$

where the response variable Y_{cka} is the a-th annular growth increment for the k-th fish from year class c. Fixed effects for the model included the following: i_a, the annular growth increment for a fish of age a; X_{ck}, a variable to represent fish captured during a particular experimental period for the k-th fish in a year class c; and $(iX)_{a,\,ck}$, an interaction term between the age of the growth increment and the experiment period. S_{cka} represents the random effect of fin ray shape with zero mean variance for k-th fish of year class c at age a. T_{cka} represents the random effect of the year the sampling occurred with zero mean variance for k-th fish of year class c at age a. U_{cka} represents the random effect of the individual fish IDs with zero mean variance for k-th fish of year class c at age a. Lastly, e_{cka} is assumed to be an independent error term with mean zero and common variance.

Condition Analyses

I used relative weight (W_r, %) as a measure of condition for juvenile (< 350 mm, fork length) and mature (350-600 mm, fork length) Lake Trout. The cutoff of 350 mm to distinguish between juvenile and mature Lake Trout was used because Lake 375 Lake Trout very rarely mature at fork lengths less than 350 mm (Rennie, pers. comm.). Relative weight was estimated for Lake Trout by first calculating their standard weight using the equation from Piccolo et al. 1993:

$$\log_{10} W_s = -5.681 + 3.2462 \log_{10} TL \tag{3.3}$$

where W_s is the weight of the Lake Trout (g) and TL is their total length (mm). Relative weight was then calculated using the formula:

$$W_r = 100(W / W_s) \tag{3.4}$$

where W_r is relative weight expressed as a percentage of W_s, W is the measured weight of the individual fish, and W_s is the length-specific standard weight (Piccolo et al. 1993). Relative weights were calculated for a wide-range of Lake Trout sizes (150-618 mm, total length). The minimum size for the application of Piccolo's equation is 280 mm. Approximately 3.91% of the fish included in our analysis were below this value, but were included to characterize juvenile fish condition which were underrepresented to begin with (9.52% juvenile vs. 90.48% mature). Average relative weights of juvenile and mature Lake Trout were compared among the periods before, during, and after the experiment using a mixed-effects ANOVA approach and the "nlme" package in R 3.1.2. Differences among and between the relative weights of juvenile and mature Lake Trout during each experimental period were evaluated using Tukey HSD post hoc tests via the "lsmeans" package in R 3.1.2. The model included fixed effects (i.e. maturity status, experiment period) with an interaction term and random effects (i.e. year the fish were captured, individual fish ID). The significance of the interaction term in the model was determined using a likelihood ratio test.

Results

Prey Community Change

Abundances (CPUE) of cyprinids and Slimy Sculpin increase during the experiment compared to the years before the experiment, but reverted within 1-2 years to pre-experiment levels following the removal of the aquaculture cage (Figures 3.1 and 3.2). There were 3.74 and 6.93-fold increases in the CPUE of cyprinid species and Slimy Sculpin, respectively, from the period before the experiment to the period during the experiment. Additionally, there were 70.03% and 74.64% decreases in the CPUE of cyprinid species and Slimy Sculpin, respectively, from the period during the experiment to the period after the experiment. In contrast, *M. diluviana* density decreased in the 4th and 5th years of the aquaculture operation (Figure 3.3). The average density of *M. diluviana* (number·m^{-2}) decreased from 87.40 m^{-2} in 2002 to 6.09 m^{-2} in 2008, a 93% decrease (Figure 3.3; Paterson et al. 2011).

Precision and Bias of Ageing Structures

Annuli were detectable for both the otolith and fin ray samples, and the range of the ages, mean ages, and standard errors were similar between the reads for each structure (Table 3.1). The percent agreement (PA) between the reads for each structure was greatest for the first and second fin ray reads (PA = 54.62%), followed by the second fin ray reads and second otolith reads (PA = 44.54%; Table 3.2). The lowest percent agreement occurred between the first fin ray reads and the first otolith reads (PA = 34.45%). Although the percent agreement between the reads was relatively low, the difference in the age estimations was typically only one year. The first and second otolith reads were within one year of each other 80.67% of the time, the first and second fin ray reads were within one year of each other 87.50% of the time, and the second otolith and fin ray reads were within one year of each other 81.51% of the time. Additionally, a paired *t*-test revealed the mean CV for the fin ray reads (mean ± SE, 5.96 ± 0.74) was significantly lower than the mean CV for the otolith reads (9.40 ± 1.03; $t = -2.84$, df = 118, $p = 0.005$). A visual inspection of the relationship between the estimated ages for the second fin ray and otolith reads revealed that the relationship was more variable at older ages (Figure 3.4). For second fin ray reads of 13 years or older, only 7.69% of the age estimations agreed with the paired second otolith age estimations (n = 13). Additionally, only 15.38% of the first and second fin ray age estimations agreed for fish whose second fin ray age estimations were 13 years or older. Due to the decrease in the agreement between the age estimations at older ages, I limited the annual growth measurements to Lake Trout that had estimated fin ray ages of 12 and younger.

Annual Growth-at-Age and Condition

The early growth of the Lake Trout appeared to be greater following the start of the aquaculture operation compared to years prior. The average annual growth ($mm \cdot year^{-1}$) for age 1-3 Lake Trout was greater in years during and after the experiment than years prior (Figure 3.5, Table C2). The average annual growth-at-age of the Lake Trout was not significantly different for any of the age classes before and during the experiment (t = 0.13-2.74, $p > 0.05$; Table C2). Increases in Lake Trout average annual growth was greatest for age 2 and 3 individuals in the period after the experiment. Tukey HSD post-hoc tests revealed the average annual growth-at-age 2 was significantly greater in the period after (73.48 ± 2.46 $mm \cdot year^{-1}$) the experiment compared to the periods before (49.32 ± 2.19 $mm \cdot year^{-1}$; t = 7.33, $p < 0.0001$) and during (55.96 ± 2.10 $mm \cdot year^{-1}$; t = 5.42, $p < 0.0001$) the experiment (Figure 3.5, Table C2). There were no other significant differences between the annual growth-at-age measurements from the period after the experiment and the annual growth-at-age measurements from the periods before and during the experiment.

Results from the growth increments ($pixels \cdot mm \cdot year^{-1}$) were similar to the back-calculated annual growth results. Growth increments of Lake Trout were largest from age 1-2 and age 2-3, and they progressively decreased following age 2. Tukey HSD post-hoc tests revealed the only statistically significant differences were between Lake Trout annual growth-at-age 2 in the period after the experiment (0.062 ± 0.008 pixels·mm·year^{-1}) compared to the periods before (0.049 ± 0.007 pixels·mm·year^{-1}; $t = 3.95$, $p < 0.01$) and during (0.050 ± 0.007 pixels·mm·year^{-1}; $t = 3.60$, $p < 0.05$) the experiment (Figure 3.6), which was consistent with the back-calculated annual growth results for that age class.

The condition (W_r, %) of both juvenile (< 350 mm) and mature (350-600 mm) Lake Trout increased during the experiment compared to years prior (Figure 3.7, Table C1). Additionally, the condition of juvenile Lake Trout remained elevated in the period after the experiment, while the condition of mature Lake Trout declined to values similar to those observed before the experiment. There was a significant interaction term between experiment period and maturity for the mixed effects model (Likelihood ratio test, $X^2 = 8.06$, df= 2, $p < 0.05$). However, Tukey HSD post-hoc tests revealed there were no statistically significant changes in either the condition of juvenile or mature Lake Trout between the experiment periods ($t = -2.05$-2.30, $p > 0.05$). The condition of juvenile and mature Lake Trout was not significantly different before the experiment (Tukey HSD, $t = 2.80$, $p > 0.05$, Figure 3.7, Table C1), but condition of juvenile and mature Lake Trout diverged following the start of the aquaculture operation. The condition of juvenile Lake Trout during the experiment was significantly greater than the condition of mature Lake Trout during the experiment (Tukey HSD, $t = 4.78$, $p < 0.0001$, Figure 3.7), and the condition of the juvenile Lake Trout continued to be greater than the condition of the mature Lake Trout after the experiment (Tukey HSD, $t = 7.53$, $p < 0.0001$). Furthermore, the condition of juvenile Lake Trout during the experiment was significantly greater than the condition of mature Lake Trout in the periods before (Tukey HSD, $t = 3.72$, $p <$

0.05) and after (Tukey HSD, $t = 4.17$, $p < 0.05$) the experiment. The condition of juvenile Lake Trout after the experiment was not significantly greater than the condition of mature Lake Trout before or during the experiment (Tukey HSD, $t = 1.54\text{-}3.26$, $p > 0.05$). Finally, the condition of juvenile Lake Trout before the experiment was not significantly different from the condition of mature Lake Trout during and after the experiment (Tukey HSD, $t = -0.25\text{-}1.48$, $p > 0.05$).

Discussion

As the abundance of prey fish increased during the aquaculture operation, so too did the early growth of Lake Trout. However, Lake Trout continued to show rapid early growth after the aquaculture operation despite relative abundance estimates of prey fish in the lake reverting to pre-experiment levels. Growth rates of fish have repeatedly been shown to be accelerated when the abundance of their prey increases (Graeb et al. 2004), and a similar fertilization experiment in an Alaskan lake showed that Lake Trout had elevated growth rates as a consequence of increased productivity and prey abundance (Lienesch et al. 2005). As such, the greater annual growth of Lake Trout during the experiment when prey fish abundances were elevated was not surprising. However, the sustained growth and condition of juvenile Lake Trout after the experiment was unexpected.

In a previous fertilization experiment at the IISD-ELA, Lake Whitefish (*Coregonus clupeaformis*) in Lake 226 maintained elevated growth after the cessation of the fertilization compared to the non-fertilized basin of the lake (Mills et al. 1987). However, the growth of Lake Whitefish in the years after cessation of the fertilization was less than their growth in the years when fertilization occured. In contrast, Lake Trout in this study exhibited the fastest growth from age 2-3 in the years after the aquaculture operation (73.48 ± 2.35 mm·year^{-1}), a drastic increase from the years during the experiment (55.96 ± 1.78 mm·year^{-1}). The average back-calculated fork length for Lake Trout at the start of age 2 during the after experiment years was 208.78 mm, and their average weight (g) at this size was about 100 grams (Figure C4). Researchers have previously reported that Lake Trout in Algonquin Park, ON, shift from feeding on profundal invertebrates to littoral invertebrates and cyprinids at about 100 grams (Sherwood et al. 2002). Thus, it is likely that the Lake Trout in this study made an ontogenetic shift to foraging on cyprinids at age 2, explaining their elevated growth at this age. Despite the trap net data showing a decrease in the relative abundance of prey fish after the aquaculture operation, prey accessibility may have remained high for immature Lake Trout. Possibly, Lake Trout predation on prey fish remained high following the aquaculture operation, but the prey fish had lower recruitment which ultimately resulted in their abundances declining. As food waste from the aquaculture operation accounted for nearly 30% of the diet of cyprinid species by the third year of the experiment (Kullman et al. 2009) and the density of *M. diluviana* drastically decreased by 2008 (Paterson et al. 2011), prey fish would have had less available food after the aquaculture operation ultimately affecting their abundance and recruitment. This is in accordance with isotopic values from cyprinids in the lake, where carbon isotope ratios ($\delta^{13}C$) of the cyprinids shifted towards the trace of the fish feed during the aquaculture operation, and then returned towards pre-experiment levels after the aquaculture operation (Kidd et al. 2017). This trend was also prevalent for other species in the lake, including Lake Trout and *M. diluviana*.

