

**Invasive spiny water flea (*Bythotrephes cederstroëmi*) and their impacts
on young-of-year walleye (*Sander vitreus*) growth**

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Abstract

Invasive species are a major threat to aquatic ecosystems, costing an estimated \$3.6 billion in impacts across Ontario. In particular, the predatory cladoceran *Bythotrephes cederströmii* (*Bythotrephes* hereafter) has had significant trophic impacts on invaded ecosystems, such as decreasing zooplankton density and biomass. Changes to the zooplankton community can impact ecosystem energy rates and dominant pathways of transfer to other organisms in a “middle-out” trophic cascade, altering predator-prey dynamics for both algae and fish. Here, I used relevant zooplankton abundances characteristic of invaded and non-invaded lakes and a bioenergetics model to evaluate whether the *Bythotrephes*-induced changes to native zooplankton is expected to alter larval walleye consumption (and therefore rates of growth). I then used observational data to evaluate the impact *Bythotrephes* has on the zooplanktivorous young-of-year (YOY) walleye. I used a back-calculation model and linear mixed effect modeling to evaluate differences in YOY walleye growth between invaded and non-invaded waterbodies, as well as within invaded waterbodies pre- and post-invasion. In the first data chapter (chapter 2), a functional response and bioenergetics model revealed larval walleye grow slower in invaded mesotrophic lakes compared to non-invaded mesotrophic lakes, and models suggest they are unlikely to survive in invaded oligotrophic lakes based on available zooplankton. In the second data chapter (chapter 3), I found that relative to similar sized non-invaded lakes, YOY walleye grow slower in small, invaded lakes, whereas large lakes show less severe effects. Overall, *Bythotrephes* has differing impacts on YOY walleye growth depending on lake characteristics such as lake size and trophic state. As growth rates are ultimately linked to reproduction, recruitment, and production,

understanding growth rates post-invasion is essential for fisheries managers to develop and anticipate adaptive management strategies.

Lay Summary

This manuscript adds to the understanding of aquatic biology by filling in knowledge gaps regarding the aggressively invasive zooplankton, *Bythotrephes cederstroemii* (*Bythotrephes* hereafter), and its impacts to invaded ecosystems. As *Bythotrephes* consumes a large portion of zooplankton in invaded lakes, this leaves native zooplanktivores with limited prey availability. Here, I evaluate how this decreased prey availability may be impacting the growth of native fishes; in particular, the economically and culturally important juvenile walleye (*Sander vitreus*). Juvenile fish growth is important because it affects adult size, recruitment (number of fish surviving to another year), and age at reproduction. Through mathematical modelling, I first found that reduced zooplankton (prey) availability in *Bythotrephes* invaded lakes leads to decreased larval walleye growth. In lakes with low productivity and therefore lower prey availability, larval walleye were predicted to not survive in the presence of *Bythotrephes*. Through an observational approach, I found that juvenile walleye grew slower in *Bythotrephes* invaded lakes, and that this relationship is modified by the size of the waterbody such that growth is more severely impacted in smaller lakes. With a better understanding of how *Bythotrephes* is impacting juvenile walleye, natural resource managers can better understand the current or potential impacts to local aquatic ecosystems threatened by invasion and adjust management actions accordingly. Overall, this research reveals trends not seen elsewhere in the literature and provides novel insights as to how an invasive species that is spreading across the country, is impacting our native fishes.

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Table of Contents

Abstract	ii
Lay Summary.....	iv
Acknowledgments.....	v
Table of Contents.....	vi
List of Tables	vii
List of figures	viii
Chapter 1: General Introduction	1
1.1 Background.....	1
1.2 Objectives.....	8
1.3 Figures.....	10
Chapter 2: Decline of young-of-year walleye growth due to <i>Bythotrephes</i> impacts predicted from bioenergetic principles	11
2.1 Abstract.....	12
2.2 Introduction.....	13
2.3 Methods	16
2.4 Results	21
2.5 Discussion	23
2.6 Tables and Figures.....	29
Chapter 3: Impact of invasive spiny water flea on the growth of young of year walleye	34
3.1 Abstract.....	34
3.2 Introduction.....	35
3.3 Methods	41
3.4 Results	52
3.5 Discussion	56
3.6 Tables and Figures.....	62
Chapter 4: Synthesis.....	73
References	81
Appendix A.....	92
Appendix B.....	95
Appendix C.....	96

List of Tables

Table 2.1. Bioenergetic parameter estimates used in this study from Johnston 1999, and D90 parameters from McDonnell and Roth 2014.	29
Table 2.2. Zooplankton abundance treatments (\pm SE) based on various invaded and non-invaded lakes of Northern Ontario. Zooplankton data from Arnott 2021 (Unpublished raw data) were collected via vertical hauls from 2m above the bottom to the surface typically at the deepest part each lake using an 80 μ m mesh plankton sampler between May-August. Methods for collecting remaining zooplankton data can be found in Kerfoot et al. (2016).	30
Table 3.1 Physical characteristics of the study waterbodies (invaded by <i>Bythotrephes cederstroemii</i> and non-invaded) located in northwestern Ontario, Canada and Minnesota, USA and which waterbodies were included in the spatio-temporal (O), temporal (T), and the spatial model (S).	62
Table 3.2 Linear mixed effects model comparisons to evaluate the significance of fixed and random effects using maximum likelihood-ratio test.	63

List of figures

- Fig. 1.1.** A female *Bythotrephes cederströmii*, a predatory cladoceran invasive to North America, shown here with embryos in her brood pouch. Photo taken by Jake Walsh (Tribune News Services 2016)..... **10**
- Fig. 2.1.** Diet proportions and prey capture success (red line) as functions of body size for the first 40 days of feeding in larval walleye (*Sander vitreus*) assuming cyclopoid copepods (yellow), calanoid copepods (grey dotted), and *Daphnia* (blue) are the exclusive prey items. Data from Johnston and Mathias (1994a, 1994b)..... **31**
- Fig. 2.2.** Predicted final a) mass, b) energy content, and c) total length of young walleye after 31 days following start of feeding in four categories of lakes (treatments), based on bioenergetics modeling. For each treatment, results are presented for two initial body sizes. Treatments are: invaded with *Bythotrephes* and mesotrophic (IM), invaded and oligotrophic (IO), not invaded and mesotrophic (NM), and not invaded and oligotrophic (NO)..... **32**
- Fig. 2.3.** Lakes in Ontario ($n=524$), Canada populating walleye (*Sander vitreus*), divided by lake trophic state based on the total phosphorus of the trophic state index (Carlson 1977). Walleye presence data are from Ontario Ministry of Natural Resources and Forestry (2020), and TP data are from the Ontario Biodiversity Council (2021) collected by the Ontario Broad Scale Monitoring program..... **33**
- Fig. 3.1** A map of the waterbodies included in this study with *Bythotrephes cederströmii* invaded (red) and non-invaded (blue) waterbodies highlighted, as well as Quetico Provincial Park (green) and Boundary Waters Canoe Area (BWCA) (beige). The three basins of Rainy Lake are labelled (North Arm, Redgut Bay, and South Arm)..... **64**
- Fig. 3.2** Walleye (*Sander vitreus*) ageing structure axis examples for both a dorsal spine (top) and an otolith (bottom). The distance between the nucleus and 1st annulus (R_i) is the radius of the ageing structure at the end of the fish's first year of growth (Watkins and Spencer 2013). The distance between the nucleus and the edge of the ageing structure (R_c) is the radius of the structure at the time of capture. **65**
- Fig. 3.3** Linear relationship between fork length and otolith radius of walleye (*Sander vitreus*), used in the Biological Intercept model for back-calculations (see text)..... **66**
- Fig. 3.4** Allometric functions on a log-log scale of ageing structure radius at capture and walleye (*Sander vitreus*) fork length at capture, using either otoliths (A) or dorsal spines (B), used in the Monastrasky Body-Proportional Hypothesis model for back-calculations (see text)..... **67**

Fig. 3.5 Back-calculated young-of-year (YOY) walleye (*Sander vitreus*) fork length (mm) estimated through the Biological Intercept method (A), or the Monastrasky Body-Proportional Hypothesis method (B) compared using dorsal spines or otoliths as ageing structures from the same fish with an overlaid to a 1:1 line (dashed line) for reference..... **68**

Fig. 3.6 Spatio-temporal trends of young-of-year (YOY) walleye (*Sander vitreus*) fork length predicted through a linear mixed effects model from 23 waterbodies in northwestern Ontario and Minnesota. YOY walleye were present in waterbodies either invaded (dark red) or non-invaded (light blue) by *Bythotrephes cederströmii* (each connected line or floating point represents one waterbody). Lengths are scaled to a standardized growing degree day (GDD, base 5°C) of 1404. **69**

Fig. 3.7 Spatio-temporal trends of young-of-year (YOY) walleye (*Sander vitreus*) fork length predicted through a linear mixed effects model from 23 waterbodies in northwestern Ontario and Minnesota. YOY walleye were present in waterbodies either large (>2000ha) or small (<2000ha) waterbodies, invaded (dark red) or non-invaded (light blue) by *Bythotrephes cederströmii*. Lengths are scaled to a standardized growing degree day (GDD, base 5°C) of 1404. **70**

Fig. 3.8 Contemporary (2000-2018) spatial trends in back-calculated young-of-year (YOY) walleye (*Sander vitreus*) length predicted from a linear mixed effects model standardized to 1404 growing degree days (GDD, base 5°C) in 22 study waterbodies (pre-invasion observations removed) invaded (dark red) or non-invaded (light blue) by *Bythotrephes cederströmii*. **71**

Fig. 3.9 A comparison of predicted young-of-year (YOY) walleye (*Sander vitreus*) lengths scaled to a standardized 1404 growing degree day (GDD, base 5°C) in the South Arm of Rainy Lake, using back-calculation methods from adult fish and correcting them for annual climatic variation or measuring YOY walleye in the field and correcting them for annual climatic variation drawn from Hansen et al. (2020). A – difference (shaded area) in YOY length estimates between methods annually; and B – 1:1 relationship in YOY walleye length estimates between methods..... **72**

Chapter 1: General Introduction

1.1 Background

Invasive species represent a major threat to many aquatic ecosystems, which can alter the pathways for material and energy exchange in native food webs (Mello and Oliveira 2016; Blackburn et al. 2019). For example, zebra mussels (*Dreissena polymorpha*) directly and indirectly cause physical, chemical, and energetic changes via phytoplankton grazing, which ultimately impacts all other members of the food web (Higgins and Vander Zanden 2010). These trophic interactions are crucial in determining how biomass at the bottom of the food web translates into ecosystem production and are therefore highly susceptible to disruption by invasive species (Hecky et al. 2004; Lefébure et al. 2013). Although potentially detrimental to freshwater lakes that provide many ecosystem services, invasive species are poorly managed in Canada (Office of the Auditor General of Canada 2019). To assist governments in improving invasive species management, there is a critical need to better understand the current and potential future impacts that invasive species have on freshwater ecosystems.

One invasive species that has been implicated as disruptive to aquatic ecosystems is *Bythotrephes cederströmii* (*Bythotrephes* hereafter; Walsh et al. 2016). *Bythotrephes* are a large (10-15mm) predatory cladoceran native to the Palearctic region and are characterized by their long, barbed caudal spine (Fig.1.1). The likelihood of a *Bythotrephes* invasion increases with propagule pressure in areas of high development and recreational fishing (Gertzen et al. 2011). Like other cladocerans, *Bythotrephes* populations can grow rapidly as females reproduce asexually during summer and produce thick over-wintering diapausing eggs in the fall following sexual reproduction (Miehls et

al. 2014). Diapausing eggs are a strong predatory defense strategy and can also assist in dispersal by viably passing through fish digestive tracts, where harvested fish can then transport *Bythotrephes* eggs to new environments (Kerfoot et al. 2011). Other antipredator defense strategies of *Bythotrephes* include diel vertical migration (DVM; Ketelaars et al. 1995; Pangle et al. 2007) and the distinguishable long-barbed tail which acts as a major predatory defense strategy against gape-limited predators (Straile and Hälbich 2000). Due to high phenotypic plasticity, *Bythotrephes*' life history and phenotypic traits are highly variable between lakes and across seasons, making invasions difficult to predict (Straile and Hälbich 2000). As an example, *Bythotrephes* population attributes and life history traits differ between the Great Lakes such as Lake Huron, Lake Erie, and Lake Michigan due to differing predation pressure and prey availability (Pothoven et al. 2012).

Bythotrephes were introduced to the Great Lakes in the 1980s in ship ballast and have since had significant trophic impacts on several invaded ecosystems as they spread to inland lakes, primarily in mesotrophic and oligotrophic systems (Sprules et al. 1990; Sorensen and Branstrator 2017). As an aggressive general mesopredator, *Bythotrephes* are a dominant predator of herbivorous zooplankton, feeding on small and large-bodied zooplankton (Strecker et al. 2006). *Bythotrephes* have a DVM similar to their prey such as *Daphnia* and other cladocerans, making prey readily available at certain times of the day (Ketelaars et al. 1995; Pangle et al. 2007). In turn, some cladoceran species alter their DVM to avoid *Bythotrephes* by occupying the hypolimnion more often (Pangle et al. 2007). This has non-lethal implications on cladoceran life-history patterns such as lower birth rate and growth rate due to inhabiting deeper and colder water. *Bythotrephes* are

known to consume zooplankton at higher rates than they are produced, causing rapid decreases in zooplankton diversity and biomass following establishment (Yan et al. 2002; Barbiero and Tuchman 2004; Kerfoot et al. 2016). In addition, *Bythotrephes* are considered “messy” consumers, consuming only ~60% of their captured prey (Yurista et al. 2010). The remaining ~40% of zooplankton biomass is redirected into the microbial food chain, making it unavailable to higher trophic levels. In Lake Mendota, Wisconsin, *Daphnia* biomass was reduced by 60% following *Bythotrephes* invasion (Gillis and Walsh 2017). A similar effect was observed in Harp Lake, Ontario in which a rapid and long-lasting reduction in native cladoceran abundance and zooplankton species richness occurred post-*Bythotrephes* invasion (Yan et al. 2002). In addition, Barth et al. (2021) found that the zooplankton size spectrum was highly variable in systems invaded by *Bythotrephes*, causing perturbations in available prey for other zooplanktivores. Alterations to the zooplankton community such as these can impact energy flow to other organisms in a “middle-out” trophic cascade, altering predator-prey dynamics for both algae and fish (Hovius et al. 2007; Rennie et al. 2011).

Bythotrephes consume greater quantities of zooplankton than some competing zooplanktivores, including young of year (YOY) walleye (*Sander vitreus*), an economically and culturally significant sportfish (Bunnell et al. 2011). Walleye are the most popular recreational fish across Canada, contributing to the \$7.9 billion influx to provincial economies, yet knowledge on the impacts of the rapidly spreading *Bythotrephes* on walleye growth is limited (Department of Fisheries and Oceans Canada 2019). Although *Bythotrephes* are consumed by some larger zooplanktivores, YOY walleye are gape-limited to *Bythotrephes* during their first few months, making

Bythotrephes difficult to consume until walleye transition into a benthivorous or piscivorous diet at ~35mm or ~50mm in length, respectively (Mathias and Li 1982; Uphoff et al. 2019). As *Bythotrephes* invasions appear to limit zooplankton abundance and may be at least temporarily unavailable to YOY walleye as prey, one might expect a decrease in food consumption by YOY walleye in invaded lakes, leading to slower early growth rates. This may be the case in Minnesota lakes, where YOY walleye size (corrected for thermal growth accumulation) has been shown to be smaller in lakes with *Bythotrephes* than in lakes without *Bythotrephes*, possibly driven by differences in prey availability (Hansen et al. 2020). As the impacts that *Bythotrephes* has on invaded aquatic ecosystems are highly variable, a holistic approach such as identifying the magnitude and direction of the effect, as well as evaluating confounding variables that may be influencing growth, is needed to evaluate *Bythotrephes* impacts on the growth of fishes such as YOY walleye and to develop a theoretical framework for predicting future impacts.

Juvenile fish growth rates are ultimately linked to reproduction, recruitment, and overall ecosystem production (Madenjian et al. 1996; Pedersen et al. 2018). This may be the result of slower juvenile growth leading to smaller end of year lengths, which can delay age at maturation, and leave YOY walleye vulnerable to size-selective over-winter mortality, resulting in poor recruitment (May et al. 2020). The growth and survival of larval and juvenile fishes is strongly influenced by temporal and spatial variation in prey availability (Nunn et al. 2011). Therefore, with knowledge of native zooplankton biomass in invaded and non-invaded lakes, one can quantify the prey available to YOY walleye and therefore consumption and growth. When combined with functional response curves,

bioenergetics models can take advantage of prey availability data to evaluate the growth of fishes when considering a mass balance energy budget, where energy allocated to metabolism, waste, and growth (losses) can be assumed to equal energy input through consumption in an equilibrium state (Deslauriers et al. 2017). Bioenergetic modeling has been used in the past to evaluate the impacts of other invasive species on the growth of fishes (Bartsch et al. 2003; Kosmenko 2015), as well as growth and feeding habits of walleye specifically (McDonnell and Roth 2014; Madenjian et al. 2018).

Another approach to understanding how the early growth rates of fishes might be impacted by *Bythotrephes* is comparing back-calculated size-at-age from archived ageing structures (e.g., otoliths and dorsal spines) across ecosystems with and without *Bythotrephes* or within an invaded lake before and after *Bythotrephes* invasion, which can reveal changes in growth not otherwise directly observable (Lorenzen 2016). Therefore, the best way to help understand mechanisms influencing YOY walleye growth may be to first use bioenergetics modelling to try and predict how organisms should respond to *Bythotrephes* invasion based on changes to the zooplankton community, and then compare these results to observational growth trends through back-calculations. Understanding how YOY walleye growth rates responds to *Bythotrephes* invasion can help us understand changes in recruitment which can be used by fisheries managers to evaluate management options and make informed decisions to ensure sustainable fisheries.

Evaluating the impacts of invasive species is challenging regardless of the approach taken. Comparative approaches (e.g., making comparisons among invaded and non-invaded systems) often have high degrees of variability due to uncontrolled variables that

differ between and within systems that can mask the effect of the response variable of interest (i.e., invasion status). As an example, Nero and Sprules (1986) compared zooplankton communities in lakes with and without *Mysis relicta*. To account for variability between study systems, they selected lakes and made comparisons in a fashion that would best help control for effects such as size, water chemistry, productivity, and prey assemblages. Other studies attempting longitudinal/temporal analyses of trends rely on long-term data series (which are rare), but also may include confounding variables such as regional climate change and other disturbances (e.g., increasing human development). Potentially, the best method for assessment may be a combined approach, taking advantage of spatial and temporal datasets to look for consistencies in the direction and magnitude of effect between the two, and controlling for variables as covariates where possible.

Climate change is another disturbance that can have significant impacts on the growth of ectotherms by altering the amount of ambient thermal energy available for growth (Angilletta et al. 2004; Chezik et al. 2014). Fish growth and maturity are directly related to temperature and growing degree days (GDD) where annual growth rate increases with longer growing seasons (Neuheimer and Taggart 2007; Pedersen et al. 2018); GDD are simply defined as the cumulative degrees above a pre-defined temperature (T_o) over time, where T_o is specific to the species of interest (Chezik et al. 2014). In particular, GDD has been found to have a strong linear relationship with immature walleye growth and can therefore explain a great deal of variance ($r^2 \geq 0.92$) in length accumulated for this species (Venturelli et al. 2010). Due to climate change, the average global GDD has been increasing by 2.5 degree days per decade (Natural

Resources Canada 2020), implying that any trends presented from longitudinal analyses should also include climate as a potential covariate to account for changes in the thermal environment as they relate to early growth rates.

Arguably, the most direct method for assessing growth rate is to capture YOY fish and measure their length through their first year to calculate growth rate (change in length/year). However, this isn't always practical as it requires specific sampling (i.e., using small mesh nets), which are not in place in many parts of the world or may not occur frequently, lending few years of YOY growth data. Therefore, back-calculations might be the only way to evaluate YOY growth over time in regions where these sampling programs aren't in place or in waterbodies with only contemporary data. However, measured YOY in a given time may not necessarily reflect back-calculated YOY size from individuals that were collected as adults.

Here, I propose to evaluate the difference in larval walleye growth rate between invaded and non-invaded systems through functional response and bioenergetics modelling. Bioenergetics modelling may reveal the direction and magnitude of effect that *Bythotrephes* is expected to have on YOY walleye. I then propose to combine both spatial and temporal approaches to examine the impacts of *Bythotrephes* invasion on back-calculated fish growth rates while including potential confounding variables in my analysis and study design. Further, to compare the use of back-calculated size at age against other previously published metrics, walleye back-calculations will be compared to measured YOY walleye lengths in the same system (both adjusted for thermal growth accumulation).

1.2 Objectives

The objective of this thesis is to evaluate the impact of *Bythotrephes* invasions on the growth rates of YOY walleye, through three sub-objectives:

1. To integrate data on zooplankton biomass, equations relating the functional response of walleye to their prey, and a larval walleye bioenergetics model to estimate larval walleye growth rates during their first month of life in lakes invaded by *Bythotrephes* and compare them to those in non-invaded lakes.

H-1: Decreased zooplankton availability in *Bythotrephes* invaded lakes will result in lower larval walleye consumption and slower growth rates compared to consumption and growth in non-invaded lakes with higher zooplankton availability.

2. To compare YOY walleye growth rates over time within waterbodies before and after *Bythotrephes* invasion, as well as among waterbodies with and without *Bythotrephes* considering potential climate drivers (e.g., GDD) and other covariates (e.g., waterbody size) which could influence early walleye growth.

H-2: Controlling for environmental covariates, YOY walleye will have slower growth rates after *Bythotrephes* invasion and in *Bythotrephes* invaded waterbodies compared to non-invaded waterbodies due to decreased prey availability.

3. To compare back-calculated YOY walleye lengths with measured YOY lengths from Hansen et al. (2020) in Rainy Lake and understand if or how the two are related.

H-3: Back-calculated lengths will be similar to the measured lengths from Hansen et al. (2020) as both methods estimate YOY walleye lengths from the same waterbody and year classes.

1.3 Figures

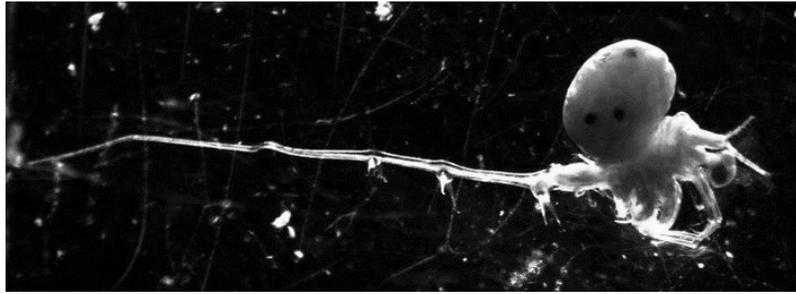


Fig. 1.1. A female *Bythotrephes cederstroemii*, a predatory cladoceran invasive to North America, shown here with embryos in her brood pouch. Photo taken by Jake Walsh (Tribune News Services 2016).

Chapter 2: Decline of young-of-year walleye growth due to *Bythotrephes* impacts predicted from bioenergetic principles

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Disclaimer

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2.1 Abstract

Invasive species are a major threat to ecosystem structure and function. For example, *Bythotrephes cederstroemii* (*Bythotrephes* hereafter) invasions have significantly reduced native zooplankton density and biomass, resulting in competitive interactions with zooplanktivorous fishes. Young of year (YOY) walleye (*Sander vitreus*) are initially zooplanktivorous and have recently been shown to display reduced rates of immature growth in *Bythotrephes* invaded lakes. Here, I combined a bioenergetics model for larval walleye with changes in the zooplankton community following *Bythotrephes* invasion to demonstrate that reduced larval walleye growth in the presence of *Bythotrephes*, are predicted solely by changes in the zooplankton prey community available for walleye, supporting field observations. The model predicted much greater impacts of *Bythotrephes* invasion on YOY walleye size in oligotrophic versus mesotrophic lakes, whereby *Bythotrephes* invasion could potentially lead to walleye recruitment failure in low-nutrient oligotrophic ecosystems. As YOY growth, survival, and recruitment are ultimately linked to adult abundance and sustainability of managed stocks, our results highlight the potential impacts of *Bythotrephes* on the sustainability of walleye populations in boreal lakes, which are critical components of local economies and of major cultural importance regionally.

Key words: Invasive species; Larvae; Percidae; Prey density; Year-class strength; Zooplankton

2.2 Introduction

The growth and survival of early life stages of fishes, especially during the first month of life, are major limiting factors to fish recruitment and may determine year-class strength (Venturelli et al. 2010; Grote et al. 2018; May et al. 2020). Mortality is often greatest in early life stages of fish, where factors such as predation, temperature, and prey availability are important predictors of larval fish survival (Hoxmeier et al. 2006). Prey availability is considered to be one of the most critical factors in larval fish survival, as inadequate food supply may lead to slower growth rates and/or decreased swimming speed, thus increasing the risk of predation (Jonas and Wahl 1998). For predatory fish like walleye (*Sander vitreus*) which are initially planktivorous, faster growing larvae will reach larger sizes sooner, making ontogenetic diet shifts to benthivory and piscivory earlier. These more rapidly growing individuals, making earlier transitions in diet show selective advantages via increased survival in their first year versus their slower-growing counterparts (Bergenius et al. 2018; May et al. 2020). However, lifetime growth and mortality are classically known to trade off against one another (Charnov 2004), such that faster growing individuals may show reduced survival due to increased exposure to predators (Biro et al. 2006). Regardless, larval walleye growth rates (and therefore mortality through to their first year of life) ultimately influence future recruitment of fish populations, and therefore the sustainability of fisheries (Anderson 1988; Post and Evans 1989; Grote et al. 2018). Understanding how prey availability affects larval growth (and mortality) is therefore critical for identifying recruitment bottlenecks at a particular life stage and represents a critical consideration for informed fisheries management decisions.

Invasive species, particularly *Bythotrephes cederstroemii* (hereafter *Bythotrephes*), have been shown to have significant impacts on the zooplankton communities of lakes they have invaded. *Bythotrephes* are a large, predatory cladoceran, and are known to consume zooplankton at higher rates than they are produced, causing rapid decreases in zooplankton diversity and biomass following establishment (Yan et al. 2002; Barbiero and Tuchman 2004; Kerfoot et al. 2016). In some lakes invaded by *Bythotrephes*, microcrustacean biomass (particularly cladocerans and cyclopoid copepods) was reduced by 40-60%, resulting in decreased prey availability for other zooplanktivores (Yan et al. 2002; Kerfoot et al. 2016; Gillis and Walsh 2017). Further, *Bythotrephes* consume more zooplankton than other zooplanktivores, including larval stages of fishes of economical and cultural significance, such as walleye (Bunnell et al. 2011). Reductions in zooplankton prey availability due to *Bythotrephes* invasion might therefore lead to reductions in the growth, survival, and recruitment rates of other zooplanktivores, including fishes.

Walleye are an important freshwater sportfish, representing 26% of all recreational fishing caught in Canada, and contributing \$7.9 billion to local economies (Department of Fisheries and Oceans Canada 2019). For iteroparous species of fishes and other vertebrates, higher rates of larval recruitment success will likely lead to more sustainable populations (Shelton and Mangel 2011). However, the response of young-of-year (YOY) walleye survival in relation to invasive species impacts on planktivore communities is largely unknown. *Bythotrephes* is not likely a prey item for YOY walleye during their zooplanktivorous phase as YOY fishes tend to adopt an aversion behaviour to *Bythotrephes* due to the difficulty of ingesting their long spine (Barnhisel 1991a,

1991b; Compton and Kerfoot 2004). As zooplanktivores, larval walleye diet typically consists of calanoid copepods, cyclopoid copepods, and *Daphnia* spp. (Graham and Sprules 1992). In Minnesota lakes, YOY walleye size (corrected for thermal growth accumulation) was reported as smaller in *Bythotrephes* invaded lakes compared to non-invaded lakes (Hansen et al. 2020). As *Bythotrephes* invasions appear to reduce zooplankton abundance, potentially limiting prey availability to zooplanktivores, one might predict a decrease in larval fish (i.e., walleye) prey consumption, leading to slower growth, but this potential link between reduced growth and zooplankton prey abundance has only been speculated (Hansen et al. 2020) and not demonstrated experimentally or theoretically.

Bioenergetics models can be used to describe the energy budget of fishes, where energetic costs for metabolism, waste loss, and growth can be balanced against the energy consumed (Deslauriers et al. 2017). In this study, I used a bioenergetics model to evaluate whether changes in the zooplankton community expected due to *Bythotrephes* invasions could alter consumption and growth of YOY walleye, in a magnitude similar to that observed elsewhere in invaded lakes (Hansen et al. 2020). The objective of this study was to integrate models describing (1) the changes observed in zooplankton communities resulting from *Bythotrephes* invasion and establishment (Dumitru et al. 2001; Yan et al. 2002; Boudreau and Yan 2003; Pangle et al. 2007), (2) a functional response model linking larval zooplanktivorous walleye consumption with zooplankton community composition and abundance (McDonnell and Roth 2014), and (3) a larval walleye bioenergetics model (McDonnell and Roth 2014), to compare predicted larval walleye growth rates in lakes invaded with *Bythotrephes* compared with non-invaded lakes after

their first month of life. In order to account for potential differences in productivity of lakes subjected to invasion, which is known to also affect the species richness and functional diversity of zooplankton (Barnett and Beisner 2007), I compared these predicted impacts in both mesotrophic and oligotrophic lakes.

2.3 Methods

2.3.1 Zooplankton abundance

To assess how larval walleye growth rate might change due to the impacts of *Bythotrephes* invasion on zooplankton community structure, I first determined zooplankton densities and basic water chemistry parameters from lakes, both invaded and non-invaded by *Bythotrephes*, across Northern Ontario and Northern Minnesota (Kerfoot et al. 2016; Arnott 2021 [Unpublished raw data]). These lakes were separated by invasion status and nutrient status/trophic state (categorized as either oligotrophic, 5-12 µg/L total phosphorus [TP], or mesotrophic 12-24 µg/L TP), based on the Trophic State Index (TSI) of Carlson (1977). For the purpose of this study, we assumed larval walleye consume exclusively preferred zooplankton, classified broadly as *Daphnia spp.*, calanoid and cyclopoid copepods (Houde 1967). Zooplankton densities from mesotrophic lakes were estimated from four *Bythotrephes* invaded study lakes described in Kerfoot et al. (2016) to attain four pre-invasion estimates (non-invaded) as well as four post-invasion estimates (invaded). Oligotrophic lake zooplankton densities were estimated from 132 non-invaded and 38 invaded lakes in Ontario (Arnott 2021 [Unpublished raw data]). To determine if zooplankton densities were different among invaded and non-invaded lakes, Kerfoot et al. (2016) conducted a one-way analysis of variance (ANOVA) to contrast zooplankton densities from invaded and non-invaded mesotrophic lakes on log-transformed data.

Similarly, I also compared zooplankton densities for oligotrophic lakes, although using a two-way ANOVA to detect differences in zooplankton density in relation to *Bythotrephes* invasion and among zooplankton taxa (classified broadly as *Daphnia spp.*, calanoid and cyclopoid copepods).

I therefore simulated larval walleye growth under four different conditions: non-invaded mesotrophic lakes (NM), non-invaded oligotrophic lakes (NO), invaded mesotrophic lakes (IM), and invaded oligotrophic lakes (IO). The comparison of outcomes for walleye between mesotrophic and oligotrophic lakes was conducted to represent the range of habitats suitable for both walleye and *Bythotrephes* occupancy (Johnson et al. 1977; Sorensen and Branstrator 2017), and to compare walleye growth rate responses to *Bythotrephes* invasion in productive (mesotrophic) versus less productive (oligotrophic) lakes. Zooplankton biomass ($\mu\text{g/L}$) was estimated from densities (individuals/L) using taxa-specific length-mass regressions and zooplankton length/mass averages reported elsewhere (McDonnell and Roth 2014).

2.3.2 Bioenergetics model

I used a bioenergetics model to determine larval growth rates over the first 31 days of life, comparing results from representative zooplankton community composition in *Bythotrephes* invaded lakes and non-invaded lakes. I chose a 31-day model to simulate the first month of food consumption, the period over which walleye are typically zooplanktivorous (Graham and Sprules 1992). At first feeding, walleye typically weigh between 0.0040 to 0.0055g (Mathias and Li 1982; Malison and Held 1996), so each treatment was run at both these weights as the initial masses for a walleye larva to capture a range of initial larvae sizes. Growth (G) was then determined through a daily energy

budget equation (Deslauriers et al. 2017) using bioenergetic parameters from Johnston 1999 (Table 2.1):

$$G_t = C_{r,t} - R_t - F_t - U_t - SDA_t \quad (\text{eq. 2.1})$$

Where growth (G ; $\text{J}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$) is the difference between realized consumption ($C_{r,t}$, $\text{J}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$) and energy losses (the sum of R_t , F_t , U_t and SDA_t). Losses are characterized as respiration (R_t , $\text{J}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$), egestion (F_t , $\text{J}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$), excretion (U_t , $\text{J}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$) and specific dynamic action (S_t , $\text{J}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$). Each of these metabolic parameters can be further broken down into functions (equations 2.4-2.15) dependent on mass (g), prey density ($\mu\text{g}/\text{L}$ wet mass), and temperature ($^{\circ}\text{C}$). I simulated daily temperature (T) using a water temperature curve from Lake Simcoe, ON based on the Julian day (J) using equation (2.2) to represent a typical larval walleye environment in temperate lakes during the first month of their life (Trudel et al. 2000).

$$T = 4.0 + 18.5 \cdot e^{-(J-207)^2/70^2} \quad (\text{eq. 2.2})$$

The resulting growth (G_t ; $\text{J}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$) was then applied to the initial mass (M_t) and energy density of a larval walleye (E_{pred} ; $3349 \text{ J}\cdot\text{g}^{-1}$; Madon and Culver 1993) using equation (2.3) and input as the mass for the proceeding time-step (M_{t+1}) for the duration of the simulation, as:

$$M_{t+1} = M_t + \frac{G_t \cdot M_t}{E_{pred}} \quad (\text{eq. 2.3})$$

The above model was run for the four treatments of prey availability described previously. If at any time step the mass dropped to 0g, the larva was considered deceased.

Growth and consumption between treatments were compared to determine how changes in prey availability due to *Bythotrephes* invasion impact larval walleye growth rates.