In addition to $\delta^{13}C$ decreasing for cyprinids, Lake Trout, and *M. diluviana* after the experiment, nitrogen isotope ratios ($\delta^{15}N$), a measure of relative trophic position (Peterson and Fry 1987), increased for Lake Trout, cyprinids, *M. diluviana*, zooplankton, and certain littoral macroinvertebrates both during and after the experiment (Kidd et al. 2017). The increased nutrient inputs into the lake likely had a bottom-up effect on the ecosystem, providing primary consumers with more food via increases in chlorophyll ɑ concentration and phytoplankton biomass in the epilimnion (Bristow et al. 2008, Findlay et al. 2009, Paterson et al. 2010). Furthermore, food pellets and waste from the aquaculture operation provided additional food to consumers in the lake (Kullman et al. 2009). As indicated by increases in their abundance, cyprinids and Slimy Sculpin likely had a surplus of food available to them during the aquaculture operation which may have resulted in increases in their condition, recruitment, and relative trophic position (Kidd et al. 2017, Mills et al. 2008). Improved condition and energy density of cyprinids and Slimy Sculpin in the lake could explain the continued rapid growth of Lake Trout observed here, as they are the primary prey for larger Lake Trout in the lake. Additionally, the productivity of the lake remained elevated in the years following the aquaculture operation, and it will likely take several years for the lake to return to its normal state (Kidd et al. 2017, Mills et al. 1987).

In contrast to my hypotheses, the 93% decline in *M. diluviana* density had no detectable negative effects on juvenile Lake Trout growth and condition. Lake Trout growth increased as mentioned previously, and the recruitment of Lake Trout also increased as evidenced by the greater percentages of age 3-4, 5-6, and 7-8 year old Lake Trout caught during and after the experiment (Figure C3). Additionally, the condition of juvenile Lake Trout increased, though not significantly, during the aquaculture operation and remained elevated after the operation, suggesting that juvenile Lake Trout had abundant prey to forage on during both experiment periods. However, results for juvenile Lake Trout condition should be interpreted with caution as they are extrapolated beyond the standard weight equation (Piccolo et al. 1993). Although there was a dramatic decline in their density, *M. diluviana* were never completely extirpated from the lake, but were restricted to a smaller portion of the lake due to hypoxia in the hypolimnion. Thus, Lake Trout may have been able to forage more efficiently on *M. diluviana* while they were confined to this smaller area. Furthermore, the density of *M. diluviana* rebounded after the lake began to recover following the aquaculture operation (Paterson, pers. comm.). A strong rebound in the abundance of *M. diluviana* in the lake could explain the rapid growth of juvenile Lake Trout after the aquaculture operation, as they are an important component of juvenile Lake Trout diets (Trippel and Beamish 1993).

Similar to juveniles, mature Lake Trout had increased condition during the aquaculture operation. However, mature Lake Trout condition subsequently decreased after the decline in prey fish abundance. Compared to years before the aquaculture operation, the prevalence of larger Lake Trout drastically increased in the periods during and after the experiment (Figures D1-2). During and after the experiment, Lake Trout were captured at sizes greater than 450 millimeters and 1,000 grams, while no fish this large were ever captured before the aquaculture operation began. The increase in the body sizes of Lake Trout was likely a result of the increased prey fish availability following the onset of the aquaculture operation. However, the larger body sizes obtained by Lake Trout during and after the experiment may not have been sustainable following the decline in the abundance of prey fish. Additionally, mature Lake Trout have greater energetic needs compared to juvenile Lake Trout because of their larger sizes and diversion of energy towards reproduction (Quince et al. 2008), and they are more reliant on larger, energy-rich prey (Trippel and Beamish 1993). Thus, the decrease in prey fish availability was almost certainly a factor in the lower condition of mature Lake Trout relative to juveniles after the experiment, and it is likely that the condition of mature Lake Trout will continue to decline as the lake returns to its oligotrophic state.

The results of this research further exemplify how increased nutrient inputs into oligotrophic lakes affects the growth and condition of Lake Trout populations via increased prey fish availability. As a variety of stressors, including climate change and anthropogenic development, have contributed to the eutrophication of freshwater systems (Bristow et al. 2008, Carpenter et al. 1998, Schindler 2006), it is important to understand how these changes will impact Lake Trout populations across North America. Although there were no negative effects on Lake Trout detected in this study, it is possible that prolonged nutrient enrichment in these systems may negatively impact Lake Trout recruitment through reductions in their optimal habitat (Lienesch et al. 2005). However, the lack of negative effects detected in this study suggests that moderate amounts of nutrient enrichment in oligotrophic lakes may positively impact the growth and productivity of Lake Trout, at least initially. Additionally, this experiment provides further context on how the growth of Lake Trout is impacted by changes in resource availability. The hypothesis that the growth rates of piscivorous Lake Trout would increase following the increase in the abundance of cyprinids and Slimy Sculpin was supported, but there were no detectable negative effects of the decline in *M. diluviana* abundance on juvenile Lake Trout growth and condition. This suggests that juvenile Lake Trout forage opportunistically and were able to subsist on alternate prey.

Although the altered growth of Lake Trout in this experiment was the result of the aquaculture operation, the effects on the ecosystem provided a unique opportunity to investigate how the growth of Lake Trout is impacted by fluctuations in prey community dynamics of lakes. Despite detecting no negative effects of the eutrophication and the decline in *M. diluviana* density on the growth and condition of Lake Trout, further examination of Lake Trout after the experiment is needed to understand how their recruitment, condition, maturity, and growth trajectories have been impacted by the lake returning to its oligotrophic state.

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Table 3.1 Range, mean, and standard error of the Lake Trout age estimations for both the first and second reads of each ageing structure (*n*= 119).

	Otolith Age			**Fin Ray Age**		
Read	Range	Mean	(SE)	Range	Mean	(SE)
Read 1	2-22	7.18	(0.33)	2-19	7.08	(0.35)
Read 2	2-23	7.27	(0.37)	2-21	7.28	(0.37)
Overall	2-23	7.19	(0.25)	2-21	7.19	(0.25)

Table 3.2 Percent agreement between the first and second age estimations for each Lake Trout ageing structure.

	Otolith 1st Read	Otolith 2nd Read	Fin Ray 1st Read	Fin Ray 2nd Read
Otolith 1st Read	100.00			
Otolith 2nd Read	40.34	100.00		
Fin Ray 1st Read	34.45	38.66	100.00	
Fin Ray 2nd Read	37.82	44.54	54.62	100.00

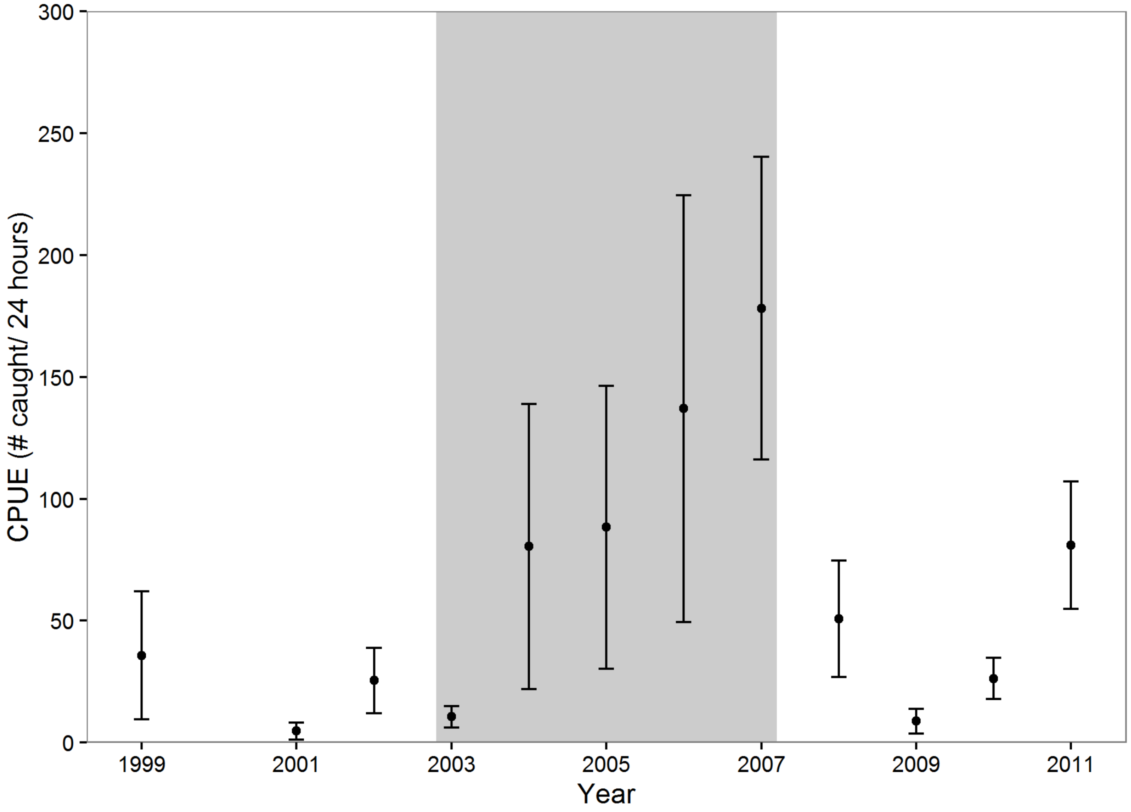

Figure 3.1 The average relative abundance (# of individuals caught/ 24 hours) of all cyprinid species in Lake 375 from 1999-2011 for all seasons. Error bars represent the standard errors for each year. The shaded box represents the years during the experimental aquaculture operation.

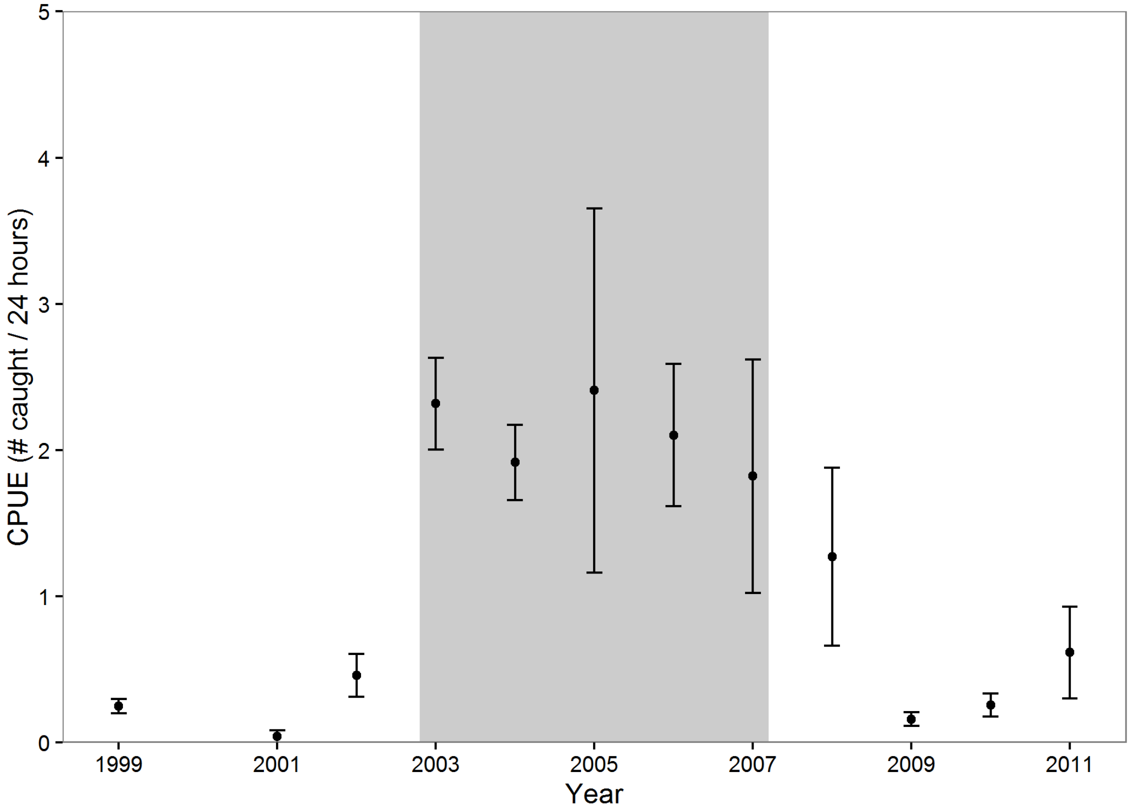

Figure 3.2 The average relative abundance (# of individuals caught/ 24 hours) of Slimy Sculpin in Lake 375 from 1999-2011 for all seasons. Error bars represent the standard errors for each year. The shaded box represents the years during the experimental aquaculture operation.

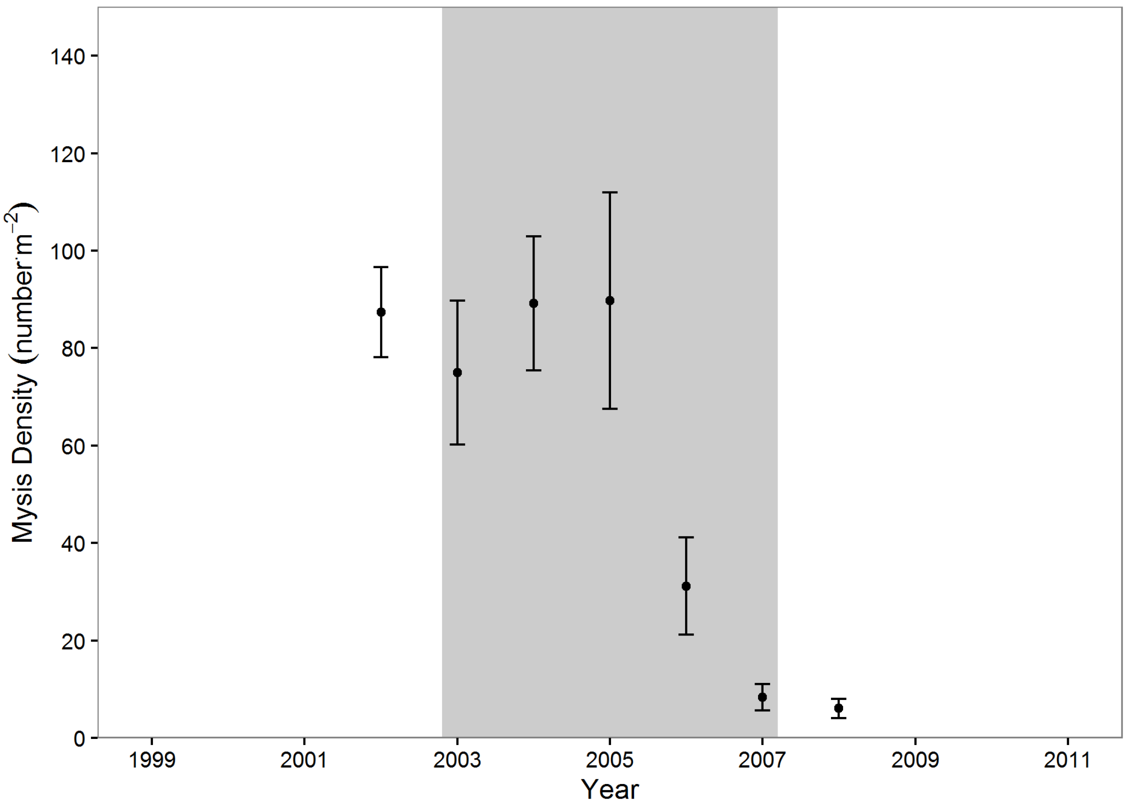

Figure 3.3 The average density (number·m^{-2}) of *M. diluviana* in Lake 375 from 2002-2008 for all seasons. Error bars represent the standard errors for each year. The shaded box represents the years during the experimental aquaculture operation. Data are reproduced from Paterson et al. 2011.

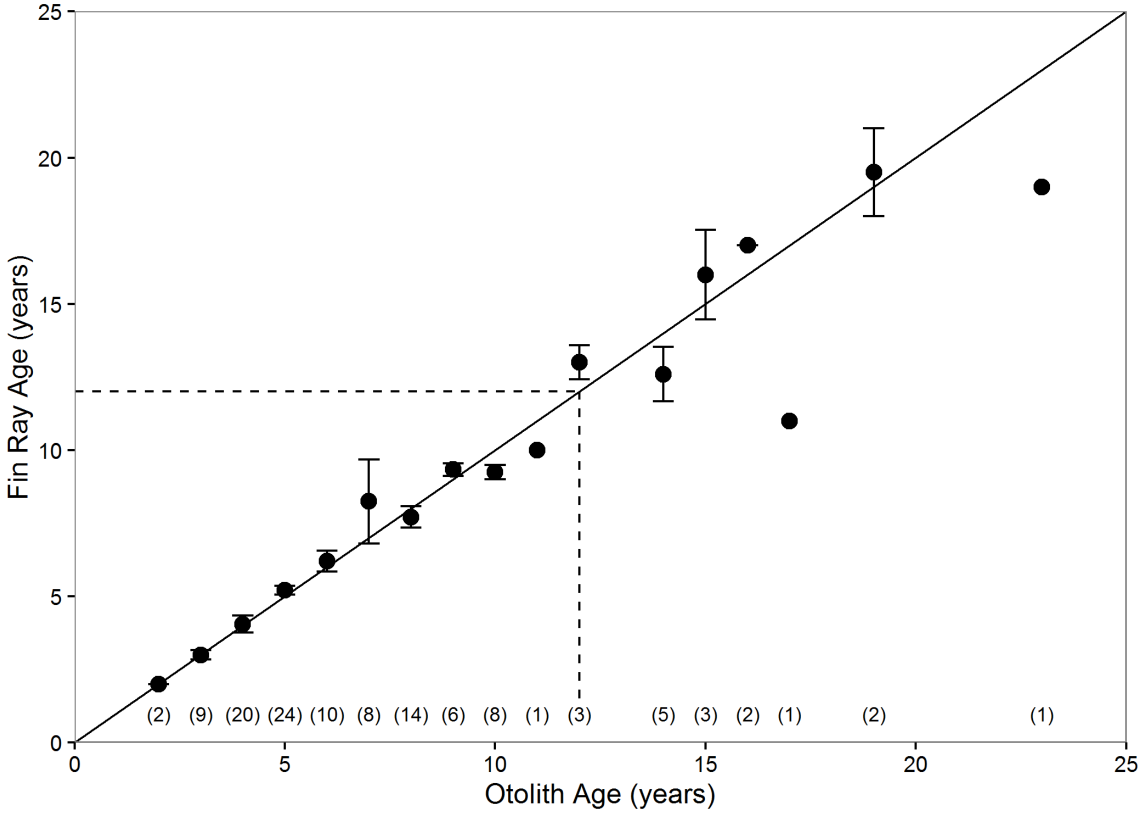

Figure 3.4 Agreement of final age estimations for paired Lake Trout fin rays and otoliths. Data points equal the mean and the error bars represent the standard errors for the paired structures at each estimated otolith age. The diagonal line represents a 1:1 line of complete agreement. The sample sizes are in parentheses above the x-axis. Dashed lines indicate the cut-off age for fish for which back-calculations were performed.

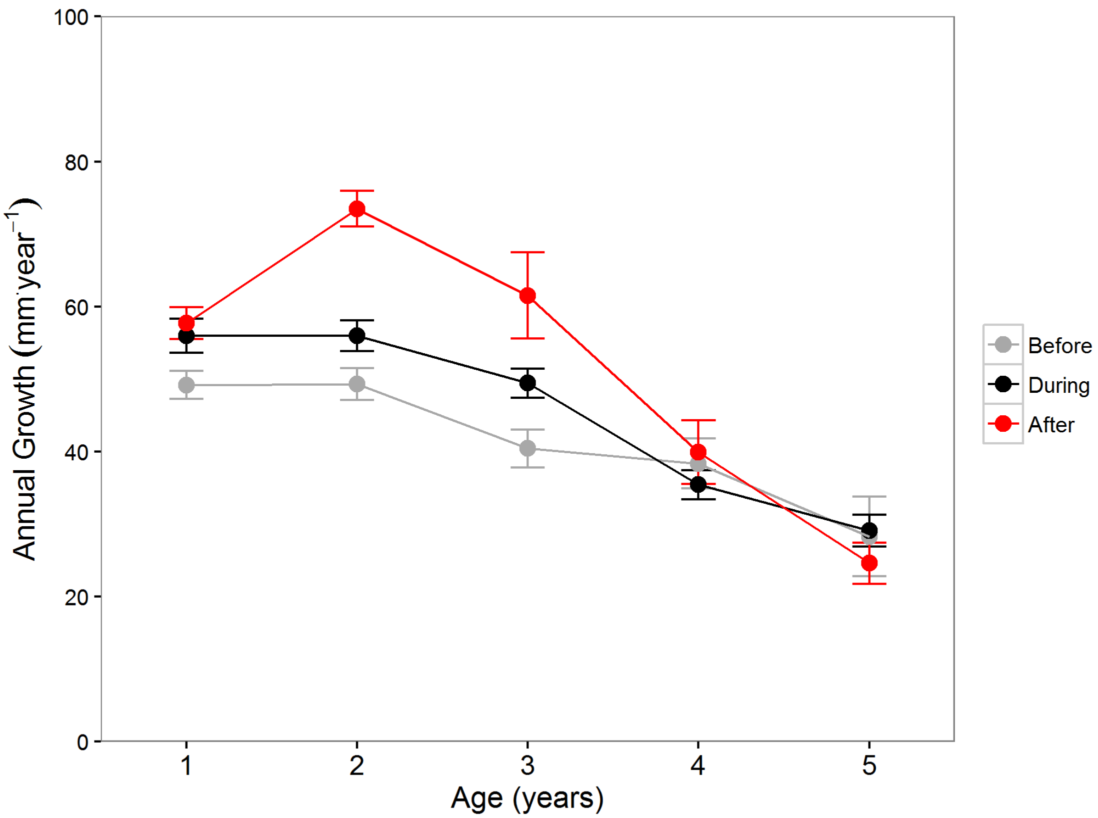

Figure 3.5 The average back-calculated annual growth (mm·year^{-1}) of individual Lake Trout for ages 1-5 before (1999-2002), during (2003-2007), and after (2008-2013) the aquaculture operation. The error bars represent the standard errors for the measurements at each age class.