2.3.3 Consumption

Species-specific realized consumption, or the energy input contributed to the specific consumption rate ($C_{j,t}$; $\text{g} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$) of each prey item (j) was based on a multi-species type II functional response model for larval walleye (McDonnell and Roth 2014):

$$C_{j,t} = \frac{C_{max,t} * \left(\frac{9P_{j,t}}{D90_{j,L}}\right)}{1 + \sum_{j=1}^n \left(\frac{9P_{j,t}}{D90_{j,L}}\right)} \quad (\text{eq. 2.4})$$

where $P_{j,t}$ is the environmental prey density ($\mu\text{g} \cdot \text{L}^{-1}$ wet mass) for prey type j at time t , and $D90_{j,L}$ is the prey density at which 90% of the maximum consumption rate (C_{max}) can be achieved for a walleye at length L (in mm). C_{max} (g of prey $\cdot \text{g}$ of fish $^{-1} \cdot \text{day}^{-1}$) is a function of consumer mass, M (g), with parameter estimates of the intercept (CA) and slope (CB) generated from an allometric and temperature dependent function (Table 2.1). Lastly, $P_{j,t}$ is multiplied by 9 so that $D90_{j,L}$ reflects the prey density in which consumption is 90% of C_{max} . I assumed that larval walleye consumed exclusively their preferred prey of calanoid copepods, cyclopoid copepods, and *Daphnia spp.*, whose proportions changed based on larval walleye length (L_t) due to gape limitation (Fig. 1; Houde 1967; Graham and Sprules 1992). I calculated $D90_{j,L}$ using equations below and parameters (Table 2.1) reported by McDonnell and Roth 2014:

$$D90_{cyclopoid,L} = \frac{cy_1 \cdot e^{-cy_2 \cdot L_t}}{1 - \left(\frac{cy_1}{1.367} \cdot 10^5\right) + \left(\frac{cy_1}{1.367} \cdot 10^5\right) \cdot e^{-cy_2 \cdot L_t}} \quad (\text{eq. 2.5})$$

$$D90_{calanoid,L} = \left\{ ca_1 \left[ca_2 \left(\frac{L_t - 16}{|L_t - 16|} \right) \right] \right\} \cdot (L_t - 16)^2 + 6.757 \quad (\text{eq. 2.6})$$

$$D90_{daphnia,L} = da_1 \cdot e^{\left[-\frac{(L_t-16)^2}{da_2}\right]} + 2.788 \quad (\text{eq. 2.7})$$

Due to gape limitation, larval walleye may not be capable of consuming larger zooplankton until they reach a certain size (Johnston and Mathias 1994a). To account for poor capture success at small body sizes, I used a walleye capture success (K_t) function using constants a_v (338.45) and b_v (-0.16) derived from laboratory studies on larval walleye length and zooplankton capture success (Johnston and Mathias 1994a):

$$K_t = \frac{100 - [a_v \cdot e^{(b_v \cdot L_t)}]}{100} \quad (\text{eq. 2.8})$$

Total realized consumption ($C_{r,t}$, $\text{J} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$) for inclusion in equation 2.1 was then calculated by summing the specific consumption rates of each prey item ($C_{j,t}$) at each time step using equation 2.9, where $E_{prey,j}$ is the energy density of the respective prey item ($E_{copepods} = 2100 \text{ J} \cdot \text{g}^{-1}$, $E_{Daphnia} = 2600 \text{ J} \cdot \text{g}^{-1}$, McDonnell and Roth 2014):

$$C_{r,t} = \sum_{j=1}^n (C_{j,t} * K_t * E_{prey,j}) \quad (\text{eq. 2.9})$$

2.3.4 Metabolic costs

To account for costs associated with metabolism from equation 2.1, I used a model 2 respiration function which is a mass and temperature-dependent model with an activity multiplier from Deslauriers et al. (2017):

$$R_t = RA \cdot M_t^{RB} \cdot F(T) \cdot ACT \quad (\text{eq. 2.10})$$

$$F(T) = V^X \cdot e^{(X \cdot (1-V))} \quad (\text{eq. 2.11})$$

where,

$$V = (RTM - T)/(RTM - RTO) \quad (\text{eq. 2.12})$$

$$X = (Z^2 \cdot (1 + (1 + \frac{40}{Y})^{0.5})^2) / 400 \quad (\text{eq. 2.13})$$

$$Z = \ln(RQ) \cdot (RTM - RTO) \quad (\text{eq. 2.14})$$

$$Y = \ln(RQ) \cdot (RTM - RTO + 2) \quad (\text{eq. 2.15})$$

where RA is the intercept for maximum standard respiration ($\text{g O}_2 \cdot \text{g}^{-1} \cdot \text{day}^{-1}$), RB is the slope for maximum standard respiration, RQ is the slope for temperature dependent respiration, and RTM and RTO are the maximum and optimal temperatures ($^{\circ}\text{C}$) for standard respiration. We included an activity multiplier (ACT) to account for energy lost to active metabolism which was set to a constant value of 1 (unitless) to remain consistent with other larval walleye bioenergetic models in the literature (Kitchell et al. 1977; Johnston 1999). Egestion (F), excretion (U), and assimilated energy (S) costs from equation 2.1 in this study are based on model 4 from Deslauriers et al. (2017) which are functions of consumption rates and temperature.

2.4 Results

2.4.1 Zooplankton

Zooplankton biomass ($\mu\text{g/L}$) for all three taxa in invaded oligotrophic lakes was significantly lower (33.3% on average) compared to non-invaded oligotrophic lakes (Two-factor ANOVA: $F_{1,500}=6.54$, $p < 0.05$). The interaction term of this ANOVA was not significant (ANOVA: $F_{2,500}= 1.72$, $p > 0.10$), revealing that *Bythotrephes* invasion resulted in the same effect among each of the three zooplankton taxa. In mesotrophic lakes, Kerfoot et al. (2016) found the biomass of *Daphnia*, calanoids, and cyclopoids to be 51.8% lower post-*Bythotrephes* invasion, with significant decreases in only some species (i.e., *Daphnia* spp., *Senecella calanoides*, *Diacyclops bicuspidatus*, and

Mesocyclops edax) and a significant increase in one species (*Tropocyclops prasinus*). Overall, zooplankton biomass was lower in invaded lakes compared to non-invaded lakes under both mesotrophic and oligotrophic conditions. Biomass of *Daphnia*, calanoids, and cyclopoids were then averaged within treatments (combination of *Bythotrephes* presence and lake trophic status) across 178 lakes in Northern Ontario and Minnesota (Table 2.2).

Larval growth under non-invaded conditions was predicted to be greater in both mesotrophic and oligotrophic lakes compared to both invaded treatments, with the mesotrophic lakes providing the fastest larval growth (0.012g/day or 0.95mm/day). Larval growth rates under the invaded-mesotrophic treatment were similar to the growth rates of the non-invaded oligotrophic treatment (Fig. 2.2).

Larval walleye successfully grew in all treatments except the invaded oligotrophic treatment (Fig. 2.2), where after 31 days larval walleye either did not survive (initial mass 0.0040g or length 9.31mm) or managed to shrink to 0.0048g or 9.89mm (initial mass 0.0055g or length 10.31mm). The model allowed a diet shift in zooplankton type depending on length in which larvae consumed cyclopoids until they reached 11mm, then a mix of calanoid and cyclopoids until 16mm where *Daphnia* began to be the dominant prey item (Graham and Sprules 1992; McDonnell and Roth 2014). In the invaded oligotrophic (both initial masses), larval walleye never grew large enough (≥ 11 mm) to shift diet. Overall, with *Bythotrephes* present, the final walleye larvae length was on average 9.68% and 118.0% shorter than non-invaded mesotrophic and oligotrophic systems, respectively.

2.5 Discussion

Using a simple bioenergetic and functional response modeling framework, I predicted lower growth rates of larval walleye based on changes in prey (zooplankton) abundance associated with *Bythotrephes* invasions. In mesotrophic lakes, our models predicted an average 9.68% shorter body length at the end of the first month compared to non-invaded mesotrophic lakes. These findings match closely with a recent field study that reported age-0 walleye were 12.8% smaller in length at the end of their first summer in lakes invaded by *Bythotrephes* compared to non-invaded systems, however they did not account for the potentially confounding effect of lake trophic state (Hansen et al. 2020). Importantly, in oligotrophic lakes, our models only predicted walleye growth under certain circumstances, suggesting that walleye in lakes below a certain trophic status might be more vulnerable to recruitment failure following *Bythotrephes* establishment. Our modelling exercise shows that these differences in YOY walleye growth patterns between lakes with and without *Bythotrephes* result directly from the distribution of total zooplankton biomass in lakes where *Bythotrephes* are established (Table 2.2). This supports speculation in the literature that *Bythotrephes*-related changes in zooplankton abundance and community composition are responsible for YOY walleye growth; both May et al. (2020) and Hansen et al. (2020) observed reduced larval walleye growth rate and concluded these reductions were due to reduced zooplankton abundances over their study period. Our findings provide evidence that that food limitation due to zooplankton community changes resulting from the predatory impacts of *Bythotrephes* is a likely mechanism for these YOY walleye growth declines observed elsewhere.

Walleye typically grow to ~30mm within their first month (Graham and Sprules 1992), and this occurred in all bioenergetic simulations except in oligotrophic lakes invaded with *Bythotrephes*, where consumption based on low prey availability was not sufficient to sustain metabolic costs (Fig. 2.2c). Larval walleye death in oligotrophic treatments was likely due to an insufficient availability of cyclopoids early in life, resulting in insufficient growth to reach the length-dependent diet shifts to calanoids at 11mm or the more energy dense *Daphnia* at 16mm (Fig. 2.1; McDonnell and Roth 2014). Because gape is dependent on fish length, decreased growth due to low prey availability delays the timing of diet shifts of larval walleye to larger, more energy dense prey. Decreased growth during the first month of life also implies that ontogenetic diet-shifts to benthic invertebrates, and ultimately, piscivory later in their first year of growth, may also be delayed (Uphoff et al. 2019). Delayed diet shifts are likely energetically detrimental, as larval walleye are confined to consuming less energy-dense prey items (zooplankton) for a longer period. Future studies that continue building on this bioenergetics approach could extend the modelling period to also incorporate length-dependent diet shifts to benthic invertebrates and piscivory, which may ultimately demonstrate how *Bythotrephes* invasions impact the timing of diet-shifts and the total growth of not just larval walleye, but ultimately growth and development into both YOY and juvenile stages.

Our results have significant implications for walleye recruitment and population growth rates in *Bythotrephes*-invaded lakes, which may ultimately impact the long-term sustainability of these populations. Maturity of walleye is typically defined by a length at maturation relationship (Ma et al. 2021), and that walleye age at maturation depends on

growth rate/time to reach the length at maturity (Venturelli et al. 2010). In addition, post-larval growth in male Chinook salmon (*Oncorhynchus tshawytscha*) has shown to be a major influence on timing of maturity (Shearer et al. 2006), suggesting that slow growing YOY walleye in *Bythotrephes* invaded lakes may have delayed maturation. Delayed maturation can act to reduce the proportion of spawning fish in the population and can have negative impacts on future recruitment (Rowe and Thorpe 1990). Our results suggest that these impacts would be exacerbated in low-nutrient lakes and/or populations that exhibit smaller sizes at first feeding; smaller initial larval sizes had a smaller final mass and length, to the extent that the smallest initial size could not maintain positive growth to the end of the 31-day period in invaded oligotrophic lakes. Further, smaller YOY walleye as a result of *Bythotrephes* invasion may also have significant implications for overwinter survival. In other closely-related percid species (yellow perch, *Perca flavescens*), smaller sized YOY individuals entering winter suffered greater mortality (Post and Evans 1989). Overall, this implies *Bythotrephes* impacts to larval walleye growth on populations in invaded lakes may also result in either delayed maturation, increased juvenile mortality (e.g., smaller initial sized larvae in oligotrophic lakes), or size-dependent overwinter mortality ultimately affecting walleye population dynamics.

Although our study found that prey availability in oligotrophic lakes invaded by *Bythotrephes* results in an energy deficiency for larval walleye, walleye persist in many invaded oligotrophic lakes such as Lake Michigan (TP=7-12 $\mu\text{g/L}$) and Lake Ontario (TP = 5.9 $\mu\text{g/L}$; Bunnell et al. 2011; Wang et al. 2012; Zorn et al. 2020). The reason our model may predict an energy deficiency for larval walleye may be due to the zooplankton densities used in this study were based on one sampling event per lake and seasonal

dynamics of zooplankton availability were not considered. Therefore, my prey availability estimates may not coincide with larval walleye first feeding (spring) and may reflect densities later in the summer when native zooplankton are more impacted by *Bythotrephes* (Kerfoot et al. 2016; Stein et al. 2017). A more accurate representation of prey availability would be daily prey density estimates for the month of the simulation (late spring); unfortunately, daily zooplankton density estimates are rare for most lake ecosystems. Another potential issue may arise from the zooplankton species selected for prey availability estimates, as I included only preferred prey, it is possible prey alternatives may be consumed by larval walleye when preferred prey are not readily available. As an example, larval walleye are known to consume chironomids (Galarowicz et al. 2006; Hoxmeier et al. 2006), and *Chaoborus* larvae (Spykerman 1974), which are not predated by *Bythotrephes* (Jokela et al. 2017), suggesting chironomids and/or *Chaoborus* could be an important diet item for larval walleye in *Bythotrephes* invaded lakes where native zooplankton may be not readily available. Lastly, this study did not consider variable temperature regimes which could have considerable impacts on walleye egg size, larvae size-at-hatch, and larval growth rate (Farmer et al. 2015), therefore, a temperature sensitivity analysis would broaden this analysis to be applicable under various climatic conditions. Considering these limitations, I believe my findings are strong as I revealed trends based on the mean zooplankton density of larval walleye preferred prey from many ecosystems and provided a mechanism for walleye growth trends seen in wild populations.

Recognizing that the impact of *Bythotrephes* on larval walleye growth was greatest in oligotrophic lakes in our study, and therefore potentially most vulnerable to

Bythotrephes invasion, I determined how many lakes across the province of Ontario, Canada (which has readily available data to address this question, see below) fall under the trophic lake classifications used in this study. I used TP and walleye presence data from lakes surveyed by the Broad Scale Monitoring (BSM) program (Ontario Ministry of Natural Resources and Forestry 2020; Ontario Biodiversity Council 2021), to categorize lakes in Ontario based on trophic state (see *Methods*; Carlson 1977), and whether they support walleye populations. Across 524 surveyed lakes, I found that most lakes were oligotrophic (61.6%) or mesotrophic (19.3%). Of those lakes, walleye were present in 36.8% of oligotrophic lakes, and 64.4% of mesotrophic lakes (Fig. 2.3). Considering that of the lakes surveyed, 91% of walleye lakes fall into the mesotrophic to oligotrophic categories, and the BSM set of lakes is intended to represent the state of fisheries in Ontario (Ontario Ministry of Natural Resources and Forestry 2020), our results suggest that walleye populations across Ontario may be vulnerable to reduced growth, and, in the case of oligotrophic lakes, potentially recruitment failure, if invaded by *Bythotrephes*.

This study aimed to determine if a change in zooplankton abundance due to *Bythotrephes* invasion could impact the growth rates of larval walleye. Our results suggest that walleye in less productive/oligotrophic lakes may be particularly at risk to *Bythotrephes* invasion, where zooplankton densities post-invasion may be insufficient to sustain larval walleye growth. In more productive/mesotrophic lakes, larval walleye growth was slower in invaded lakes, but comparable to that of non-invaded oligotrophic lakes. Bioenergetics models have been used in the past to determine changes in fish growth due to invasive species (e.g., Johnston 1999; McDonnell and Roth 2014), but this is the first I know of to evaluate the impacts of *Bythotrephes* invasions on larval walleye

specifically. Importantly, I have linked observed decreases in growth rate of larval walleye to the decreased prey availability in *Bythotrephes* invaded lakes, expanding our knowledge on the impacts of invasive species to freshwater fisheries.

2.6 Tables and Figures

Table 2.1. Bioenergetic parameter estimates used in this study from Johnston 1999, and D90 parameters from McDonnell and Roth 2014.

Symbol	Description	Value
Consumption		
CA	Intercept for maximum consumption	0.51
CB	Slope for maximum consumption	-0.42
CTO	Optimum temperature for consumption (°C)	25
CTM	Maximum temperature for consumption (°C)	28
CQ	Slope for temperature dependence of consumption	2.3
Respiration		
RA	Intercept for maximum standard respiration	0.056
RB	Slope for maximum standard respiration	-0.22
RTO	Optimum temperature for standard respiration	27
RTM	Maximum temperature for standard respiration	32
RQ	Slope for temperature dependence of respiration	2.1
ACT	Activity coefficient	1.0
SDA	Specific dynamic action coefficient	0.15
Waste losses		
FA	Intercept for proportion of consumed food egested	0.428
FB	Coefficient for egestion vs. temperature	-0.222
FG	Coefficient for egestion vs. feeding level	0.631
UA	Intercept for proportion of consumed food excreted	0.0292
UB	Coefficient for excretion vs. temperature	0.58
UG	Coefficient for excretion vs. feeding level	-0.299
D90 estimation		
Ca ₁	Baseline calanoid shape parameter	8.55
Ca ₂	Modifying calanoid shape parameter	-6.226
Cy ₁	Cyclopoid D90 value at length 0	1.11 x 10 ⁵
Cy ₂	Cyclopoid shape parameter	1.167
Da ₁	Peak value of <i>Daphnia</i> curve	4323.9
Da ₂	<i>Daphnia</i> shape parameter	38.033

Table 2.2. Zooplankton abundance treatments (\pm SE) based on various invaded and non-invaded lakes of Northern Ontario. Zooplankton data from Arnott 2021 (Unpublished raw data) were collected via vertical hauls from 2m above the bottom to the surface typically at the deepest part each lake using an 80 μ m mesh plankton sampler between May-August. Methods for collecting remaining zooplankton data can be found in Kerfoot et al. (2016).

Treatment	Invasion status	Trophic status	<i>n</i>	<i>Daphnia</i> (μ g/L)	Calanoid (μ g/L)	Cyclopoid (μ g/L)	Total (μ g/L)
NM	Non-invaded	Mesotrophic	4	192.02 \pm 1 ^a	69.86 \pm 1 ^a	32.87 \pm 1 ^a	294.75 ^a
NO	Non-invaded	Oligotrophic	132	161.9 \pm 442.2 ^b	52.51 \pm 148.3 ^b	13.21 \pm 20.00 ^b	227.71 ^b
IM	Invaded	Mesotrophic	4	55.20 \pm 1 ^a	75.23 \pm 1 ^a	21.29 \pm 1 ^a	151.72 ^a
IO	Invaded	Oligotrophic	38	28.51 \pm 65.21 ^b	14.13 \pm 15.84 ^b	6.20 \pm 7.13 ^b	48.85 ^b

Data source: ^a Kerfoot et al. 2016 ; ^b Arnott, *unpublished data*.

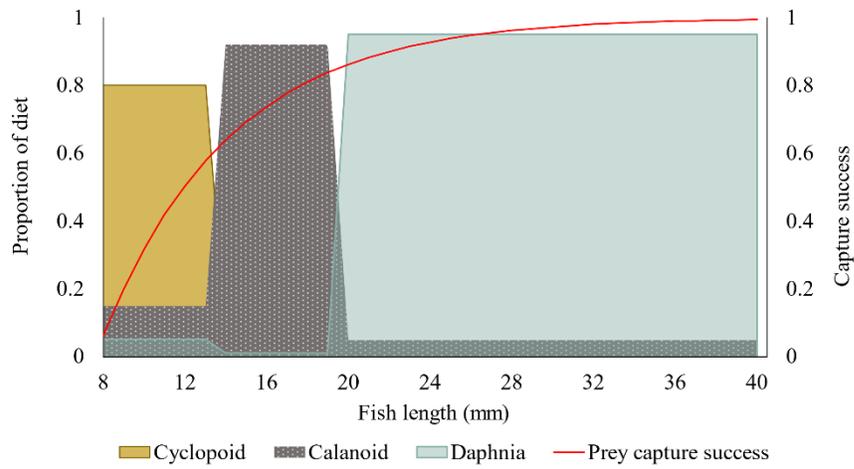


Fig. 2.1. Diet proportions and prey capture success (red line) as functions of body size for the first 40 days of feeding in larval walleye (*Sander vitreus*) assuming cyclopid copepods (yellow), calanoid copepods (grey dotted), and *Daphnia* (blue) are the exclusive prey items. Data from Johnston and Mathias (1994a, 1994b).

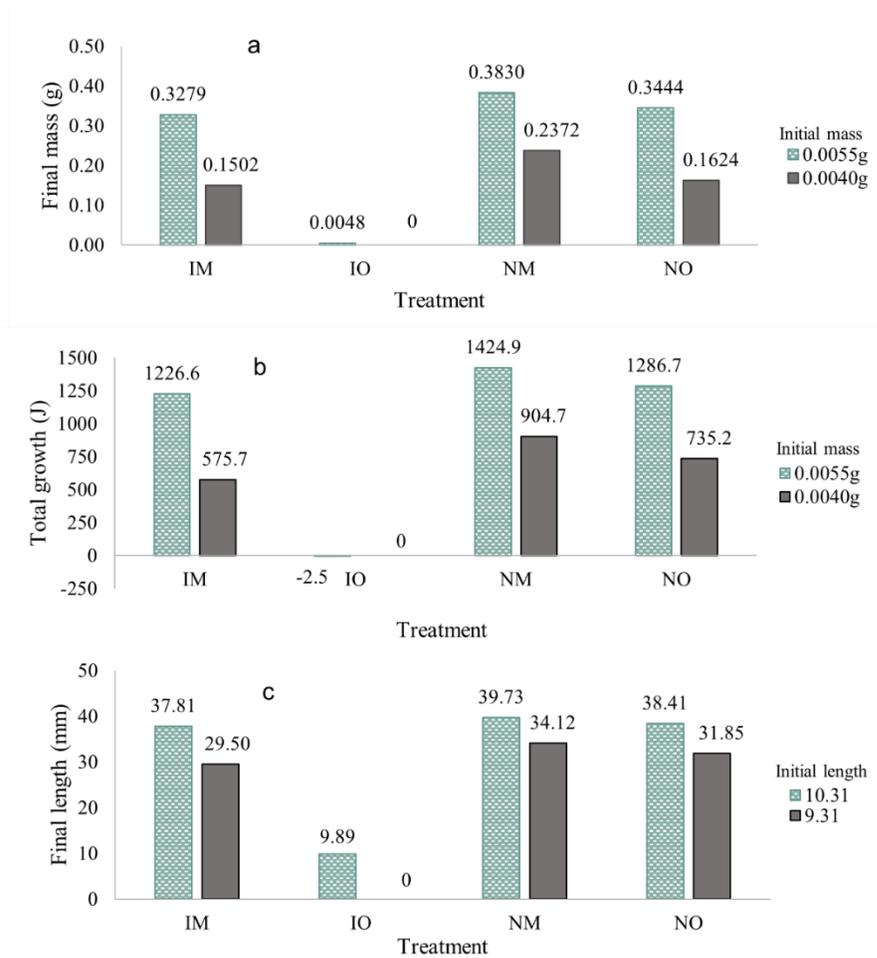


Fig. 2.2. Predicted final a) mass, b) energy content, and c) total length of young walleye after 31 days following start of feeding in four categories of lakes (treatments), based on bioenergetics modeling. For each treatment, results are presented for two initial body sizes. Treatments are: invaded with *Bythotrephes* and mesotrophic (IM), invaded and oligotrophic (IO), not invaded and mesotrophic (NM), and not invaded and oligotrophic (NO).

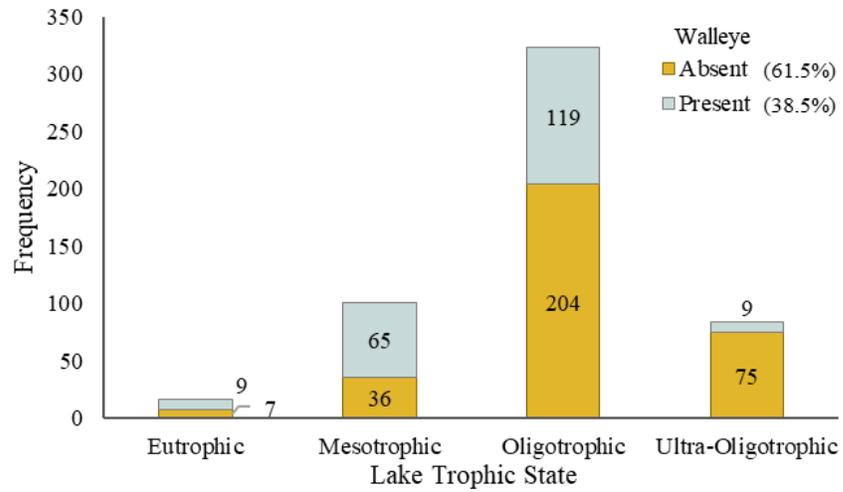


Fig. 2.3. Lakes in Ontario ($n=524$), Canada populating walleye (*Sander vitreus*), divided by lake trophic state based on the total phosphorus of the trophic state index (Carlson 1977). Walleye presence data are from Ontario Ministry of Natural Resources and Forestry (2020), and TP data are from the Ontario Biodiversity Council (2021) collected by the Ontario Broad Scale Monitoring program.

Chapter 3: Impact of invasive spiny water flea on the growth of young of year walleye

3.1 Abstract

The invasive spiny water flea, *Bythotrephes cederstroemii* (*Bythotrephes* hereafter), poses significant threats to the ecosystems they invade, by decreasing native zooplankton biomass and potentially decreasing prey availability for zooplanktivores. Here, I used a linear mixed effects model to evaluate the impact of *Bythotrephes* invasion on back-calculated size of the zooplanktivorous young-of-year (YOY) walleye (*Sander vitreus*), while considering the potential impact of climate as a covariate. For small waterbodies (<2000ha), I found that YOY walleye grew slower in *Bythotrephes*-invaded compared to non-invaded waterbodies. In contrast, for large waterbodies (>2000ha) YOY walleye growth showed negative but less severe changes in growth with *Bythotrephes* invasion. By contrast, the same analysis applied over time to only large waterbodies (the only lake size class to support pre- and post-invasion comparisons) did not reveal any changes in YOY growth. I also compared model-predicted YOY walleye lengths (scaled to a standardized GDD) to those from another study based on YOY collection surveys and found my predicted lengths to be significantly larger, potentially due to differing cohort sampling (measuring YOY length vs back-calculating YOY length from adult fish). Overall, this study provides novel insights to the impacts of an invasive species on fish growth using back-calculation methods revealing trends not reported elsewhere. As juvenile growth is linked to fish recruitment, reproduction, and production, it is essential to evaluate the potential impacts *Bythotrephes* has on native fishes for fisheries managers to make informed management decisions.

3.2 Introduction

Invasive species have been establishing themselves in Canadian coastal and inland lakes at a rate of 15 species per decade, some causing detrimental ecological impacts such as the disruption of food webs, population dynamics, energy transfer, and lake productivity (Department of Fisheries and Oceans Canada 2004; Kelly et al. 2013; Sturtevant et al. 2019). Increasing interest from the scientific community has helped document invasive species impacts, particularly for invasives that have successfully invaded habitats over a large geographic region. One such species is the large predatory cladoceran *Bythotrephes cederströmii* (previously *Bythotrephes longimanus*, hereafter *Bythotrephes*). *Bythotrephes* are considered a threat to invaded ecosystems due to their high population growth rates and documented direct and indirect impacts on aquatic food webs (Strecker et al. 2011; Kelly et al. 2013). *Bythotrephes* possess a novel barbed spine that typically measures 60% of their total body length and serves as a deterrent to predation by gape-limited fish (Barnhisel 1991b; Ketelaars et al. 1995). While larger predators can consume *Bythotrephes*, knowledge surrounding the potential indirect impacts of *Bythotrephes* on zooplanktivorous fish that are unable to consume *Bythotrephes* as prey, remains limited (Straile and Hälbich 2000).

In *Bythotrephes* invaded lakes, native zooplankton diversity, species richness, and biomass have been shown to rapidly decrease after invasion (Dumitru et al. 2001; Yan et al. 2002; Boudreau and Yan 2003; Barbiero and Tuchman 2004; Foster and Sprules 2009). Prey items for *Bythotrephes* such as the cladoceran *Daphnia* have been shown to modify their daily vertical migrations (DVM) to migrate lower in the water column as an avoidance behaviour in response to *Bythotrephes* predation, which can have negative

impacts such as slowing *Daphnia* growth rates due to increased occupancy of colder water temperatures (Pangle and Peacor 2006). Lakes invaded by *Bythotrephes* that also support additional native predatory invertebrate species can leave limited refuge for zooplankton prey. For example, the large predatory zooplankter *Mysis relicta*, remain near the bottom of lakes during the day and move up higher in the water column at night (Bunnell et al. 2011). In contrast, *Bythotrephes* inhabit the epilimnion and metalimnion of lakes with minimal DVM, leaving limited refuge for other zooplankton at all times of the day in lakes with both *Bythotrephes* and *Mysis* (Bunnell et al. 2011). In addition to high consumption rates, *Bythotrephes* are known to be “messy” eaters where only a portion of their prey is actually consumed, redirecting a substantial proportion of pelagic energy down the food chain into the microbial loop, and reducing net energy transfer to higher trophic level species, such as fish (Yurista et al. 2010). The combined impacts of altered zooplankton community structure, lower native zooplankton biomass, and redirected food chain pathways all suggest that food availability may be greatly reduced for native zooplanktivores in lakes invaded by *Bythotrephes*.

While *Bythotrephes* are known to outcompete most native invertebrate zooplanktivores (Foster and Sprules 2009), their impacts on zooplanktivorous fish are less well documented. Small zooplanktivorous fish (<100mm in total length) have been shown to have long handling times and difficulty consuming *Bythotrephes*, to the extent that some species such as yellow perch (*Perca flavescens*) have been shown to adopt an avoidance from feeding on *Bythotrephes* (Barnhisel 1991a, 1991b). An economically and culturally significant sportfish, walleye (*Sander vitreus*), are zooplanktivorous during their first year and as such may be at risk in *Bythotrephes* invaded lakes through

competition for shared resources. During the first few months of life, young-of-year (YOY) walleye are zooplanktivorous until they transition to benthivory and then piscivory during their first year (Galarowicz et al. 2006). In the presence of invasive *Bythotrephes*, lower prey availability may cause YOY walleye to have reduced consumption, leading to slower growth. A study by Hansen et al. (2020) in northern Minnesota lakes comparing those invaded by *Bythotrephes* with non-invaded lakes revealed that YOY walleye lengths (adjusted for thermal growth accumulation) were significantly smaller in invaded lakes. The authors speculated that this reduced growth resulted from lower prey availability in lakes invaded by *Bythotrephes*. As early growth rates are fundamentally linked to adult size, over-winter survival, recruitment, and ultimately ecosystem productivity, it is essential for fisheries management to understand the impacts *Bythotrephes* has on the growth rates of native fishes (Post and Evans 1989; Lester et al. 2004; Lorenzen 2016; Pedersen et al. 2018; May et al. 2020).

When assessing growth trends over time or across a broad geographical range, the effects of climate must be considered because growth is dependent on temperature in poikilotherms such as fish. As such, in temporal studies, changes to the ambient thermal energy due to a warming climate will likely also alter optimal thermal habitat, metabolic rates, and therefore available energy for growth (King et al. 1999; Angilletta et al. 2004). A climate metric commonly used to quantify the thermal environment as it relates to poikilotherms is growing degree days (GDD), which is the cumulation of daily average temperatures above a certain threshold temperature (T_0) between two time periods, where T_0 depends on the species of interest (Neuheimer and Taggart 2007; Chezik et al. 2014). Venturelli et al. (2010) showed a linear relationship between immature walleye growth

and GDD which explained a great deal of variance in fish length across lakes spanning a broad geographical distribution ($r^2 \geq 0.92$). It is important to consider climate as a covariate when evaluating temperature-dependent processes, especially on a longitudinal scale because global GDD has been increasing by 2.5 degree days per decade and annual variation in temperature may influence trends (Natural Resources Canada 2020).

Larval walleye growth is predicted to be lower in habitats with low abundance of zooplankton such as *Daphnia* (McDonnell and Roth 2014), indicating that factors impacting zooplankton abundance may also influence walleye growth. Lake trophic status may influence YOY walleye growth because zooplankton abundance and biomass tend to increase with lake productivity, likely due to increased available resources (Blancher 1984; Canfield and Jones 1996). In addition, lake size and depth are correlated with planktonic diversity and size (Johnson et al. 1977; Dodson 1992), which are critical factors that influence growth efficiency in some zooplanktivorous fish and may impact walleye recruitment (Pazzia et al. 2002; Hansen et al. 2015). Specifically, high prey diversity offers alternatives that may be more readily available or energetically beneficial in size compared to a habitat with a low diversity in available prey sizes (Sherwood et al. 2002). As lakes exhibit high levels of heterogeneity, it is important to consider covariates such as lake size, depth, and trophic state when evaluating fish growth.

Harvest can induce changes in the life history traits of fish, including rapid phenotypically plastic responses and/or longer-term evolutionary responses (Walsh et al. 2006; Dunlop et al. 2007). It is common in fisheries for juvenile growth to increase and for age at maturation to decrease, perhaps because growth is a plastic trait that is highly density dependent, such that lower density may increase the available resources per

capita, therefore increasing growth and likely earlier maturity (Dunlop et al. 2018). Faster growing larvae reach larger sizes and make ontogenetic diet shifts earlier compared to their slower-growing counterparts, and therefore may have size-selective advantages via increased survival in their first year (Bergenius et al. 2018; May et al. 2020). In *Bythotrephes* invaded lakes, although native zooplankton abundance may be reduced, faster growing YOY walleye may have a size-selective advantage by attaining a larger gape sooner, and therefore the ability to consume larger prey items not impacted by the invasion such as benthic invertebrates or even *Bythotrephes* as prey more rapidly than slower growing individuals. Therefore, YOY walleye populations may already have a size-selective advantage and the ability to consume *Bythotrephes*, suggesting YOY walleye in lakes with high fishing pressure may be less impacted by *Bythotrephes* invasions compared to waterbodies without high fishing pressure.

The determination of early growth rate from adult ageing structures through back-calculation can be a powerful tool that can provide a window into past ecological conditions. Back-calculations can be used to estimate lengths of age classes that are rarely sampled in typical fisheries surveys, such as YOY cohorts, and have been used to calculate fish growth rate over time periods not otherwise observable through population-based size-at-age relationships which rely only on captured fish through standard surveys (Francis 1990; Vigliola and Meekan 2009; Government of Ontario 2020). Population-based size-at-age relationships tend to mask intercohort variability in mortality and life history traits, whereas back-calculations provide information on individual growth trajectories and provide more power to detect cohort-specific patterns (Vigliola and Meekan 2009). Back-calculations performed on adult fish implicitly only characterizes

growth patterns in those individuals that survived to adulthood, possibly biasing conclusions around only a small portion of individuals in their cohort that survive to adulthood. However, the use of back-calculation remains advantageous by revealing growth trends for a life stage that is rarely sampled for or is not otherwise observable.

To assess the impacts of *Bythotrephes* on the growth rates of YOY walleye, I used ageing structures (i.e., otoliths and dorsal spines) collected from walleye in Ontario and Minnesota lakes to back-calculate size-at-age at the end of their first year, which is used here as a proxy for juvenile growth rate. These back-calculated growth rates were compared before and after *Bythotrephes* invasion in waterbodies with historical data, as well as among a larger dataset of invaded and non-invaded waterbodies focused on more contemporary data. The objectives of this study were to first compare back-calculated YOY walleye growth rates over time within waterbodies before and after *Bythotrephes* invasions, and secondly, between waterbodies with and without *Bythotrephes*. In each case relevant potential covariates of growth were considered in these analyses (i.e., GDD). I hypothesize that YOY walleye will have slower growth rates after *Bythotrephes* invasion and in *Bythotrephes* invaded waterbodies compared to non-invaded waterbodies, due to decreased prey availability after controlling for potential climate impacts. In addition, the research by Hansen et al. (2020) was partly conducted on the south arm of Rainy Lake, which is also included in my analysis. This overlap in data allows me to address my last objective to compare the back-calculated YOY walleye lengths in this study to the measured YOY walleye lengths from Hansen et al. (2020), both adjusted for thermal growth accumulation, for the same cohorts in the south arm of Rainy Lake where data on both metrics were available.

3.3 *Methods*

3.3.1 *Study area*

This study used data from 23 waterbodies in northwestern Ontario and Minnesota which varied primarily based on the presence of *Bythotrephes* (Fig. 3.1, Table 3.1). Long-term data sets were available for the selected study waterbodies dating back to the early 1980's, including government archives of walleye ageing structures and biometrics upon catch (Table 3.1). In addition, five lakes were sampled in 2021 to increase the number of lakes and/or year classes to be included (Table 3.1). All fish handling in 2021 as a part of this study was approved by the Lakehead Animal Care Committee (AUP #1468680). Most study waterbodies were located in Quetico Provincial Park (QPP) in Ontario, created in 1913, as well as the Boundary Waters Canoe Area (BWCA) in Minnesota which has been a federally designated wilderness area since 1964. Both areas uniquely lack the influence of high human disturbance (e.g., intense fishing pressure, eutrophication) compared to other waterbodies in the region. Beginning in 2003, some waterbodies within these areas have been observed to have become invaded by *Bythotrephes*, while others have remained non-invaded. This provided the opportunity for a natural whole-ecosystem experiment on waterbodies with comparable fishing pressure and environmental variables to evaluate the impacts of *Bythotrephes* across invaded and non-invaded waterbodies, as well as within waterbodies before and after *Bythotrephes* invasion.

The Rainy Lake complex, Namakan Lake, and Sand Point Lake were also included in my analysis as walleye ageing structure archives were available annually for all three systems back to the early 1990s. These waterbodies are large and support

popular fisheries bordering Ontario, Canada and Minnesota, USA. Including these waterbodies allowed me to compare growth rates between large and popular fisheries, alongside relatively non-impacted waterbodies in QPP and BWCA. Rainy Lake has three basins (Red Gut Bay, North Arm, and South Arm; Fig. 3.1) among which fishing pressures and fish communities vary, so each basin was treated as an independent waterbody for the purposes of this analysis. Rainy Lake has been recreationally and commercially fished since the 1940s for various species, including walleye. In efforts to improve walleye populations, fingerling and fry stocking occurred in the late 1980s and commercial walleye fishing quotas were decreased in 1994 (Ontario Ministry of Natural Resources [OMNRF] and Minnesota Department of Natural Resources [MDNR] 2004). Sand Point Lake is connected to Namakan Lake, and both support popular recreational fisheries, though commercial walleye quotas in both lakes were eliminated in 2001 and 2002, respectively (OMNRF and MDNR 2004).

As harvest tends to reduce population density and therefore increase growth (Dunlop et al. 2007), fishing pressure may be a confounding factor influencing the interpretation of growth in my analyses. Therefore, in study waterbodies with high fishing pressure such as the three basins of Rainy Lake, Namakan Lake, and Sand Point Lake, I expected to see faster growing YOY walleye compared to other study waterbodies with low fishing pressure, regardless of the impacts of invasive *Bythotrephes*. In populations with higher harvest pressure, I expect YOY walleye to have larger body sizes because of their faster growth rates, which could reduce *Bythotrephes* impacts owing to larger YOY gape sizes that would permit consumption of *Bythotrephes*.