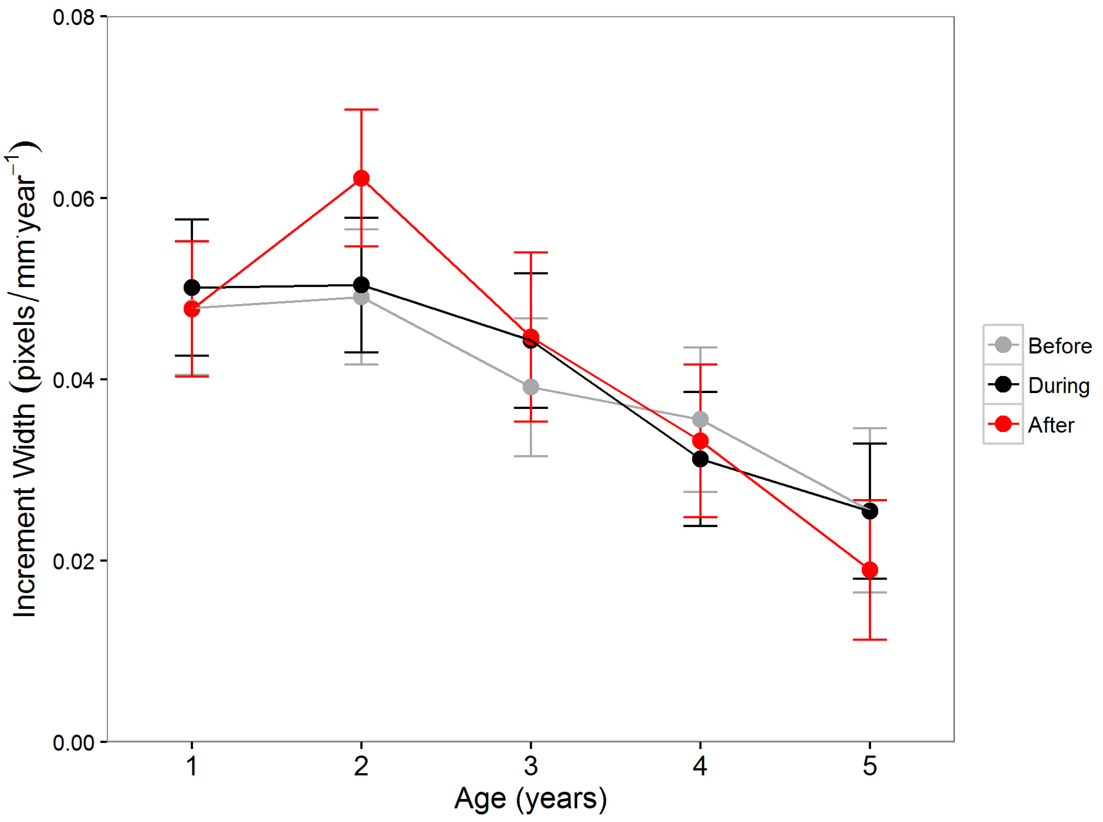

Figure 3.6 The average predicted growth-at-age measured as increment width (pixels·mm·year^{-1}) for age 1-5 Lake Trout before (1999-2002), during (2003-2007), and after (2008-2013) the aquaculture operation. The error bars represent the standard errors for the measurements from the mixed-effects model.

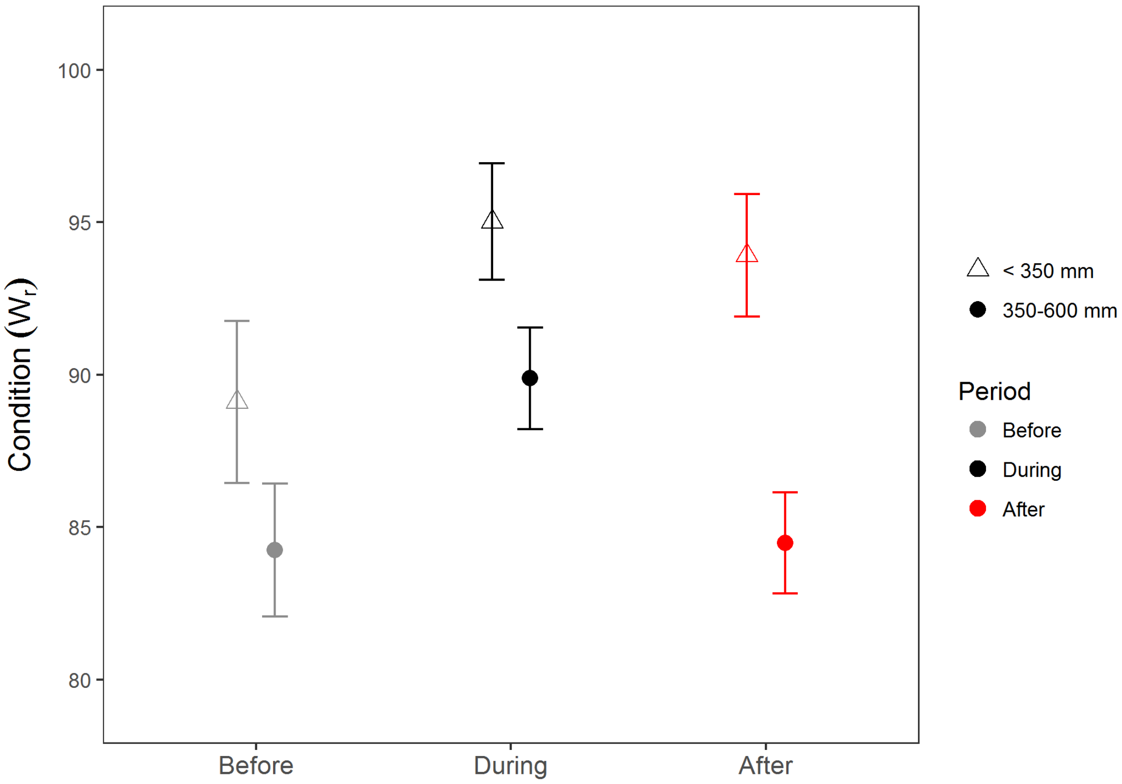

Figure 3.7 The average condition of juvenile (< 350 mm) and mature (350-600 mm) Lake Trout expressed as relative weight (W_r, %) before (1999-2002), during (2003-2007), and after (2008-2013) the aquaculture operation. The error bars represent the standard errors for the measurements.

Chapter Four: Synthesis Discussion

In this thesis, I examined how prey community composition and dynamics influence growth and life history strategies of aquatic apex predators common to the Canadian Boreal Shield. This was accomplished by using standardized netting data from the province of Ontario to compare the influence of the offshore prey community on the life history variation of Northern Pike and Lake Trout (Chapter 2), as well as retrospectively analyzing changes in the early growth and condition of Lake Trout in response to temporal shifts in prey community dynamics of a single lake (Chapter 3). The availability of offshore, energy-rich Cisco in Boreal Shield lakes appears to influence the growth and life history strategies of both Northern Pike and Lake Trout, where both species reach significantly larger asymptotic lengths when Cisco are more abundant. Additionally, Northern Pike have slower early growth rates and lower mortality rates in lakes with greater abundances of Cisco. The widespread influence of Cisco availability on the life history traits of Northern Pike suggests that they behave more as generalists, rather than nearshore specialists, when offshore prey are abundant. For Lake Trout in lakes without offshore prey fish, the availability of smaller nearshore prey fish appears to have a large influence on their early growth and life history. Results on the early life history of Lake Trout here reveal that juvenile Lake Trout have elevated growth rates and condition in response to nutrient enrichment and drastic increases in the abundance of small prey fish. Together, the results of this research suggest that the availability of energy-rich prey fish is critical to the growth of aquatic apex predators throughout their ontogeny, and the life history strategies of these predators varies with respect to such prey availability.

The influence of Cisco on the growth and life history variation of Northern Pike and Lake Trout observed across the Boreal Shield was consistent with previous case studies on aquatic apex predatory species (Kaufman et al. 2006, Trippel and Beamish 1989). Lake Trout have been shown to grow more efficiently in lakes with prey fish compared to lakes without prey fish (Pazzia et al. 2002), and the availability of Cisco has been shown to influence both the asymptotic size and size at maturity of Lake Trout in Lake Opeongo (Martin 1970, Shuter et al. 2016). However, my research is to first to quantify the influence of the offshore prey community on growth and life history variation of Northern Pike across the Canadian Boreal Shield. In the primary literature, Northern Pike in North America have almost always been associated with nearshore energy pathways. While Northern Pike are reliant on nearshore littoral habitat during their early growth and life history, the results of this research suggest that Northern Pike may make ontogenetic shifts to feeding on offshore Cisco when they are abundant. As Cisco are an energy-dense and productive mid-trophic-level fish (Bryan et al. 1996, Rypel and David 2017), foraging on them is potentially profitable for aquatic apex predators. Furthermore, the availability of Cisco may allow Northern Pike and other aquatic apex predators to grow more efficiently, slowing down their rate of senescence and allowing them to live and reproduce longer.

While the life history analyses here provide strong evidence for a widespread use of offshore prey by Northern Pike, further research is necessary to understand how and when Northern Pike incorporate themselves into offshore food webs. Previous research has shown that larger Northern Pike are more active and occupy deeper habitat than do smaller Northern Pike (Casselman and Lewis 1996, Chapman and Mackay 1984, Kobler et al. 2008), supporting the conclusion that an ontogenetic shift to foraging on Cisco likely occurs during Northern Pike's later life history stages. To test this hypothesis, a combination of dietary and stable isotope analyses could be used on a broad range of Northern Pike size classes in Cisco lakes to determine at what age and size their diet shifts to offshore resources occur, as well as how their prey utilization varies by season. Such information would be vital for fisheries managers, as it would further their understanding of Northern Pike foraging ecology, provide insight on how to attain desirable life histories of Northern Pike, and inform them how to effectively implement management decisions in the face of environmental change. For lakes with multiple coexisting apex predators, similar dietary studies would provide insights into resource partitioning and the dynamics of intraguild predation between aquatic apex predators. Understanding the dynamics of intraguild predation is crucial to understanding the delicate balance of aquatic ecosystems and how that balance might shift in response to changes in the environment. For example, it may provide insight on how warming climates influence foraging behaviors and resource use of multiple predatory fishes.

When larger offshore prey fish are absent, the availability of smaller prey fish appears to be critical for the early growth of Lake Trout in oligotrophic Boreal Shield lakes. Following nutrient enrichment caused by an experimental aquaculture operation in a small Boreal Shield lake, I showed that the abundance of small prey fish in the lake drastically increased, ultimately resulting in faster early growth rates and better condition of Lake Trout. The growth of the Lake Trout was significantly faster when they were two years of age. Lake Trout in this lake typically weighed about 100 grams at the start of age 2, which is the size that Lake Trout in similar systems switch to foraging on littoral minnows and invertebrates (Sherwood et al. 2002). Despite a 93% decrease in the density of *M. diluviana,* an important prey species for juvenile Lake Trout (Trippel and Beamish 1993), no negative effects on the early growth and condition of Lake Trout were detected in this study. This suggests that juvenile Lake Trout are opportunistic and can subsist on a variety of prey during their early life histories, such as profundal invertebrates, littoral invertebrates, and small prey fish. Furthermore, investigating the influence that near shore prey species might have on the growth and life history strategies of Lake Trout provides insights into how these populations might shift in response to climate change, as optimal Lake Trout habitat is projected to decrease and nearshore prey may become less available (Dillon et al. 2003, Dolson et al. 2009, Plumb and Blanchfield 2009). In the absence of offshore prey fish, Lake Trout may experience significant stunting in their growth if nearshore prey fish become less available due to warming water temperatures.

Overall, this thesis has shown that growth and life history variation of aquatic apex predators both within and among Canadian Boreal Shield lakes is strongly influenced by prey community structure and dynamics. Specifically, energy in the form of available prey fish is a major driver of the life history strategies with which we observe in aquatic apex predators throughout their development. The results of this thesis contribute more evidence on how prey community dynamics help shape the growth potential and evolution of life history strategies of fishes, and such bottom up effects should continue to be considered when investigating and managing predators in the natural world.

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Appendix A. Relationships among the fixed effects included in the Northern Pike and Lake Trout life history analyses.