3.3.2 *Fish Growth*

Back-calculation models can be used to determine fish growth and assess population health which are commonly used in fisheries assessments as fish growth influences biomass production, mortality, and reproduction (Dunlop et al. 2007; Lorenzen 2016). Various models have been used to back-calculate size-at-age of fish, such as Monartyrsky's Body-Proportional Hypothesis (MBPH) method, and the Biological Intercept (BI) method. While the Fraser Lee method is the most popular back-calculation method, it was not chosen in the current study as it may inaccurately back-calculate walleye size-at-age (Meerbeek and Hawkins 2013) and is constrained by the assumption that the ageing structure-fish length isometric relationship passes through a zero intercept (Vigliola and Meekan 2009). This assumption can lead to Lee's Phenomenon where growth rate calculations become less accurate when applied to ageing structures from mature fish experiencing reproductive investment (Francis 1990). However, the BI method can accommodate for Lee's Phenomenon by including a biologically-determined intercept based on a relationship between fish and ageing structure size, allowing the model to be less sensitive to mature fish ageing structure-length relationships (Campana 1990). In addition, the MBPH includes an allometric curve rather than an isometric function of ageing structure size and fish length, which has also been shown to result in more accurate back-calculated size-at-age estimates (Smedstad and Holm 1996). As such, I back-calculated size-at-age using both the BI and MBPH method to be used in analysis.

Otoliths were the primary ageing structure used in this analysis and are considered the most accurate structure for age determination in fishes (Watkins and Spencer 2013).

Where otoliths were unavailable, dorsal spines were used in lieu to back-calculate size-at-age. To ensure that back-calculated size-at-age based on the two different ageing structures could be integrated into a single data set meaningfully, I compared the back-calculated YOY fork length from both otoliths and dorsal spines from a subset of fish that had both ageing structures available using a paired two-sample t-test to determine if a correction factor to make comparisons between structures were necessary. If a consistent significant difference between the back-calculated lengths was found between the two structures, the mean relative difference between them was used to convert dorsal spine back-calculation estimates as otolith back-calculation estimates.

To select fish for my analyses, I used selection criteria to account for attributes of fish age and/or collection that could potentially bias back-calculated growth estimates. First, age estimates from dorsal spines sections tend to be inaccurate for female walleye >600mm or male walleye >450mm in fork length, while otoliths tend to be inaccurate for fish >10 years old (Koenigs et al. 2015; Dembkowski et al. 2017). To account for this, I only used otoliths from walleye originally aged as ≤ 10 years old and used dorsal spines from walleye that were less than the length boundaries for accurate age estimates when assigning fish to year classes. This method also helps to improve the ageing structure-length relationships used in the back-calculation methods from becoming disproportionate as ageing structures in old fish might continue to grow after the fish's length stops growing (Vigliola and Meekan 2009). Second, sampling gear varied between surveys; for example, various organizations conduct surveys in Ontario using gill nets, trap nets, and public surveys (creel), whereas the Minnesota surveys typically use a combination of gill nets and/or trap nets (MDNR 2017; Ontario Government 2020). I

therefore constrained fish selection to avoid net-selectivity for fast-growing fish by creating sampling gear-specific catch curves to determine fully recruited size classes (peak catch) for each of the four gear types (i.e., gill net, trap net, creel, or a combination of gill and trap nets), where the size class just greater than the peak catch size became the lower threshold of fish to be included in this analysis (Smith et al. 2012, Appendix A). In situations where the sample size was too small after the application of these criteria, I chose to not use that waterbody in my analysis ($n < 6$ for each age class, Appendix B). Last, fish lengths acquired from the Minnesota DNR were measured as total length, rather than fork length. Therefore, I converted these total lengths to fork lengths through the fork length-total length regression developed using the fish data used in this study (Appendix C).

For the purpose of this study, growth rates were defined as the fork length at the end of the first year of growth (mm). I used a Laxco™ LMC 4000 Trinoc Microscope at 4X magnification with a Laxco™ SEBACAM5C mounted camera to image otolith annuli using the crack-and-burn method or mounted and sectioned-dorsal spine annuli (Watkins and Spencer 2013). I then measured the distance (mm) to 5 decimal places from the nucleus of the structure to each annulus along the same transect from the images (Fig. 3.2; Borkholder and Edwards 2001; Watkins and Spencer 2013), using the program SebaView (Laxco Inc. 2019). To back-calculate size-at-age and growth rate, I used both the BI model (eq. 3.1) and MBPH model (eq. 3.2) model as described previously:

$$L_i = L_c + (R_i - R_c) \frac{L_c - L_0}{R_c - R_0} \quad (\text{eq. 3.1})$$

$$L_i = \left(\frac{R_i}{R_c}\right)^b L_c \quad (\text{eq. 3.2})$$

where L_c and R_c are the fork length of the fish (mm) and radius of the otolith/dorsal spine section at capture (mm, R_c in Figure 3.2), respectively, and L_i and R_i are then the fork length (mm) of fish and the otolith/dorsal spine section radius (mm) at the age of interest (in this case, the first annulus, R_i in Figure 3.2), corresponding to a measured annulus on the ageing structure. The BI model also requires an estimate of the fork length of fish and the otolith/dorsal spine section radius at the time of hatch (L_0 and R_0). At hatch, walleye can range between 6 mm to 10 mm in length (Johnston 1997; Bozek et al. 2011) at which time they do not possess a dorsal spine (McElman 1983). Therefore, when dorsal spine samples were used for back calculations, L_0 was set to 6 mm and R_0 was set to zero. However, I suggest future analysis using a range of L_0 values (6mm to 10mm) to account for variation in size at hatch that may be associated with egg dry mass (Johnston 1997). To calculate the size of an otolith at hatch (R_0) for the BI model, I used all available walleye data from my study waterbodies to develop a linear function between otolith radius at capture (R) and fork length (L) using equation (3.3):

$$L_i = a + bR_i \quad (\text{eq. 3.3})$$

To estimate b for the MBPH model in equation (3.2), I constructed an allometric function between ageing structure radius at capture (R) and fork length (L) using equation (3.4):

$$L_i = aR_i^b \quad (\text{eq. 3.4})$$

All back-calculated YOY walleye lengths were quality checked by plotting length-frequency histograms for each back-calculation method. Any lengths that were clearly

outside of what is biologically possible for a YOY walleye cohort were removed (e.g., lengths >350mm).

3.3.3 *Climate as a covariate*

Since the late 1940's, northwestern Ontario has experienced an increase of 1.4°C in average annual temperature, making it the most rapid warming area in all of Ontario (Ontario Centre for Climate Impacts and Adaptation Resources 2009). Therefore, to address my first objective comparing back-calculated YOY walleye growth rates over time within waterbodies before and after *Bythotrephes* invasions, I needed to first consider potential climate impacts on growth rates of fishes. To do this, I used local weather station (Atikokan, ON) air temperature as a proxy for water temperature to calculate $GDD \geq 5 \text{ }^\circ\text{C}$ (Honsey et al. 2019):

$$GDD = \left[\frac{T_{max} + T_{min}}{2} \right] - T_o \quad (\text{e.q 3.5})$$

Where T_{max} and T_{min} are the maximum and minimum daily temperature respectively and T_o is the base temperature in which I chose to use 5 °C because this temperature is recommended in the literature (Chezik et al. 2014), and is suggested to be metabolically relevant to the growth of walleye (Honsey et al. 2019). I calculated the cumulative GDD for the first growing season (May 1st to December 31st) for each fish based on their birth year (Chezik et al. 2014), and standardized all GDD values by subtracting the mean GDD for all years to center the values around zero.

3.3.4 *Linear mixed effects modelling*

I used a linear mixed effect (LME) modelling approach to evaluate the effect of *Bythotrephes* invasion on YOY walleye growth, including relevant covariates that might

influence this relationship. I used R (R Core Team 2021) and R package lme4 (Bates et al. 2015) to conduct all statistical analyses. Waterbody characteristics such as prey availability, competitor species and density, mean growing season temperature, waterbody size, and waterbody depth are all known to be influential on fish growth (Nero and Sprules 1986; Madenjian et al. 1996; Quist et al. 2004; Eloranta et al. 2015, Massie et al. 2021). Therefore, I used a categorical variable for waterbody size of small waterbodies (≤ 2000 ha in surface area) and large waterbodies (> 2000 ha). A categorical vs. continuous variable was chosen for lake size because a small number of waterbodies in my analysis (e.g., the three basins of Rainy Lake) are 2-10 times larger than other study waterbodies, which would give them high leverage in the analysis if left as a continuous variable. Further, the distribution of lake size in my study is bimodal, as it is represented by many small lakes, many large lakes, and only few medium sized lakes. The categorization applied divides the sample size of lakes almost equally between the two size classes (12 small [three invaded, nine non-invaded], and 11 large [ten invaded, one non-invaded]). Waterbody trophic state was determined using the Trophic State Index using either total phosphorus (TP), Secchi depth (SD; mm) found in Carlson (1977, their Table 1), or from a predetermined status using unknown methods found elsewhere in the literature (e.g., page 60 of the Ontario-Minnesota Boundary Waters Fisheries Atlas describes the trophic status of Namakan Lake). Using these criteria, four lakes were identified as mesotrophic, 19 as oligotrophic, and two lakes with unknown trophic state. GDD was calculated as previously described. Prey availability, competitor species and density information were available for only very few waterbodies and were therefore not included in the analysis.

The general LME modelling approach sought to test the fixed effect of *Bythotrephes* invasion (categorical for invaded or non-invaded) on the growth of YOY walleye (continuous variable) while controlling for fixed covariates of GDD (continuous variable), waterbody size (categorical fixed effect), maximum waterbody depth (continuous fixed effect) and waterbody trophic status (categorical fixed effect). We also included waterbody and fish birth years as discrete random effects.

The LME modelling approach was done using three subsets of data to create three LME models. First, I created a temporal model by using a subset of invaded waterbodies to achieve my first objective to compare YOY walleye growth rates over time within waterbodies before and after *Bythotrephes* invasions. Next, I created a contemporary spatial model by using a subset of contemporary data (fish born in 2000-2018) to address my second objective of comparing YOY walleye growth between waterbodies with and without *Bythotrephes*. For invaded waterbodies included in the contemporary spatial model, I only included the fish that were alive after the *Bythotrephes* invasion, removing all pre-invasion fish so that I was considering only post-invasion samples for invaded waterbodies. Lastly, I used the entire dataset of spatial and temporal data to evaluate the effect of *Bythotrephes* invasion on the growth of YOY walleye on a spatio-temporal scale to consider inter-system and inter-annual variability.

I evaluated the significance of individual terms in the model using model comparisons and a likelihood-ratio test using the *anova()* function in R to estimate whether the inclusion of each variable of interest contributed a significant proportion of variance to the model. For example, to test the significance of *Bythotrephes* invasion, the following model comparison was applied:

$$\text{YOY length} \sim \text{Bythotrephes invasion} + \text{GDD} + \text{Waterbody size} + \text{Trophic status} + \text{Maximum waterbody depth} + (1 | \text{Waterbody ID}) + (1 | \text{Birth year}) \quad (\text{e.q 3.6})$$

$$\text{YOY length} \sim \text{GDD} + \text{Trophic status} + \text{Waterbody size} + \text{Maximum waterbody depth} + (1 | \text{Waterbody ID}) + (1 | \text{Birth year}) \quad (\text{e.q 3.7})$$

Evaluating interactions in an LME model can reveal that one variable changes how another variable effects the response variable; for example, waterbody size (due to increased resources and food web complexity) may change how *Bythotrephes* invasions impact YOY walleye lengths. Therefore, I compared the additive model (optimal model between e.q 3.6 and 3.7) with a model containing an interaction between *Bythotrephes* invasion and each of my fixed effect covariates: waterbody size (e.q 3.8), GDD (e.q 3.9), maximum waterbody depth (e.q 3.10), and trophic status (e.q 3.11):

$$\text{YOY length} \sim \text{Bythotrephes invasion} * \text{Waterbody size} + \text{GDD} + \text{Trophic status} + \text{Maximum waterbody depth} + (1 | \text{Waterbody ID}) + (1 | \text{Birth year}) \quad (\text{e.q 3.8})$$

$$\text{YOY length} \sim \text{Bythotrephes invasion} * \text{GDD} + \text{Waterbody size} + \text{Trophic status} + \text{Maximum waterbody depth} + (1 | \text{Waterbody ID}) + (1 | \text{Birth year}) \quad (\text{e.q 3.9})$$

$$\text{YOY length} \sim \text{Bythotrephes invasion} * \text{Trophic status} + \text{Waterbody size} + \text{GDD} + \text{Maximum waterbody depth} + (1 | \text{Waterbody ID}) + (1 | \text{Birth year}) \quad (\text{e.q 3.10})$$

$$\text{YOY length} \sim \text{Bythotrephes invasion} * \text{Maximum waterbody depth} + \text{Waterbody size} + \text{GDD} + \text{Trophic status} + (1 | \text{Waterbody ID}) + (1 | \text{Birth year}) \quad (\text{e.q 3.11})$$

Finally, I evaluated the significance of fixed effects not involved in significant interactions by comparing the fit of a model without the effect, with the full model using

maximum likelihood ratio tests (Table 3.2). Significance of random effects of lake and year were evaluated for significance, either against the fully additive model (eq. 3.6) or against the model with a significant interaction term identified.

To present the results of the models graphically, I used the final models of each subset (temporal, spatial, and spatio-temporal) to predict YOY walleye length at a standard GDD to adjust lengths for thermal growth, choosing a GDD value of 1404 which was previously considered the median end of summer degree day for waterbodies in the study region, corresponding with the end of summer fish length accumulation (Hansen et al. 2020). The predicted lengths adjusted for thermal growth were then plotted to compare differences among groups (invaded vs. non-invaded, or pre- vs. post-invasion).

3.3.5 *Method comparison*

Hansen et al. (2020) measured YOY walleye lengths in various waterbodies including the south arm of Rainy Lake between 1983 and 2018 and adjusted their lengths for thermal growth, to assess the impacts of *Bythotrephes*. Considering Hansen and colleagues collected data from one of the same systems generating back-calculated YOY sizes here based on my analysis, during the same period as the current study, it presented an opportunity to compare YOY sizes based on back-calculations with measured lengths, both adjusted for annual climatic variation. As the lengths taken from the Hansen et al. (2020) were measured as total length, I converted these to fork length through the fork length-total length regression made previously (Appendix C). I then used the third LME model using spatio-temporal data to predict YOY walleye lengths for the South arm of Rainy Lake at 1404 GDD for years 1983-2018. I chose to use the spatio-temporal model

as it used the most data and I therefore believed it to predict the most accurate YOY walleye lengths. The difference in the lengths for each year that both studies had in common was then calculated and compared using a paired *t*-test.

3.4 Results

Based on my selection criteria for size cut-offs and net selectivity, 996 walleye born between 1974 and 2018 using either dorsal spines or otoliths were included in the analysis, representing 23 waterbodies. The linear relationship between fork length and otolith radius from equation (3.3) revealed the otolith size at hatch was 0.0054mm, which was used in the application of the BI back-calculation method (Fig. 3.3). The slope coefficient (*b*) for the otolith and dorsal spine allometric functions for the MBPH model were 1.22 and 0.878, respectively (Fig. 3.4). When comparing otolith and dorsal spine back-calculated YOY length using structures from the same fish, the BI model back-calculated YOY lengths were not significantly different between dorsal spines and otoliths of the same fish (Fig. 3.5a; Paired two sample *t*-test, $t = -1.06$, $df = 15$, $p = 0.304$). In contrast, the MBPH back-calculated YOY lengths from dorsal spines were significantly different when compared to lengths back-calculated from otoliths, where structures were from the same fish (Fig. 3.5b; Paired two sample *t*-test, $t = 4.18$, $df = 15$, $p = 0.0008$). In addition, ~30% of YOY walleye were predicted to be unrealistically small (<80mm) or negative values using the BI model. Based on these observations, I selected the MBPH method to generate back-calculated YOY lengths. Back-calculations using dorsal spines were corrected using a multiplier of 1.17 based on the average relative paired difference between otolith and spine back-calculated size at YOY (Fig. 3.5b).

Of the initial 23 study waterbodies, seven large waterbodies and one small waterbody had long-term data sets to support the temporal model (e.g., those with at least one age class represented pre-invasion as well as post-invasion; Table 3.1). From the back-calculated YOY walleye lengths using the MBPH method, the optimal temporal LME model was as follows:

$$\text{YOY length} \sim \text{GDD} + (1 | \text{Waterbody ID}) + (1 | \text{Birth year}) \quad (3.12)$$

Importantly, including invasion status in the model did not explain a significantly greater portion of variance compared to a model without it (Chi-squared test, $X^2 = 0.73$, $p=0.39$). In addition, I found no significant interactions between *Bythotrephes* invasion and either waterbody size (Chi-squared test, $X^2 = 1.47$, $p=0.23$), GDD (Chi-squared test, $X^2 = 0.42$, $p=0.52$), trophic status (Chi-squared test, $X^2 = 0.46$, $p=0.50$), or maximum waterbody depth (Chi-squared test, $X^2 = 1.08$, $p=0.30$). An LME model including waterbody ID explained a significant portion of variance compared to a model excluding it (Chi-squared test, $X^2 = 38.2$, $p<0.0001$). An LME model including fish birth year also explained a significant amount of variance compared to a model excluding it (Chi-squared test, $X^2 = 25.5$, $p<0.0001$). Including waterbody size did not explain a significant amount of variation and was therefore excluded from the LME model (Chi-squared test, $X^2 = 0.036$, $p=0.85$). In addition, maximum waterbody depth did not explain a significant amount of variance (Chi-squared test, $X^2 = 1.88$, $p=0.17$), and was therefore excluded from the model. Lastly, trophic state did not explain more variance and was therefore excluded from the temporal model (Chi-squared test, $X^2 = 0.33$, $p=0.56$).