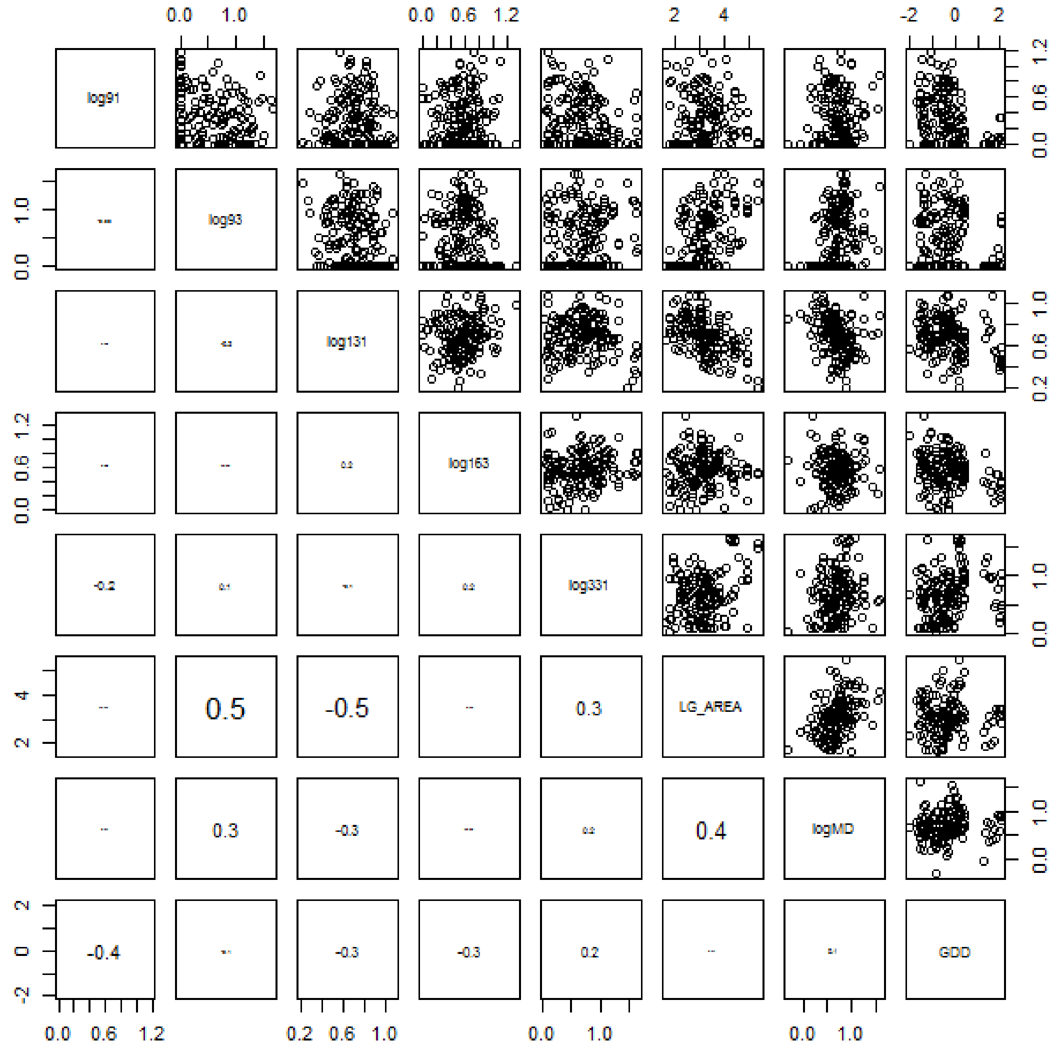

Figure A1. Multi-panel scatterplot of the fixed effects investigated in the FWIN female Northern Pike life history analyses. The top right panels display the relationships between paired variables, the lower left panels display Pearson correlation coefficients between paired variables. Variables that are more correlated are represented by larger correlation coefficients. The variable names that match the abbreviations in the figure can be found in Table 2.1.

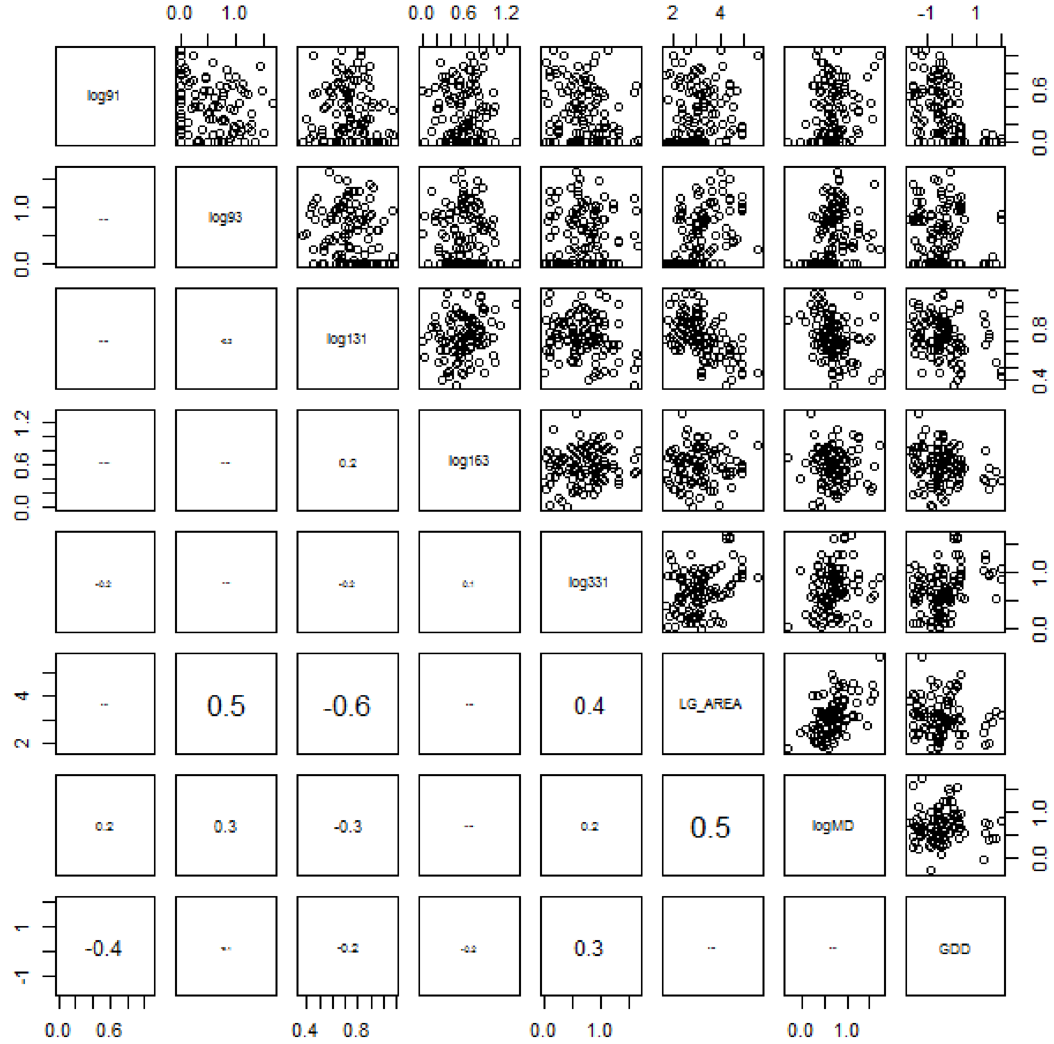

Figure A2. Multi-panel scatterplot of the fixed effects investigated in the FWIN male Northern Pike life history analyses. The top right panels display the relationships between paired variables, the lower left panels display Pearson correlation coefficients between paired variables. Variables that are more correlated are represented by larger correlation coefficients. The variable names that match the abbreviations in the figure can be found in Table 2.1.

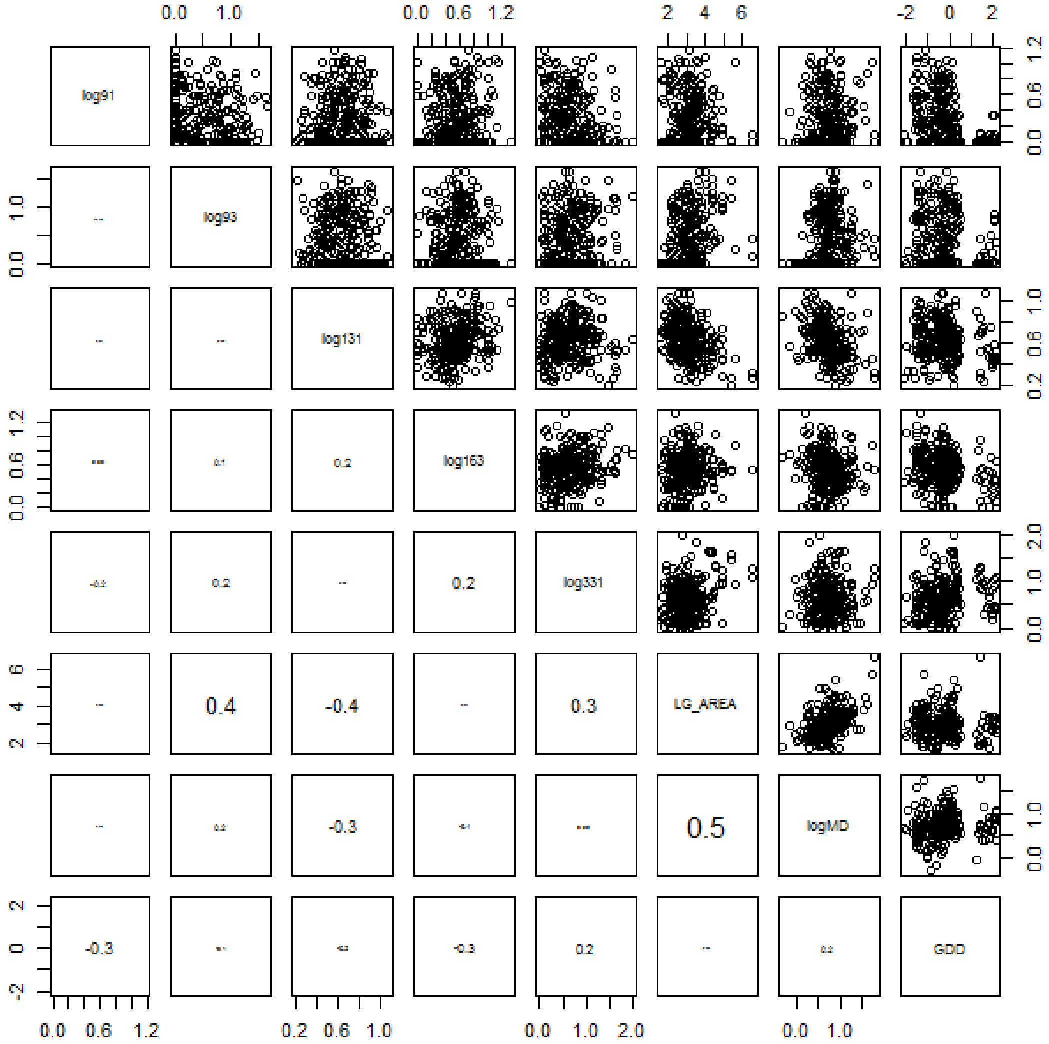

Figure A3. Multi-panel scatterplot of the fixed effects investigated in the FWIN Northern Pike relative abundance life history analysis. The top right panels display the relationships between paired variables, the lower left panels display Pearson correlation coefficients between paired variables. Variables that are more correlated are represented by larger correlation coefficients. The variable names that match the abbreviations in the figure can be found in Table 2.1.

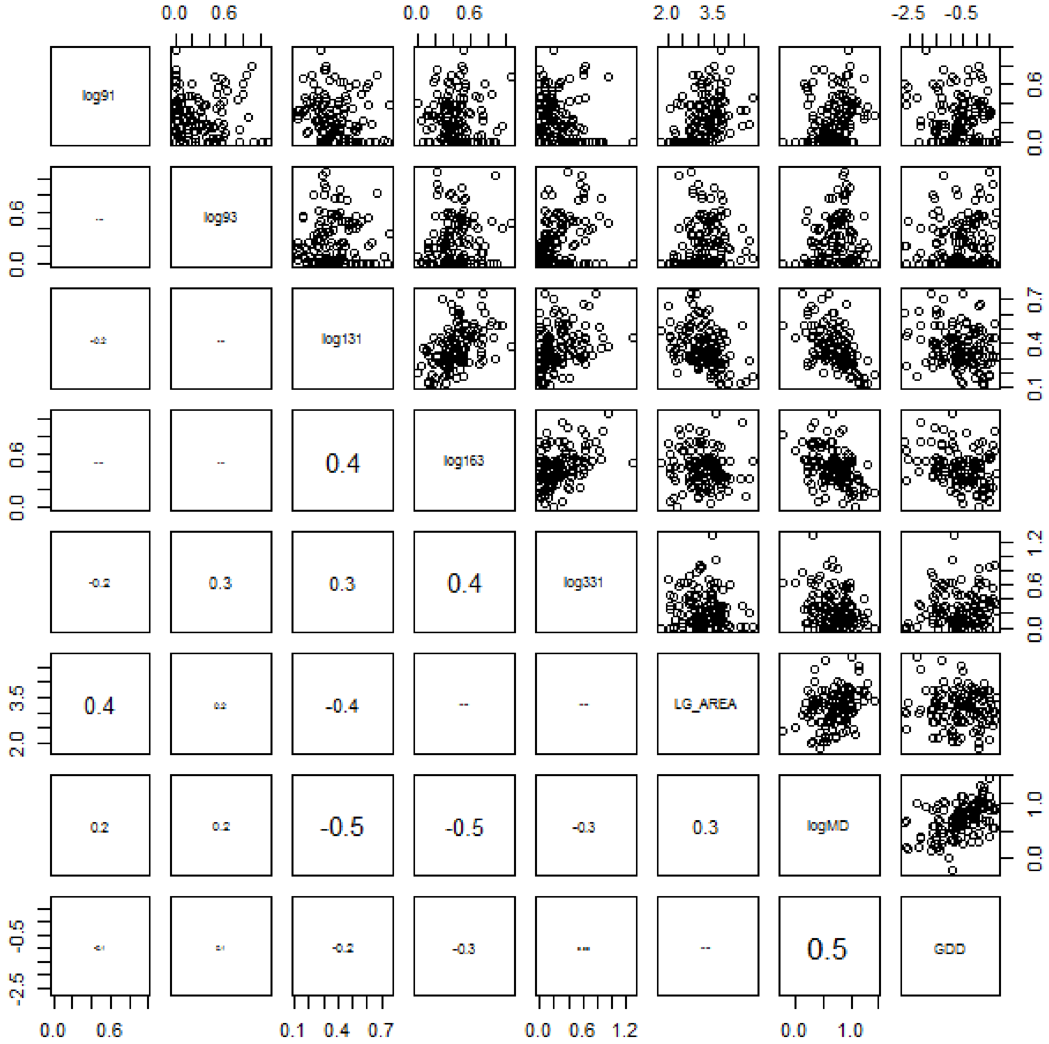

Figure A4. Multi-panel scatterplot of the fixed effects investigated in the BsM Northern Pike life history analyses. The top right panels display the relationships between paired variables, the lower left panels display Pearson correlation coefficients between paired variables. Variables that are more correlated are represented by larger correlation coefficients. The variable names that match the abbreviations in the figure can be found in Table 2.1.

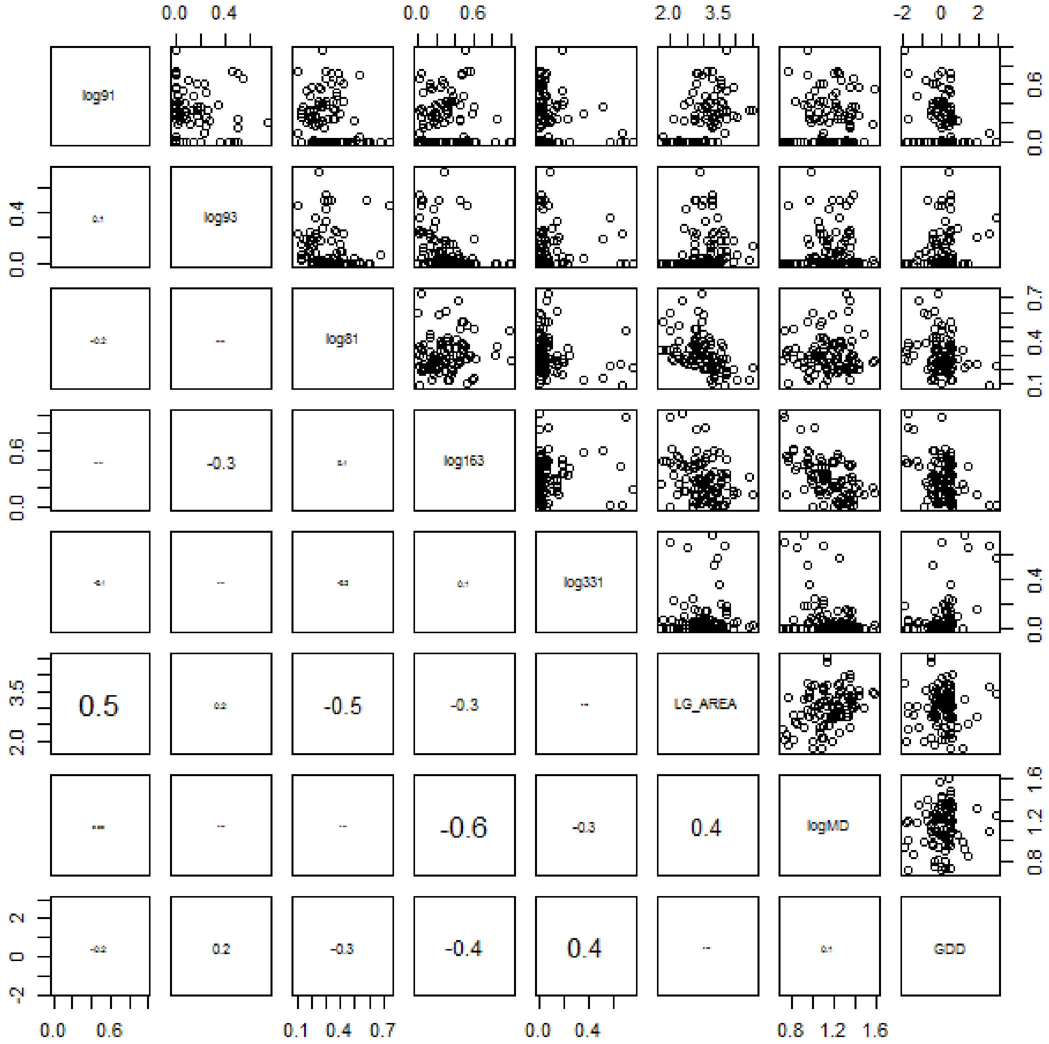

Figure A5. Multi-panel scatterplot of the fixed effects investigated in the BsM Lake Trout life history analyses. The top right panels display the relationships between paired variables, the lower left panels display Pearson correlation coefficients between paired variables. Variables that are more correlated are represented by larger correlation coefficients. The variable names that match the abbreviations in the figure can be found in Table 2.1.

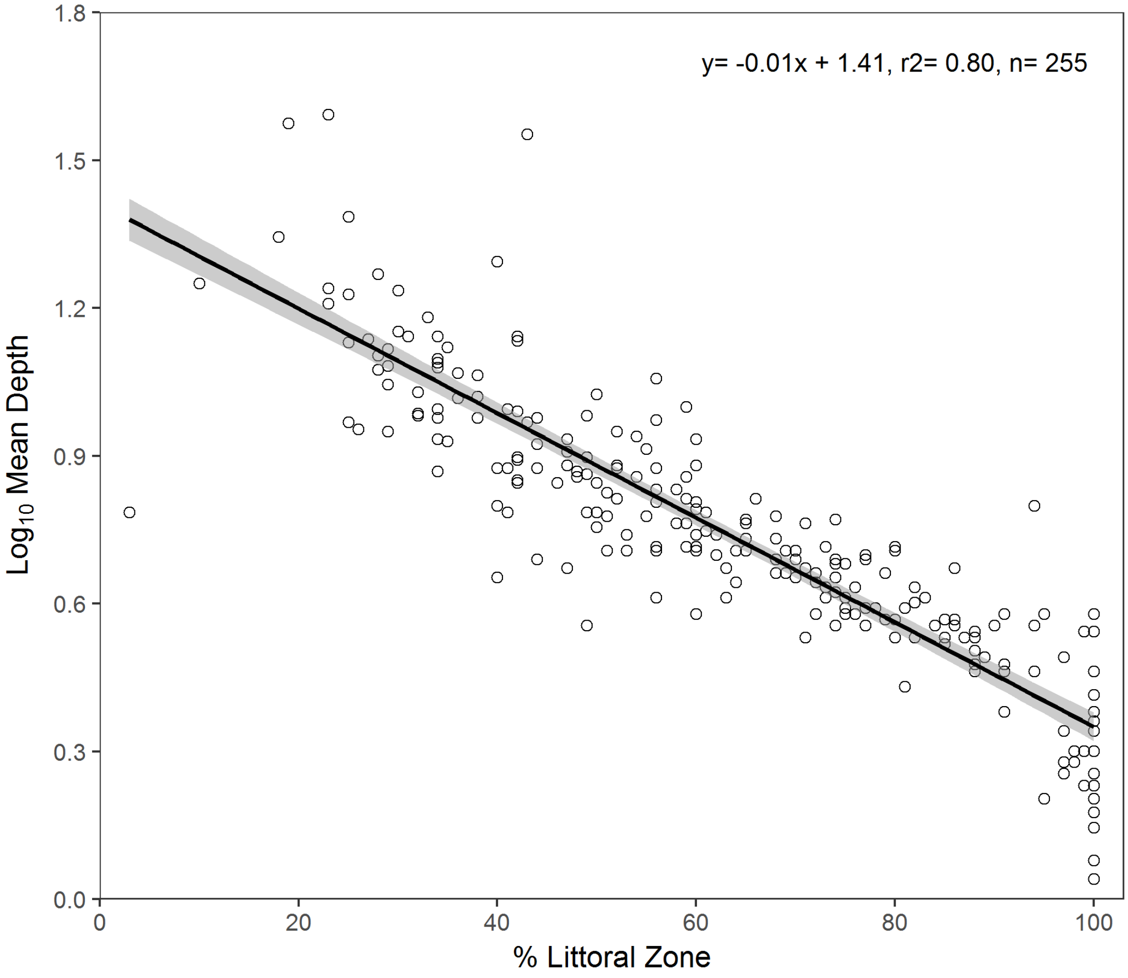

Figure A6. Relationship between mean depth and percentage of littoral habitat for a subset of lakes in the FWIN dataset (*n* = 255). The solid lines represent the relationship (Linear regression, y = -0.01x + 1.41, r^2 = 0.80) and the shaded area represents the 95% confidence intervals.

Appendix B. Chapter Three ageing and back-calculation methodology, validation.