The optimal contemporary spatial model included data from 2000 – 2018 from 22 study waterbodies (all waterbodies except Lac la Croix had data for fish born after 2000) and the optimal contemporary spatial LME model was as follows:

$$\text{YOY length} \sim \text{Bythotrephes invasion} + \text{GDD} + (1 | \text{Waterbody ID}) \quad (3.13)$$

Including invasion status as a fixed effect in the contemporary spatial model explained a significantly greater portion of variance compared to a model without it (Chi-squared test, $X^2 = 6.03$, $p=0.014$). I found no significant interaction terms between *Bythotrephes* invasion and either waterbody size (Chi-squared test, $X^2 = 0.11$, $p=0.74$), GDD (Chi-squared test, $X^2 = 0.07$, $p=0.79$), trophic status (Chi-squared test, $X^2 = 0.34$, $p=0.56$), or maximum waterbody depth (Chi-squared test, $X^2 = 0.04$, $p=0.84$). I excluded trophic state from the model as a fixed effect because it did not explain a significantly greater portion of variance when included (Chi-squared test, $X^2 = 0.60$, $p=0.74$). In addition, maximum water depth did not explain a significant portion of variance and was not included in the model (Chi-squared test, $X^2 = 0.25$, $p=0.62$). The inclusion of waterbody ID as a random intercept in the contemporary spatial LME model explained a significantly greater portion of variance compared to a random slope model (LLR test, $LLR= 1.02$, $df=8,6$, $p=0.60$), or a model with only fixed effects (LLR test, $LLR = 20.94$, $df=6,5$, $p<0.0001$). However, I found that including fish birth year did not explain a significant amount of variance compared to a model including it and was therefore excluded from the LME model (Chi-squared test, $X^2 = 0.46$, $p=0.49$). After scaling predicted values to a standardized GDD of 1404, YOY walleye length appeared to be smaller in invaded waterbodies compared to non-invaded waterbodies (Fig. 3.8).

The optimal spatio-temporal LME model was as follows:

$$\text{YOY length} \sim \text{Bythotrephes invasion} * \text{Waterbody size} + \text{GDD} + \quad (3.14)$$

$$(1 | \text{Waterbody ID}) + (1 | \text{Birth year})$$

I found that waterbody size had a significant interaction with the effect of *Bythotrephes* invasion on YOY lengths (Fig. 3.6; Chi-squared test, $X^2 = 4.18$, $p=0.041$). All other evaluations of interaction terms were not significant such as between *Bythotrephes* invasion and either GDD (Chi-squared test, $X^2 = 0.10$, $p=0.75$), trophic status (Chi-squared test, $X^2 = 0.57$, $p=0.75$), or maximum waterbody depth (Chi-squared test, $X^2 = 0.50$, $p=0.48$). As with the temporal and spatial models, I excluded maximum waterbody depth as it did not explain more variance compared to a model that included it (Chi-squared test, $X^2 = 2.46$, $p=0.12$). In addition, I found that trophic state did not explain a significant amount of variance and was therefore excluded from the model (Chi-squared test, $X^2 = 0.62$, $p=0.73$). The inclusion of waterbody ID as a random intercept in the spatio-temporal LME model explained a significantly greater portion of variance compared to a random slope model (log-likelihood test, likelihood ratio= 0.0000016, $df=8,6$, $p=1.0$), or a model with only fixed effects (LLR test, $LLR = 230.1$, $df=6,5$, $p<0.0001$). In addition, including fish birth year also explained more variance than a model without it and was therefore included in the model ($X^2 = 19.05$, $p<0.0001$). The average predicted values from the optimal spatio-temporal LME model standardized to a common GDD of 1404 (i.e., end of the summer growing season), in small, invaded waterbodies, appeared to be smaller than in small, non-invaded waterbodies, with an average difference of 19.2 mm or 13% (Fig. 3.7). For large waterbodies, YOY lengths appeared to not differ greatly between invaded and non-invaded waterbodies with an average difference of 3.98 mm or 3% smaller in invaded waterbodies (Fig. 3.7).

A comparison of GDD-standardized YOY walleye lengths between this study and that of Hansen et al. (2020) for YOY walleye born in 1991 to 2018 in the South Arm of Rainy Lake found significant differences between the two datasets; the average back-calculated GDD-standardized YOY length from the South arm of Rainy Lake was 138.1 mm, on average 26.2 mm larger than the mean GDD-standardized value of 111.9 mm from Hansen et al. (2020; paired t-test; $t=-8.57$, $df=33$, $p<0.001$; Fig. 3.9).

3.5 Discussion

Here, I used data from fish born between 1974 and 2018 across 23 waterbodies to reveal supporting evidence of reduced YOY walleye growth in the presence of *Bythotrephes*, where this impact is potentially amplified in smaller waterbodies. Additionally, growth of YOY walleye in large waterbodies from my dataset appear to be less sensitive to invasion. On average, YOY walleye were shown to grow 13% slower in small, invaded waterbodies, relative to small, non-invaded waterbodies in this study. It is widely documented that invaded waterbodies have lower zooplankton diversity and biomass post-invasion (Yan et al. 2002; Barbiero and Tuchman 2004; Walsh et al. 2016), providing fewer resources for zooplanktivores such as YOY walleye, which is consistent with my observations in small, invaded waterbodies in the current study. However, it is important to note that in the spatio-temporal model that indicated a significant interaction between waterbody size and *Bythotrephes* invasion, that small waterbodies made up only 18% of the invaded waterbodies. As such, these results should be interpreted with some caution, recognizing that it is limited from a lack of data on small lakes with long-term datasets that are also invaded by *Bythotrephes*. Regardless, this may be of concern for fisheries managers as slower growth rates in fishes can lead to weaker age-class strength

and poor recruitment (Anderson 1988; May et al. 2020). This study used back-calculated YOY size from adult walleye, thus focusing on early growth rates of individuals that were able to survive to adulthood. Therefore, in small waterbodies, *Bythotrephes* impacts to YOY walleye are apparent even in the individuals that survive to adulthood.

Bythotrephes have been spreading rapidly across inland lakes in North America and these findings illustrate the importance of invasive species management especially in small lakes, to protect fish stocks in waterbodies vulnerable to *Bythotrephes* invasions (Kerfoot et al. 2011).

The method comparison in this study revealed that the back-calculated lengths (scaled to a standardized GDD) in this study were larger than the measured lengths (also scaled to a standardized GDD) from Hansen et. al (2020), using the same large lake study system (south arm of Rainy Lake). A potential reason for the differing length estimates (and therefore differing conclusions regarding growth trends in large waterbodies between studies), is that the walleye used in this study are likely among the fastest growing individuals of their year class, having survived their first winter and into adulthood. By contrast, Hansen and colleagues measured YOY walleye collected in their first year from waterbodies, of which ~ 90% likely did not survive beyond their first winter and into adulthood (Johnson et al. 1996). First year walleye survival is typically <10% due to size-selective mortality through both risk of predation or starvation (Post and Evans 1989; Johnson et al. 1996; Grote et al. 2018). As such, it is plausible that the ~10% of YOY survivors in the south arm of Rainy Lake included in the current study had faster early growth rates and therefore had longer lengths, having survived to adulthood, compared to the ill-fated remaining ~90% of their cohort. Faster growing YOY walleye

within the same cohort have been shown to experience earlier ontogenetic shifts compared to their slower growing counterparts, purportedly due to passing gape limitation (Uphoff et al. 2019). Faster growing YOY walleye likely have a size-selective advantage to be able to consume larger prey-classes, such as small fish or even *Bythotrephes*, earlier than their smaller counterparts. If larger individuals were more likely to survive due to size-selective advantages (i.e., earlier ontogenetic shifts), it makes sense that the YOY lengths back-calculated in this study would be larger compared to the lengths from Hansen et al (2020).

As described in previous studies, *Bythotrephes* seem to have negative impacts on percids in large lakes generally, including studies examining both yellow perch and walleye (Staples et al. 2017; Hansen et al. 2020). While in the spatio-temporal model in the current study, I found weak effects of *Bythotrephes* invasion on YOY walleye growth in large waterbodies, and no effect of *Bythotrephes* in the temporal model, I found invasion impacts on small waterbodies in the spatio-temporal model and impacts of *Bythotrephes* in all sized lakes the contemporary spatial model. The results from both the spatio-temporal and the temporal model suggests that there may be some factors regarding large waterbodies specifically that might be influencing how *Bythotrephes* affects the growth of YOY walleye. Besides potential impact such as size-selective advantages as described above as well as density dependent growth, most of the large waterbodies in this study have relatively high fishing pressure which may increase mortality, reduce the population density, therefore potentially cultivating faster growth due to increased resources per capita (Dunlop et al. 2007; Dunlop et al. 2018). Considering YOY walleye growth was shown to be less impacted in large waterbodies, it

is possible that density dependent growth due to high fishing pressure in addition to larger size potentially having size-selective advantages may be dampening the effects of *Bythotrephes* invaded conditions. Though unavailable for most waterbodies at the time of the current study, this suggests that collecting data on fishing pressure and walleye density at both juvenile and adult life stages would provide additional insight to the impacts they have on YOY walleye growth.

Food web complexity may also act to reduce the impacts of *Bythotrephes* to YOY walleye in the larger waterbodies in this study. Large waterbodies tend to have higher food web complexity (Post et al. 2000), which along with adaptive foragers can buffer environmental disturbances (Kondoh 2003), possibly including stabilizing against impacts of invasive species such as *Bythotrephes*. In addition, large waterbodies tend to have higher habitat complexity and lake connectedness leading to higher species richness (Tonn and Magnuson 1982). Higher zooplanktonic and fish species richness in large waterbodies may provide YOY walleye prey alternatives post-invasion to species whose populations are less affected by *Bythotrephes*. As an example, larval smelt are shown to be abundant in *Bythotrephes* invaded waterbodies and may be readily available for YOY walleye once they are large enough to consume them as an alternative to the already impacted native zooplankton community (Dumitru et al. 2001; Bunnell et al. 2011). Overall, species richness in large waterbodies may be indirectly altering the severity of effects that *Bythotrephes* has on YOY walleye growth.

In the contemporary spatial model, I found *Bythotrephes* invasion to negatively affect YOY walleye growth in both small and large waterbodies. It is important to note in the spatio-temporal model that YOY walleye in large non-invaded waterbodies appeared to

have shorter lengths than YOY walleye in small non-invaded waterbodies (Fig. 3.7), suggesting YOY walleye may be smaller in large waterbodies regardless of *Bythotrephes* invasion status. As most of the invaded waterbodies in the contemporary spatial model were large (nine out of eleven), the difference between invaded and non-invaded waterbodies on a spatial scale might be driven by large lakes typically having smaller YOY walleye. The contemporary spatial model did however include two small, invaded waterbodies that the model suggests has smaller YOY walleye, which supports the spatio-temporal model in that YOY walleye may be smaller in small, *Bythotrephes* invaded waterbodies. I suspect that if the sample size of small and large lakes was more evenly distributed across *Bythotrephes* invaded and non-invaded categories, the resulting contemporary spatial LME model may have results more similar to the spatio-temporal model such that the effect of *Bythotrephes* invasion on YOY walleye growth was influenced by waterbody size.

Aquatic ecosystems have been greatly impacted by human influence in the past, especially with regards to invasive species. Here, I presented evidence for the potential impacts of the invasive *Bythotrephes* on the growth of YOY walleye by comparing invaded and non-invaded waterbodies, but also by comparing invaded waterbodies before and after invasion. I accounted for inter- and intra-system variability (e.g., climate change through GDD) through statistical models and was able to evaluate the impact of *Bythotrephes* on YOY walleye growth. My results suggest the impact *Bythotrephes* has on YOY walleye may be dependent on waterbody size, in that YOY walleye grew slower and reached shorter YOY sizes in small, invaded waterbodies, compared to non-invaded small waterbodies. Further, the mechanism for these growth declines are very likely due

to *Bythotrephes* induced effects on the zooplankton community (Chapter 2). Comparing my results with those reported elsewhere, I found that YOY walleye in large waterbodies that survive to adulthood appeared to be less vulnerable to impacts of *Bythotrephes* invasions, potentially due to density dependence influencing faster growth rates, size-selective advantages, or that waterbody characteristics such as adaptive foragers may be buffering the observed impacts to YOY walleye. A potential interaction between waterbody size and the effect of *Bythotrephes* on YOY fish growth has not been previously reported in the literature. In small waterbodies, slower growth in the fastest growing individuals might have negative consequences to walleye recruitment because decreased growth is correlated with delayed maturity potentially reducing the proportion of spawning individuals in the population (Rowe and Thorpe 1990, Shearer et al. 2006), suggesting walleye recruitment may be in decline in *Bythotrephes* invaded lakes. Fisheries managers can use this information to make informed management decisions such as identifying recruitment bottlenecks in *Bythotrephes* invaded lakes and stocking walleye fry that are passed this bottleneck and therefore less impacted by *Bythotrephes*.

3.6 Tables and Figures

Table 3.1 Physical characteristics of the study waterbodies (invaded by *Bythotrephes cederströmii* and non-invaded) located in northwestern Ontario, Canada and Minnesota, USA and which waterbodies were included in the spatio-temporal (O), temporal (T), and the spatial model (S).

Waterbody Name	Surface Area (ha)	Mean Depth (m)	Max Depth (m)	Trophic state	Invasion Year	Survey year(s)	Statistical Model
Agnes (ON)	2,982	19.6	79.3	Oligotrophic	-	1985, 2010, 2016, 2017	O & S
Agnes (MN)	423	Unknown	9.1	Oligotrophic	-	2016	O & S
Fall*	913.7	4	9.7	Mesotrophic	2014	2012, 2017	O, S & T
Beaverhouse	1,958	22.3	64.7	Oligotrophic	-	1996, 2010, 2016	O & S
French*	284	12.5	26	Oligotrophic	2009	2021	O & S
Kawnipi*	4,480	17	77.6	Unknown	2008	2021	O & S
Lac la Croix*	5,771	34	51.2	Unknown	2010	1994, 1999, 2003, 2017	O & S
Loon*	5,754	Unknown	26	Oligotrophic	2009	2001, 2008, and 2015	O, S & T
McAree	879	12.7	37.2	Oligotrophic	-	1996, 1997, 2007, 2010, 2016	O & S
Minn	479	5.9	39.6	Oligotrophic	-	1999, 2008, 2010, 2016	O & S
Namakan*	10,100	13.6	45.7	Oligotrophic	2006	2006-2019	O, S & T
North Arm*	34,570	7.96	41	Oligotrophic	2006	1997, 2002, 2007, 2018	O, S & T
Olifaunt	561	12.9	39.4	Oligotrophic	-	2011	O & S
Oriniack	301	Unknown	5.18	Oligotrophic	-	2018	O & S
Pickerel*	5,754	17.7	74.7	Oligotrophic	2008	1981, 1982, 2010, 2015, 2021	O, S & T
Poohbah*	1,530	16.1	70	Mesotrophic	2016	2010 and 2016	O & S
Redgut Bay*	8,320	6.89	31.2	Oligotrophic	2006	1998, 2003, 2008, 2016, 2018	O, S & T
Robinson	421	12.7	35.1	Oligotrophic	-	1985, 1999, 2021	O & S
Saganagons*	2,470	6.9	31.3	Oligotrophic	2003	2010, 2016, 2021	O & S
Sand point*	3,450	Unknown	56	Mesotrophic	2007	2007-2015, 2017-2020	O, S & T
South Arm*	27,260	11.5	49.1	Oligotrophic	2006	1999, 2004-2006, 2008-2015, 2017-2020	O, S & T
Wolseley	1,307	12.6	40	Oligotrophic	-	1997, 2011, 2016	O & S
Your	164	5.1	20.8	Mesotrophic	-	2010, 2016	O & S

*Indicates a lake invaded by *Bythotrephes cederströmii*

O – spatio-temporal model including all data; S – spatial model including contemporary data (2000-2018) while excluding pre-invasion data; T – temporal model including only invaded waterbodies with pre- and post-*Bythotrephes* invasion data

Table 3.2 Linear mixed effects model comparisons to evaluate the significance of fixed and random effects using maximum likelihood-ratio test.

Models being compared	Effect being tested
YOY length ~ <i>Bythotrephes</i> invasion + GDD + Waterbody size + Trophic status + Maximum waterbody depth + (1 Waterbody ID) + (1 Birth year) YOY length ~ GDD + Waterbody size + Trophic status + Maximum waterbody depth + (1 Waterbody ID) + (1 Birth year)	<i>Bythotrephes</i> invasion
YOY length ~ <i>Bythotrephes</i> invasion + GDD + Waterbody size + Trophic status + Maximum waterbody depth + (1 Waterbody ID) + (1 Birth year) YOY length ~ <i>Bythotrephes</i> invasion + Waterbody size + Trophic status + Maximum waterbody depth + (1 Waterbody ID) + (1 Birth year)	GDD
YOY length ~ <i>Bythotrephes</i> invasion + GDD + Waterbody size + Trophic status + Maximum waterbody depth + (1 Waterbody ID) + (1 Birth year) YOY length ~ <i>Bythotrephes</i> invasion + GDD + Trophic status + Maximum waterbody depth + (1 Waterbody ID) + (1 Birth year)	Waterbody size
YOY length ~ <i>Bythotrephes</i> invasion + GDD + Waterbody size + Trophic status + Maximum waterbody depth + (1 Waterbody ID) + (1 Birth year) YOY length ~ <i>Bythotrephes</i> invasion + GDD + Waterbody size + Maximum waterbody depth + (1 Waterbody ID) + (1 Birth year)	Trophic status
YOY length ~ <i>Bythotrephes</i> invasion + GDD + Waterbody size + Trophic status + Maximum waterbody depth + (1 Waterbody ID) + (1 Birth year) YOY length ~ <i>Bythotrephes</i> invasion + GDD + Waterbody size + Trophic status + (1 Waterbody ID) + (1 Birth year)	Maximum waterbody depth
YOY length ~ <i>Bythotrephes</i> invasion + GDD + Waterbody size + Trophic status + Maximum waterbody depth + (1 Waterbody ID) + (1 Birth year) YOY length ~ <i>Bythotrephes</i> invasion + GDD + Waterbody size + Trophic status + Maximum waterbody depth + (1 Birth year)	Waterbody ID
YOY length ~ <i>Bythotrephes</i> invasion + GDD + Waterbody size + Trophic status + Maximum waterbody depth + (1 Waterbody ID) + (1 Birth year) YOY length ~ <i>Bythotrephes</i> invasion + GDD + Waterbody size + Trophic status + Maximum waterbody depth + (1 Waterbody ID)	Fish birth year