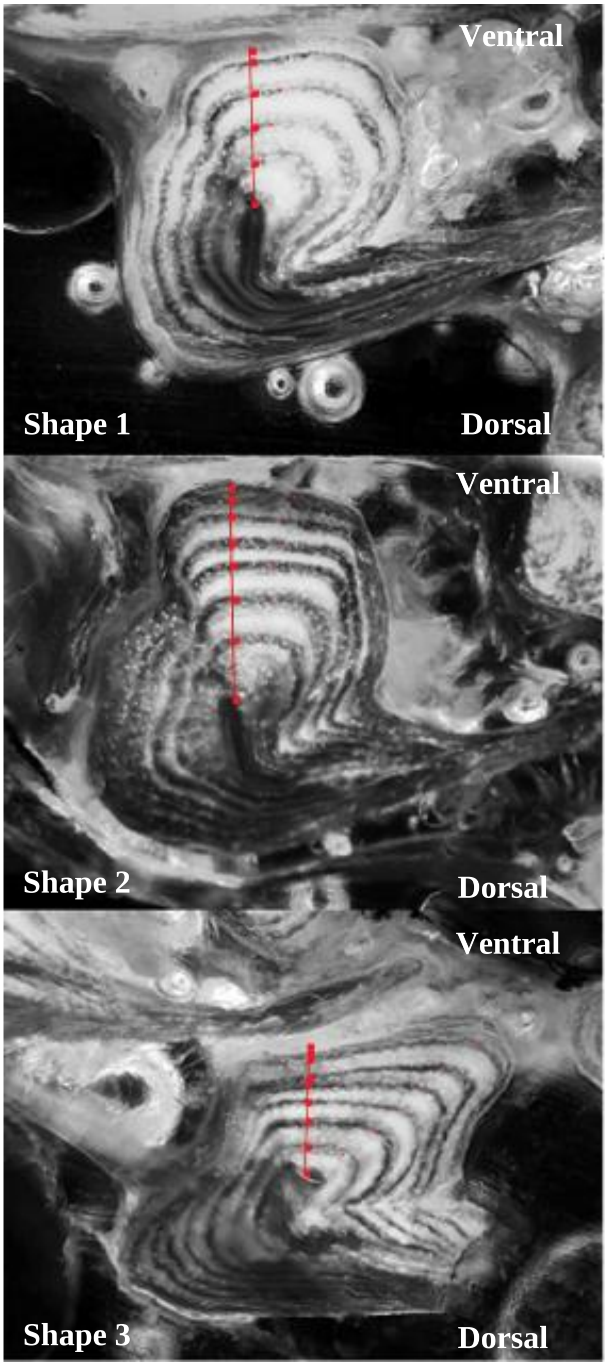

Figure B1. Digital images of the three distinct shapes of the Lake Trout pectoral fin ray cross-sections. The red dots represent marked annuli. The red lines represent the axes of measurement for the back-calculations on the anterior portion of the fin rays.

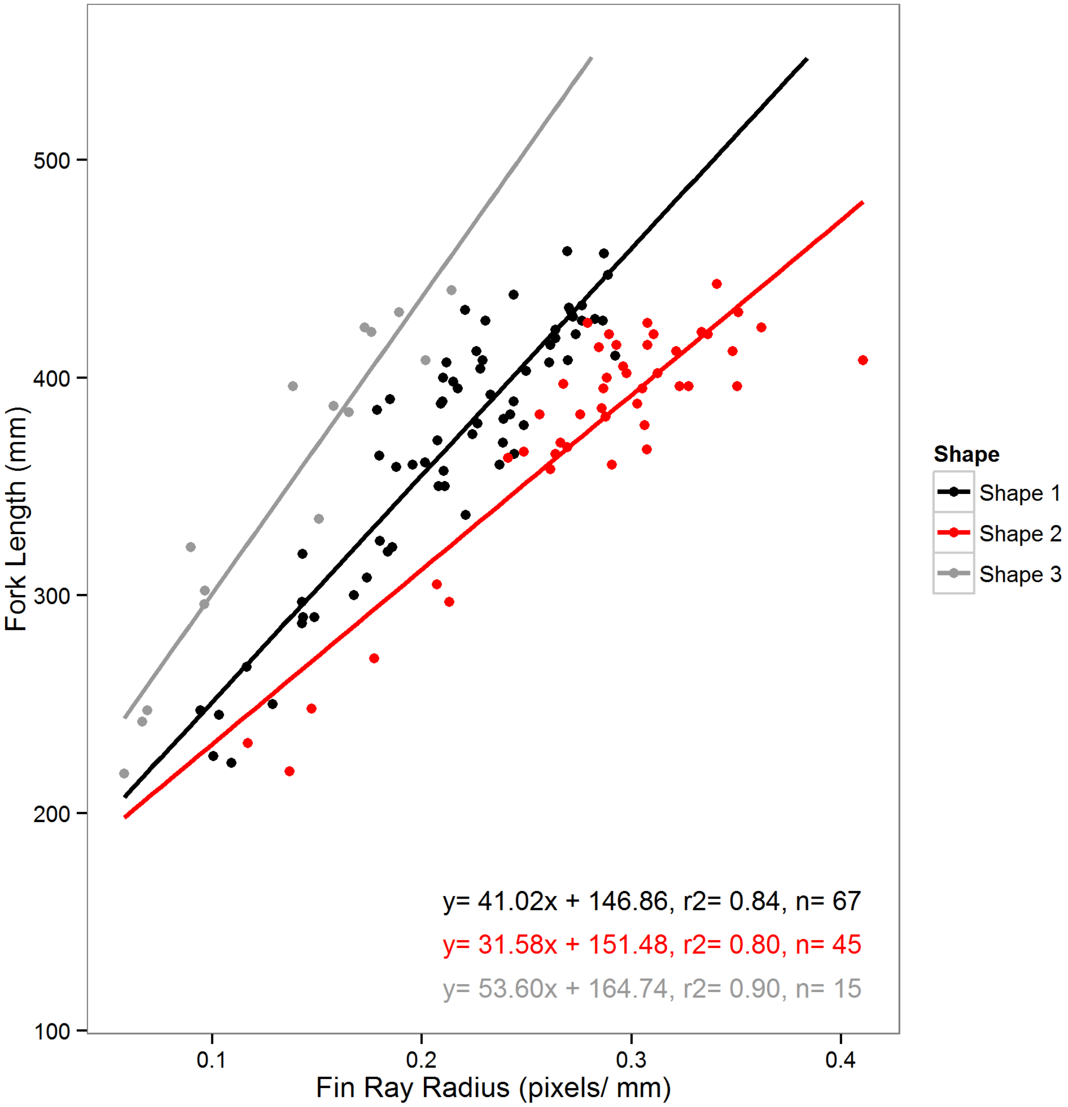

Figure B2. Linear relationship between fork length (mm) and fin ray radius (pixels·mm) for each shape of the pectoral fin ray cross-sections. Equations, r-squared values (r^2), and sample sizes (*n*) are displayed in the same colors as each fin ray shape.

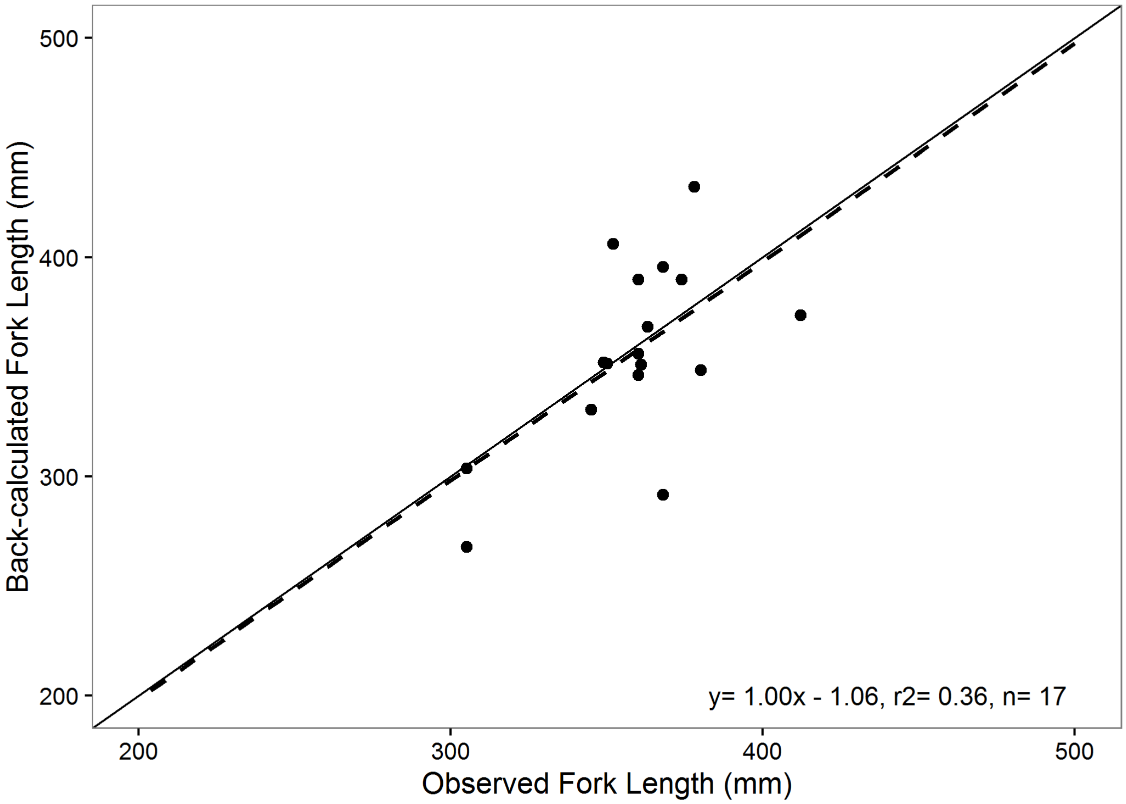

Figure B3. Relationship between the back-calculated fork lengths and the initial observed fork lengths of a subset of Lake 375 Lake Trout. The solid line represents a perfect relationship and the dashed line is the linear relationship between the measurements. The equation, r-squared value (r^2), and sample size (*n*) are displayed on the plot.

Appendix C. Chapter Three condition and length-at-age tables, shifts in Lake Trout size and age structure, and relationship between fork length and weight for Lake 375 Lake Trout.

Table C1. The average condition of juvenile (< 350 mm) and mature (350-600 mm) Lake Trout expressed as relative weight (W_r, %) in the years before (1999-2002), during (2003-2007), and after (2008-2013) the aquaculture operation ± one standard error from the mixed-effects model. Sample sizes for each group are in parentheses.

	Immature (< 350 mm)	Mature (350-600 mm)
Before	89.11 ± 2.45 % (23)	84.24 ± 1.92 % (183)
During	95.03 ± 1.73 % (63)	89.89 ± 1.47 % (439)
After	93.94 ± 1.85 % (48)	84.47 ± 1.45 % (651)

Table C2. Average back-calculated annual growth (mm·year^{-1}) of the Lake Trout in the years before, during, and after the aquaculture operation ± one standard error from the mixed-effects model. Sample sizes for each group are in parentheses. Superscripted letters indicate whether or not the means within each age class are significantly different among experiment periods. If the means in each age class contain the same letter they are not significantly different. Means in bold represent significant differences.