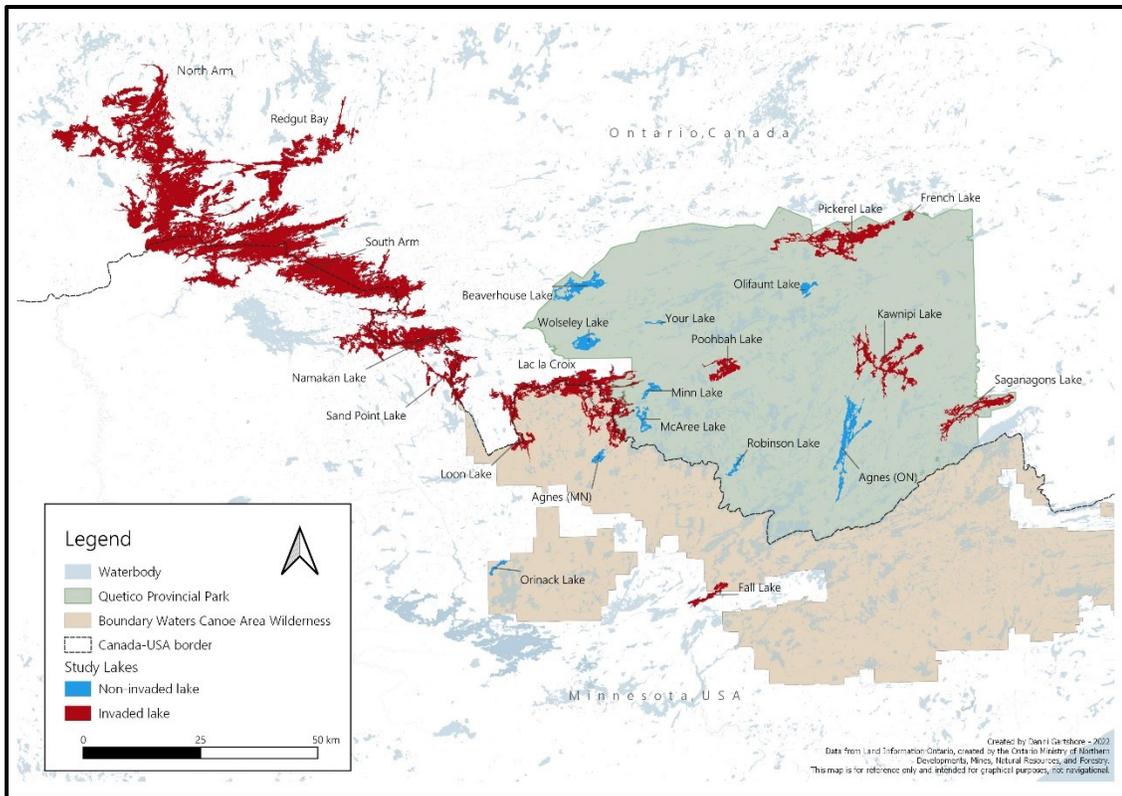


Fig. 3.1 A map of the waterbodies included in this study with *Bythotrephes cederstroemii* invaded (red) and non-invaded (blue) waterbodies highlighted, as well as Quetico Provincial Park (green) and Boundary Waters Canoe Area (BWCA) (beige). The three basins of Rainy Lake are labelled (North Arm, Redgut Bay, and South Arm).

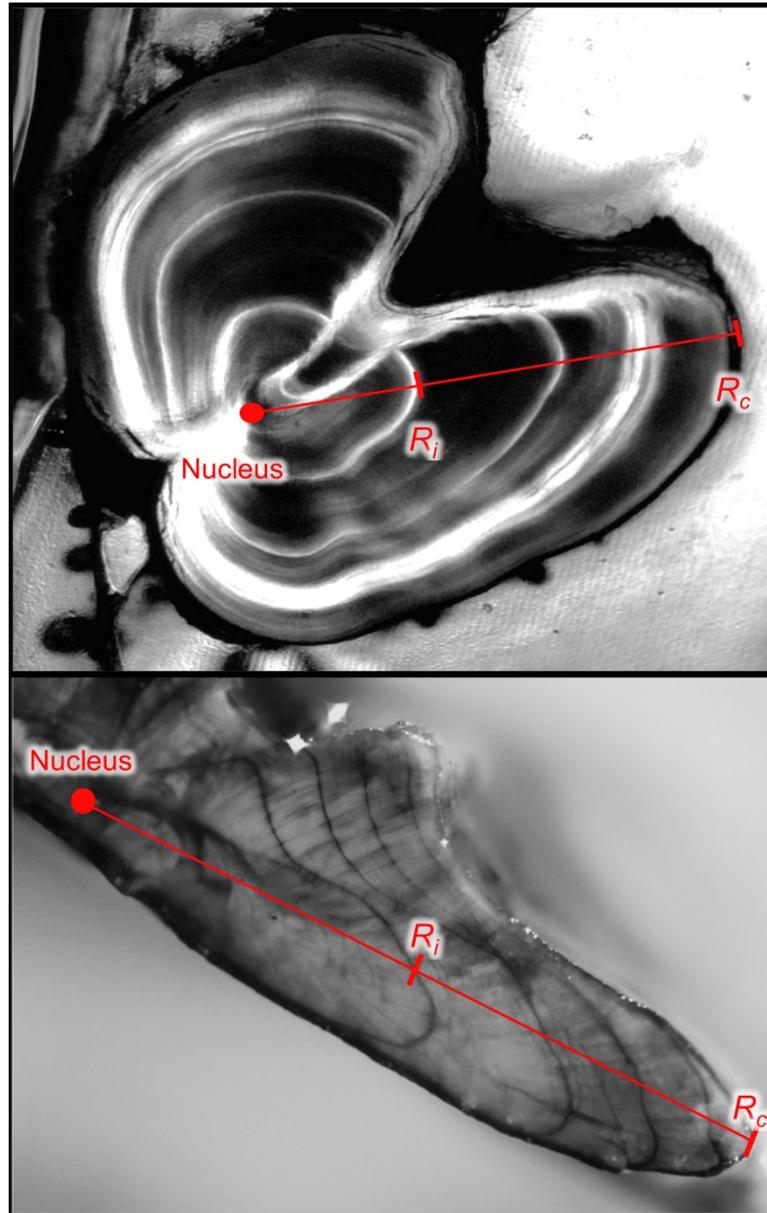


Fig. 3.2 Walleye (*Sander vitreus*) ageing structure axis examples for both a dorsal spine (top) and an otolith (bottom). The distance between the nucleus and 1st annulus (R_i) is the radius of the ageing structure at the end of the fish's first year of growth (Watkins and Spencer 2013). The distance between the nucleus and the edge of the ageing structure (R_c) is the radius of the structure at the time of capture.

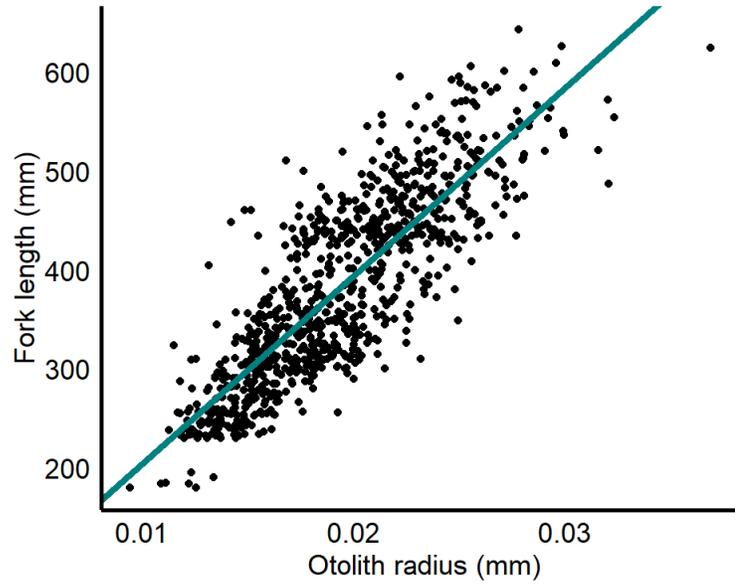


Fig. 3.3 Linear relationship between fork length and otolith radius of walleye (*Sander vitreus*), used in the Biological Intercept model for back-calculations (see text).

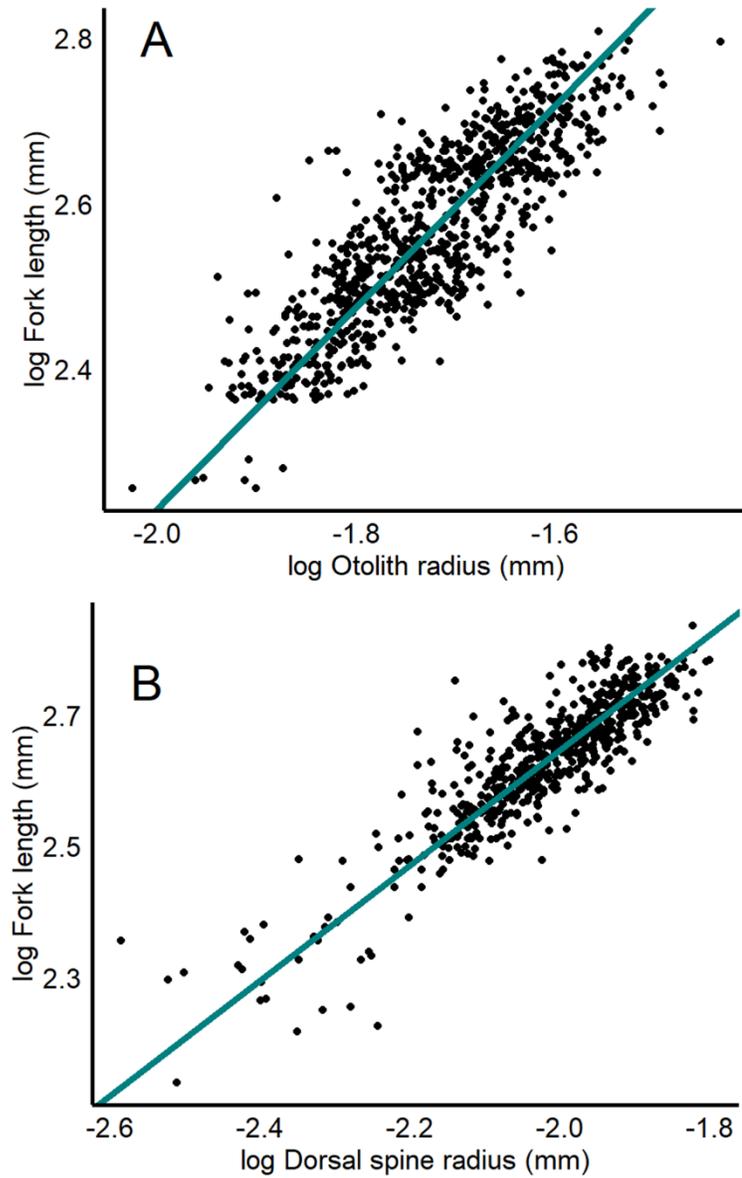


Fig. 3.4 Allometric functions on a log-log scale of ageing structure radius at capture and walleye (*Sander vitreus*) fork length at capture, using either otoliths (A) or dorsal spines (B), used in the Monastrasky Body-Proportional Hypothesis model for back-calculations (see text).

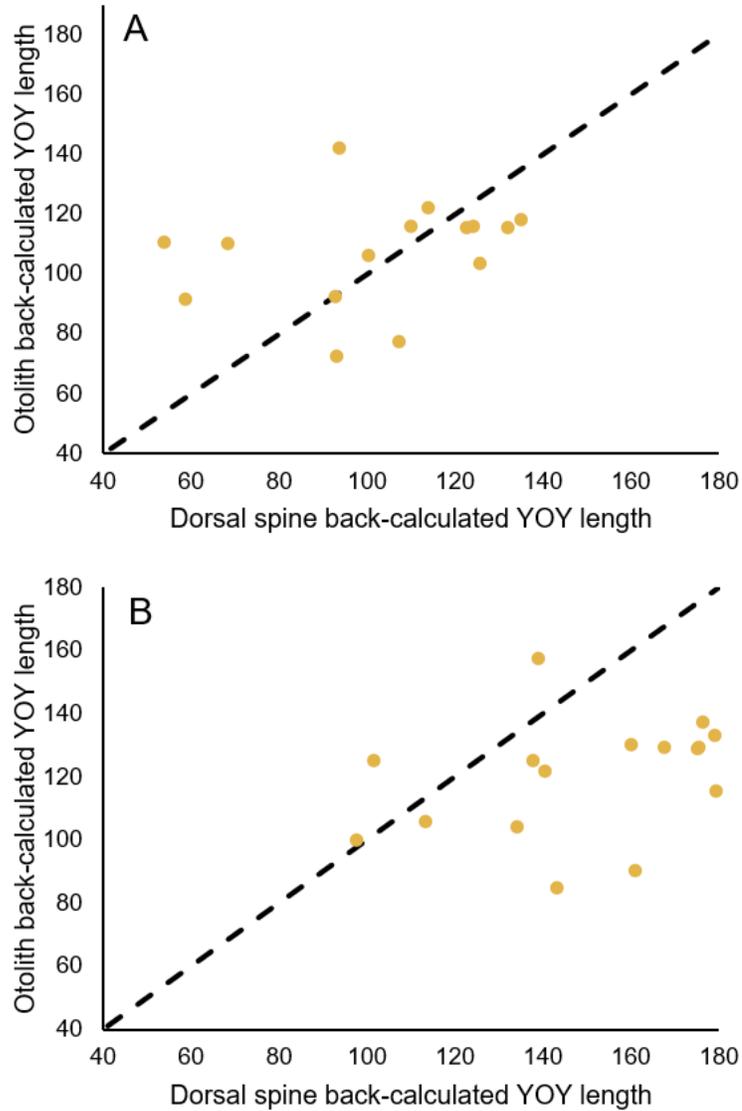


Fig. 3.5 Back-calculated young-of-year (YOY) walleye (*Sander vitreus*) fork length (mm) estimated through the Biological Intercept method (A), or the Monastrasky Body-Proportional Hypothesis method (B) compared using dorsal spines or otoliths as ageing structures from the same fish with an overlaid to a 1:1 line (dashed line) for reference.

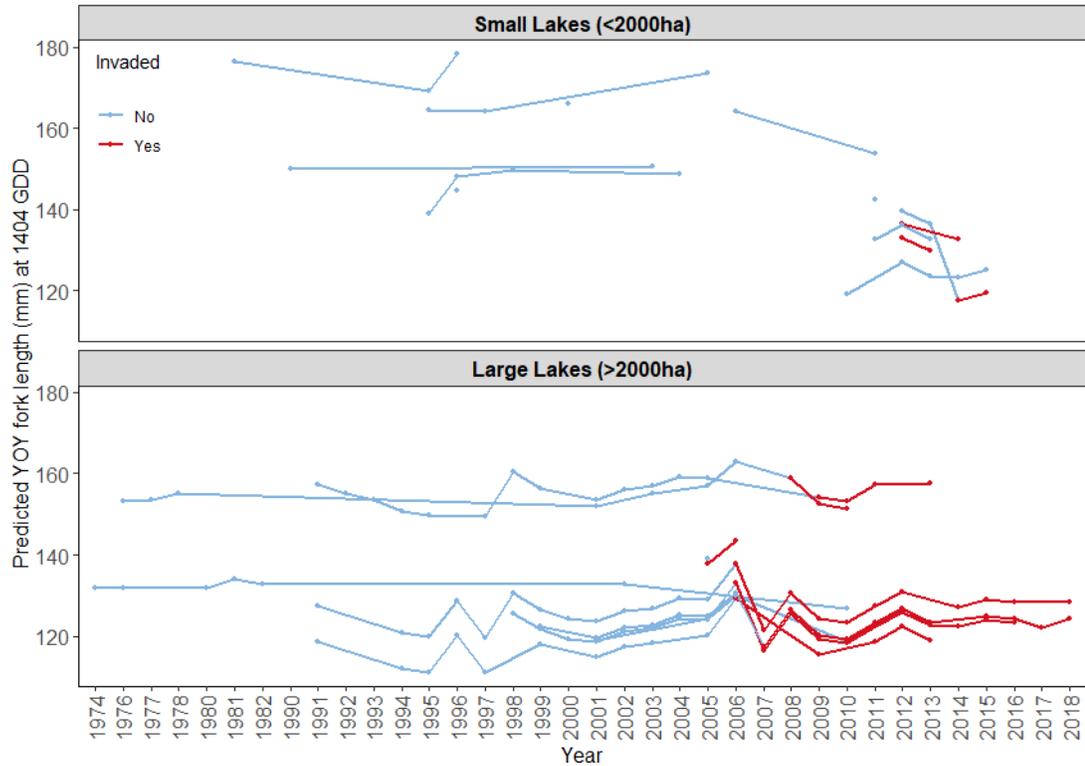


Fig. 3.6 Spatio-temporal trends of young-of-year (YOY) walleye (*Sander vitreus*) fork length predicted through a linear mixed effects model from 23 waterbodies in northwestern Ontario and Minnesota. YOY walleye were present in waterbodies either invaded (dark red) or non-invaded (light blue) by *Bythotrephes cederströmii* (each connected line or floating point represents one waterbody). Lengths are scaled to a standardized growing degree day (GDD, base 5°C) of 1404.

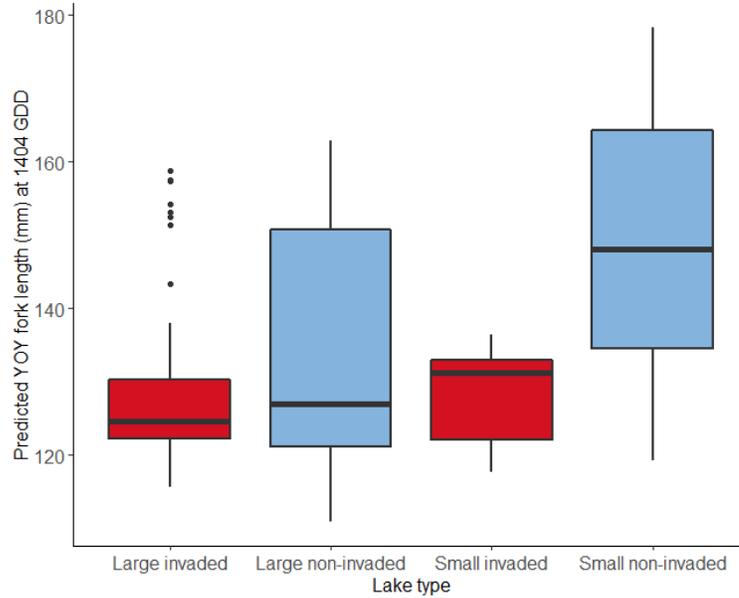


Fig. 3.7 Spatio-temporal trends of young-of-year (YOY) walleye (*Sander vitreus*) fork length predicted through a linear mixed effects model from 23 waterbodies in northwestern Ontario and Minnesota. YOY walleye were present in waterbodies either large (>2000ha) or small (<2000ha) waterbodies, invaded (dark red) or non-invaded (light blue) by *Bythotrephes cederstroemii*. Lengths are scaled to a standardized growing degree day (GDD, base 5°C) of 1404.