Age	1	2	3	4	5
Before	49.17 ± 1.94^{a} (56)	49.32 ± 2.19^{a} (44)	40.42 ± 2.61^{a} (31)	38.35 ± 3.43^{a} (18)	28.29 ± 5.50^{a} (7)
During	55.98 ± 2.33^{a} (39)	55.96 ± 2.10^{a} (48)	49.42 ± 2.00^{a} (53)	35.43 ± 2.00^{a} (53)	29.06 ± 2.19^{a} (44)
After	57.70 ± 2.19^{a} (44)	**73.48 ± 2.46^{b} (35)**	61.53 ± 5.94^{a} (6)	39.90 ± 4.39^{a} (11)	24.61 ± 2.85^{a} (26)

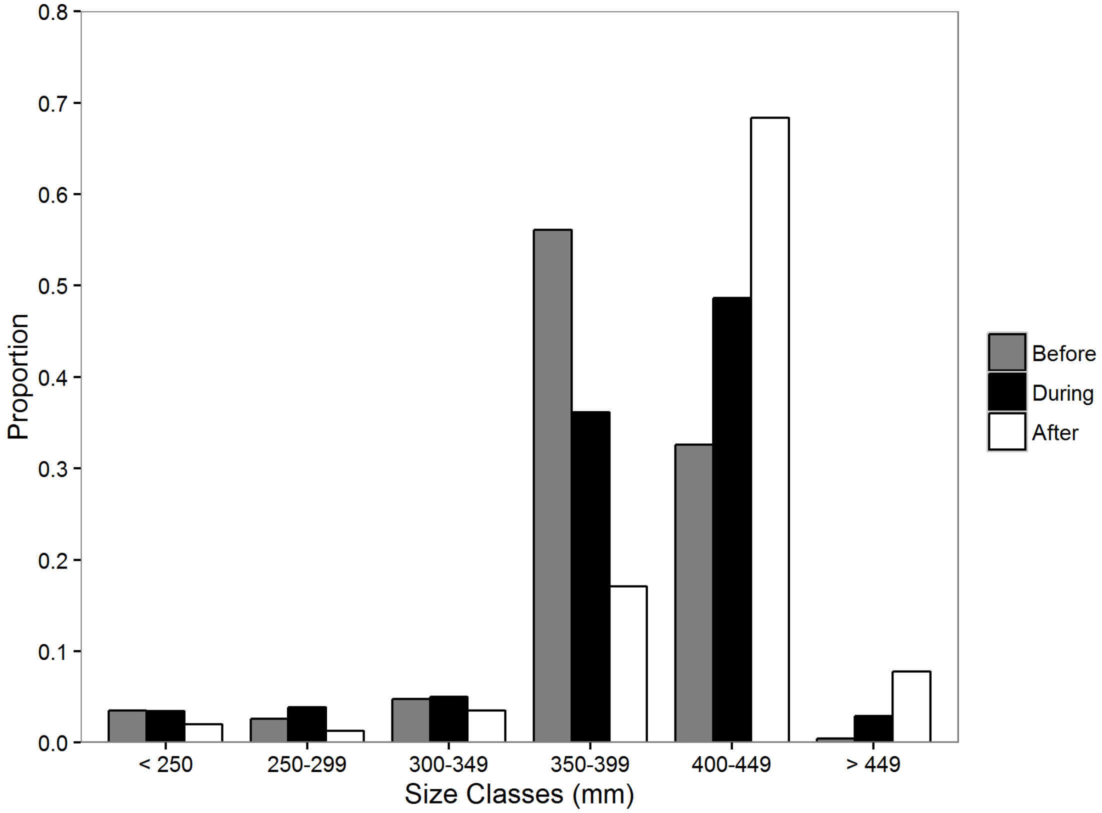

Figure C1. Proportion of captured Lake 375 Lake Trout in different size classes (mm) before (1999-2002), during (2003-2007), and after (2008-2013) the aquaculture experiment.

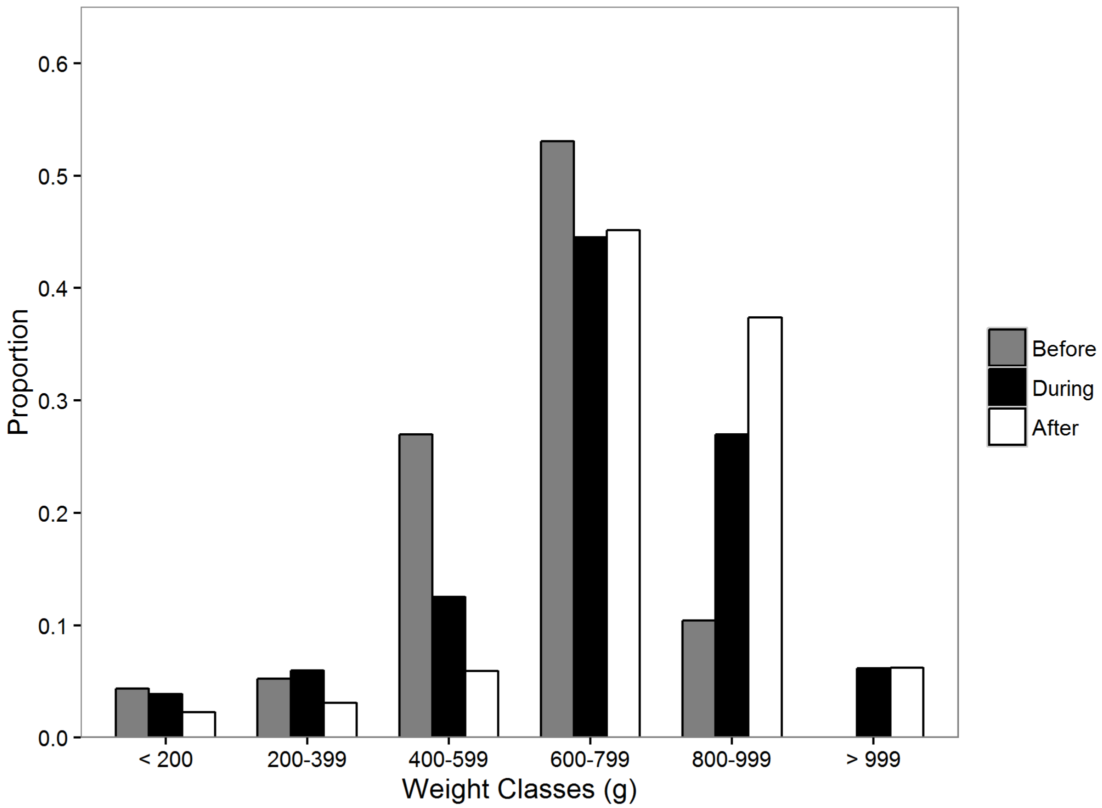

Figure C2. Proportion of captured Lake 375 Lake Trout in different weight classes (g) before (1999-2002), during (2003-2007), and after (2008-2013) the aquaculture experiment.

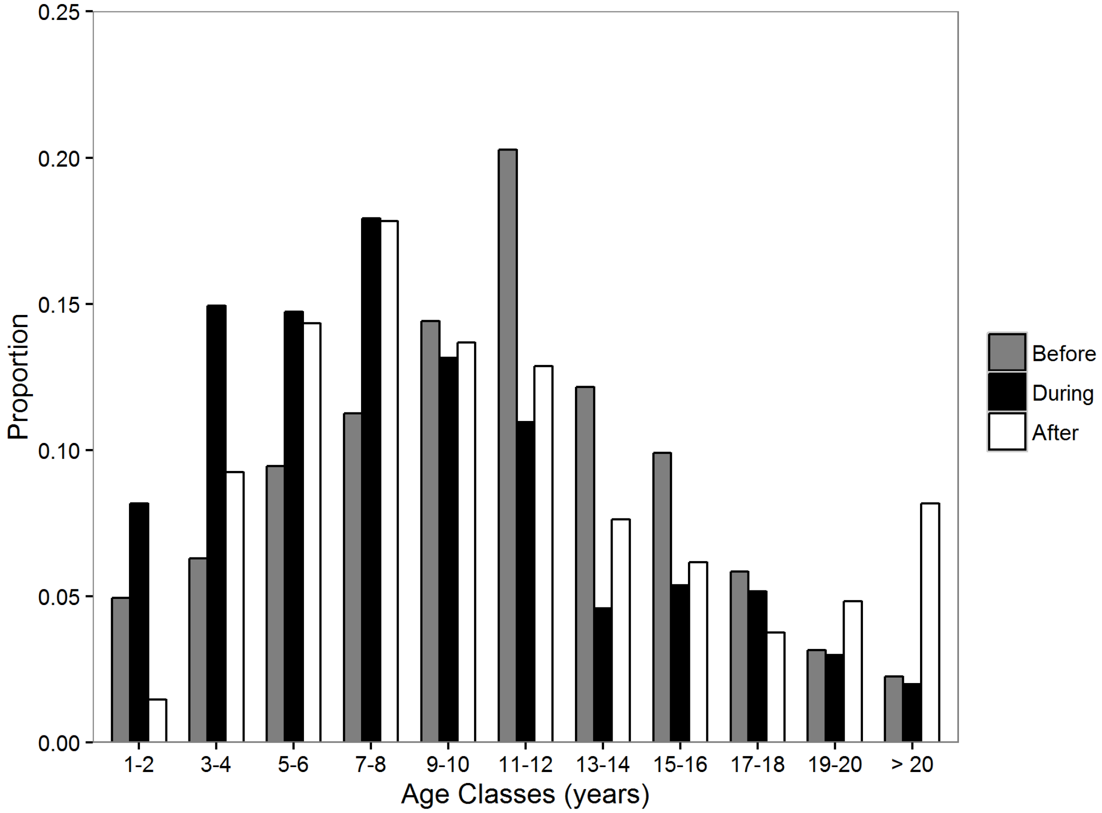

Figure C3. Proportion of captured Lake 375 Lake Trout in different age classes (years) before (1999-2002), during (2003-2007), and after (2008-2013) the aquaculture experiment.

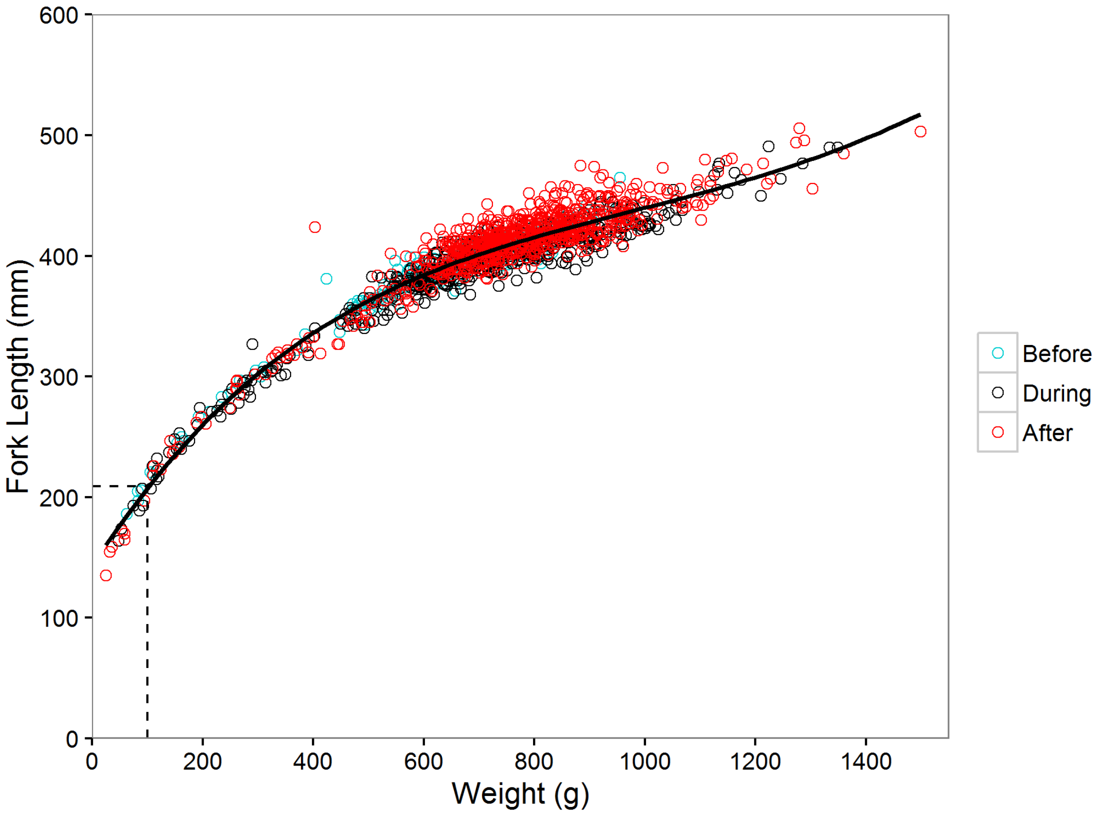

Figure C4. Relationship between Lake 375 Lake Trout fork length (mm) and weight (g). Different colored points represent the years before (1999-2002), during (2003-2007), and after (2008-2013) the aquaculture operation. The relationship was fit using a polynomial regression (r^2 = 0.91). Dashed lines represent the average fork length of Lake Trout at 100 g (~ 208 mm).