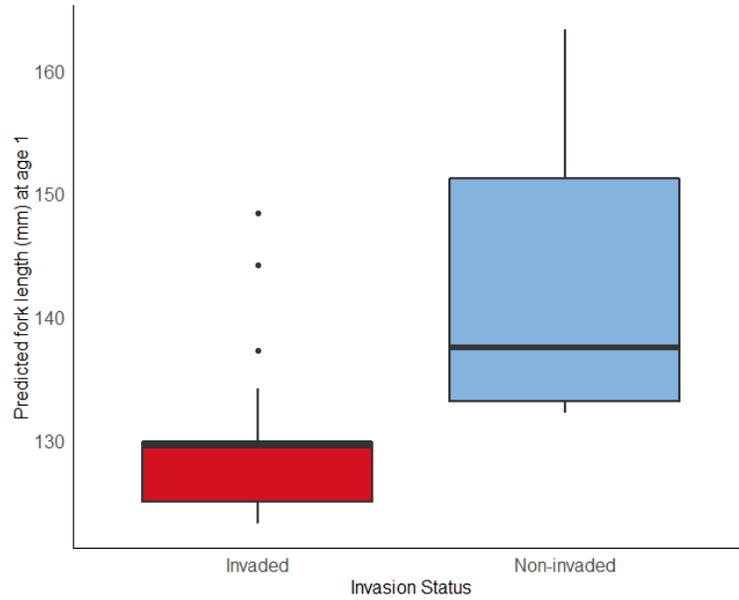


Fig. 3.8 Contemporary (2000-2018) spatial trends in back-calculated young-of-year (YOY) walleye (*Sander vitreus*) length predicted from a linear mixed effects model standardized to 1404 growing degree days (GDD, base 5°C) in 22 study waterbodies (pre-invasion observations removed) invaded (dark red) or non-invaded (light blue) by *Bythotrephes cederstroemi*.

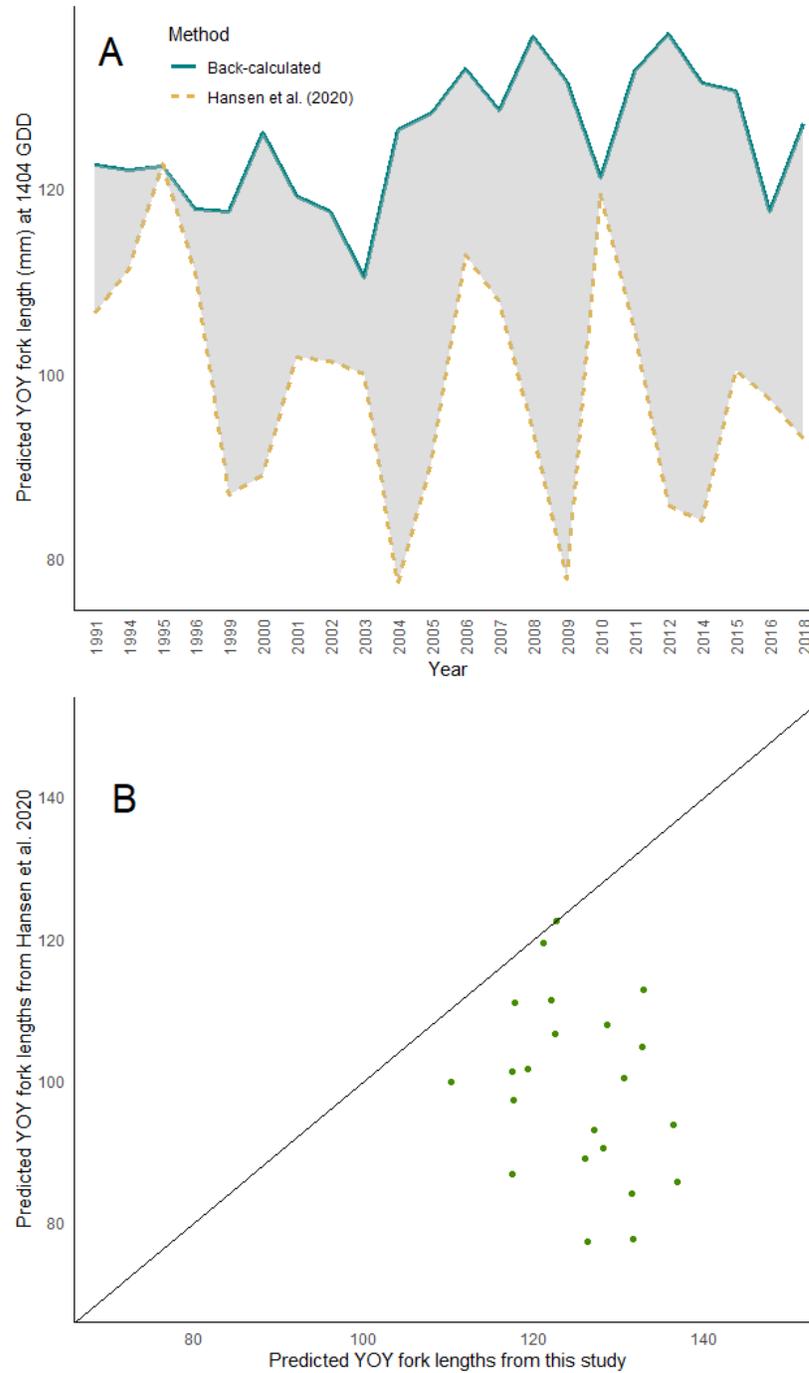


Fig. 3.9 A comparison of predicted young-of-year (YOY) walleye (*Sander vitreus*) lengths scaled to a standardized 1404 growing degree day (GDD, base 5°C) in the South Arm of Rainy Lake, using back-calculation methods from adult fish and correcting them for annual climatic variation or measuring YOY walleye in the field and correcting them for annual climatic variation drawn from Hansen et al. (2020). **A** – difference (shaded area) in YOY length estimates between methods annually; and **B** – 1:1 relationship in YOY walleye length estimates between methods.

Chapter 4: Synthesis

In this thesis, I evaluated the impacts of the invasive *Bythotrephes* on the growth rates of the culturally and economically important walleye during their zooplanktivorous phase. Using a bioenergetics modelling approach, my results highlight a probable mechanism for young walleye growth declines via food limitation due to competition with *Bythotrephes* considering different lake trophic states. Although a similar bioenergetics model has been used before (McDonnell and Roth 2014; Kosmenko 2015), this is the first time it has been tailored to evaluate the impacts *Bythotrephes* has on YOY walleye growth explicitly. Using the spatio-temporal data of back-calculated YOY walleye lengths, this study evaluated covariates (e.g., waterbody size, GDD, etc.) in order to reveal trends that would have otherwise been masked if covariates were ignored, or if only a temporal analysis was conducted. Then, to evaluate whether YOY walleye are impacted by *Bythotrephes* invasions in some lakes with high fishing pressure, and in some lakes less subject to anthropogenic impacts, I back-calculated YOY walleye size-at-age and compared fish growth rates over time within waterbodies before and after *Bythotrephes* invasion, as well as among waterbodies with and without *Bythotrephes* considering potential climate drivers (e.g., GDD) as a covariate. I found that YOY walleye may be growing slower in small, *Bythotrephes* invaded waterbodies, however factors associated with the large waterbodies in this study such as fishing pressure may be buffering the impact of *Bythotrephes* invasions on YOY walleye growth. This study provides novel insights due to the predominance of relatively unimpacted waterbodies in my study systems (i.e., lakes from Quetico Provincial Park and the Boundary Waters Canoe Area), allowing me to evaluate the impacts of *Bythotrephes* on the growth of YOY

walleye with minimal human intervention (e.g., heavy fishing pressure, walleye stocking, and water level management) compared to other studies which included large waterbodies with relatively high anthropogenic influence (Staples et al. 2017; Hansen et al. 2020).

In the first data chapter (chapter two), I found that larval walleye were shown to grow slower in invaded waterbodies due to *Bythotrephes* induced decreased prey availability, regardless of lake trophic state. Specifically, in invaded mesotrophic waterbodies, YOY walleye showed decreased consumption as well as slower growth compared to non-invaded mesotrophic waterbodies. In invaded oligotrophic waterbodies, larval walleye showed extremely low consumption, and were predicted to not survive on the available zooplankton alone. In the second data chapter (chapter three), I found that YOY walleye grew 13% slower in small, invaded waterbodies compared to small non-invaded waterbodies, whereas YOY walleye in large waterbodies grew only 3 % slower and were therefore less severely impacted than in small waterbodies. The results from chapter two provide a theoretical mechanism for trends reported elsewhere (Staples et al. 2017; Hansen et al. 2020), and for trends revealed in chapter three, such that observed larval walleye growth decreases in small waterbodies may be due to *Bythotrephes* induced lower zooplankton abundance. However, in chapter three, YOY walleye showed less severe impacts in response to *Bythotrephes* in large waterbodies. In summary, the bioenergetics model (chapter two) conclusions provide a mechanism for the decreases in YOY walleye growth predicted from the linear mixed effects model from chapter three.

In chapter two, I found waterbody trophic status influenced YOY walleye growth whereas in chapter three I found trophic state to not be a significant factor. In chapter

two, the bioenergetics model predicted the zooplankton density available for larval walleye forage in *Bythotrephes* invaded oligotrophic waterbodies was insufficient to sustain larval walleye growth. However, in chapter three, trophic state was excluded from all linear mixed effects models, and YOY walleye had stable growth rates pre- and post-invasion in some oligotrophic waterbodies. For example, all three basins of Rainy Lake as well as Namakan and Sand Point Lake are invaded by *Bythotrephes* and are oligotrophic (Christensen and Maki 2015), however they sustain healthy walleye populations. The reason for the discrepancy between chapters may be first due to the prey availability estimates in the bioenergetics model in chapter two were solely based on preferred prey items for the first month of feeding (cyclopoids, calanoids, and *Daphnia* sp.; Houde 1967). This may be imprecise as larval walleye have shown to consume other prey items such as chironomids (Hoxmeier et al. 2004), which are not known to be impacted by *Bythotrephes* invasions. As such, a holistic bioenergetics model would include more length-dependent diet shifts to other species such as chironomids. The second reason for the discrepancy between chapters may be due to the methods for attaining trophic state, as each lake was classified based on differing metrics (i.e., TP, Secchi depth) from varying time periods and sources. Lastly, most of the waterbodies in chapter three were oligotrophic, the remaining were either mesotrophic or unclassified and not distributed evenly across invasion states (Table 3.1), suggesting trophic state as a variable may have weak statistical power and therefore little influence on model-predicted growth trends. Although the significance of trophic state differed between chapters, the trends revealed from each chapter remain strong and helped to achieve the main objective of evaluating the impacts of *Bythotrephes* on the growth of YOY walleye.

In addition to trophic status, this study revealed that waterbody size may be influencing YOY walleye growth rates and how they are impacted by *Bythotrephes* invasions. In chapter 3, I found that YOY walleye in large waterbodies were less impacted by *Bythotrephes*. Food-chain length has shown to increase with ecosystem size (Post et al. 2000), suggesting large waterbodies may have higher food-web complexity than smaller waterbodies. Food-web complexity can act as a buffer to environmental disturbances through the ability of adaptive foragers to reconstruct the food web (Kondoh 2003). With higher food-web complexity, it is possible that food-web dynamics in large waterbodies were not severely impacted by *Bythotrephes* invasions. In addition, large waterbodies tend to have higher resource availability, habitat diversity and therefore species richness (Tonn and Magnuson 1982). Large waterbodies in this study may have higher zooplankton species richness and therefore more prey alternatives for YOY walleye. As zooplankton species information was not available for this study, I believe this could have provided insight into how reduced prey species richness associated with waterbody size influences the severity of impacts that *Bythotrephes* has on YOY walleye growth.

Back-calculated lengths from this study were consistently larger than the measured lengths corrected for thermal growth from Hansen et al. (2020), possibly due to differences in cohort sampling (YOY vs. adults). In addition, Hansen et al. (2020) typically found 12 % slower YOY walleye growth in large, invaded waterbodies whereas this study found just 3% slower growth. When comparing findings between studies, it is important to note that Hansen et al. (2020) captured and measured the YOY fish that existed in the year they were collected. Measuring YOY fish growth in the field may not

be a good predictor of adult size as ~90% of YOY fish will be lost due to size-selective winter mortality in their first year (Post and Evans 1989; Johnson et al. 1996). By contrast, back-calculating YOY size suggests I am evaluating the size of the remaining ~10% of surviving individuals of their cohort, which in this study were likely the larger individuals in a given cohort. Thus, many smaller walleye in the averages estimated by Hansen et al. (2020) would likely have been lost over winter and the largest/faster growing individuals survived to become adults and included in this study. Another study by Staples et al. (2017) further supports this by mentioning that although they found decreased YOY yellow perch growth post-*Bythotrephes* invasion, the MDNR reported catching 2-3 times more large-bodied yellow perch compared to pre-invasion surveys. This suggests that YOY fish may adapt faster growth after invasion as previously predicted because growth is inherently plastic (Lorenzen 2016), or that recruitment is not affected by the observed *Bythotrephes* impacts to growth. In summary, my approach is likely to be less sensitive in identifying growth trends among a YOY population, rather the trends revealed here have implications on *Bythotrephes* impacts to the small portion of YOY walleye within a cohort that survive to adulthood.

In small waterbodies, I observed slower YOY walleye growth in invaded systems, but because these were from back-calculations of surviving adults, the small portion of YOY walleye that survived to adulthood may have decreased growth. More so than from observed YOY size, this has major management implications regarding recruitment. It is well known that growth is a highly plastic trait (Lorenzen 2016), suggesting YOY growth is not a predictor of growth during later life stages. However, early life stage growth has been considered a population sink as it is correlated with YOY mortality (Oele et al.

2019), suggesting YOY walleye populations in invaded systems may have higher mortality compared to non-invaded systems or populations with higher YOY growth. Although growth may be subject to evolutionary effects through prolonged and size-selective harvesting pressure (Dunlop et al. 2007; Lorenzen 2016), it remains outside the scope of this study. Nonetheless, fisheries managers can use the information from this study to make informed management decisions in *Bythotrephes* invaded lakes such as identifying recruitment bottlenecks in YOY walleye populations and consider reducing harvest pressure, or stocking walleye fry beyond that life stage with the aim of circumvent the impacts of *Bythotrephes*.

The impacts that invasive species have on aquatic ecosystems is highly variable, making it difficult to predict their potential impacts to a newly invaded system. Theoretical frameworks for predicting impacts of invasive species have been developed, but with poor validation of hypotheses (Ricciardi et al. 2013). In addition, walleye growth is shown to be highly variable between systems based on GDD, prey availability, density dependence, lake characteristics such as Secchi depth, lake size, and maximum depth (Neuheimer and Taggart 2007; van Poorten and Walters 2016; Pedersen et al. 2018; Massie et al. 2021), some of which I was able to control for in the analyses conducted here (Chapter 3). A theoretical framework such as a decision tree can be created by uniting the diverse scientific work on aquatic invasive species and fish growth to predict the impacts that *Bythotrephes* may have to YOY walleye and further predict the health of fish populations based on lake ecosystem characteristics. With more data collected on fishing pressure, prey and competitor species, and more walleye data collected temporally in small, invaded waterbodies, we can better understand the variables

influencing the impact that *Bythotrephes* has on YOY walleye growth. Furthermore, we can create a decision tree for resource managers to classify waterbodies where walleye populations may be at risk if *Bythotrephes* invade or to predict YOY walleye growth trends in already invaded lakes. Theoretical frameworks and decision trees are beneficial for resources managers to determine trends that could be predicted based on lake characteristics, which would otherwise be timely and costly through field sampling, as well as allowing managers to make proactive changes to invasive species management to maintain the fisheries sustainability.

This research filled in various gaps in knowledge, and though I experienced many strengths and limitations in my methods, I remain confident in the general patterns. The data contained a large sample size of waterbodies and fish on both spatial and temporal scales, which gives me confidence in the findings in chapter two. However, I was unable to accurately evaluate the temporal trends in YOY walleye growth pre- and post-invasion in small waterbodies due to a sample size of one. In addition, most of the large, invaded waterbodies in chapter three experienced high fishing pressure with harvest size limits which, as previously mentioned, may influence YOY walleye growth by selecting for faster growing juveniles. A greater range of temporal data in small, invaded waterbodies as well as data in large waterbodies with low fishing pressure would benefit this analysis and is suggested for future research, however, finding such systems with existing data is challenging. Other studies evaluating the impacts of *Bythotrephes* on YOY walleye have had smaller sample sizes and have typically been conducted on large study waterbodies with intensive fisheries and management, including stocking (Staples et al. 2017; Hansen et al. 2020). In comparison, I had the ability to use many relatively unimpacted

waterbodies to determine *Bythotrephes* impacts to YOY walleye accounting for confounding variables (i.e., lake size, GDD) and included some waterbodies with high fishing pressure, giving me confidence in the results found in chapter three.

In summary, both chapter two and chapter three in this manuscript support the hypothesis that YOY walleye are growing slower in waterbodies invaded by *Bythotrephes*, and that this decline is most likely due to decreased prey availability. Collectively, the findings in this thesis suggest this relationship may differ based on both waterbody size and trophic state. With known waterbody characteristics, findings in this study can provide resource managers with guidelines for expectations on the current or potential impact that *Bythotrephes* may have on walleye populations to make well-informed decisions for their fisheries.

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Appendix A.

To avoid net-selectivity for fast-growing fish, I created catch curves by gear type to determine fully recruited size classes of walleye. Walleye used in this study were sampled by various organizations with varying gear types such as gill nets, trap nets, creel sampling, and mixed net methods. For each gear type, I created a catch curve and used the peak catch as the lower threshold for fish selection (Table A1; Smith et al. 2012). For example, Fall Walleye Index Netting (FWIN) surveys in Ontario are sampled with overnight multi-mesh gill nets and the peak catch of samples available for this study was between 250-300mm (Figure A1; Government of Ontario 2020). Therefore, fish ≥ 301 mm were considered fully recruited to the gear and used as the lower threshold when selecting walleye from FWIN surveys to be used in this study.

Table A1. Walleye fork lengths used as the lower threshold when selecting walleye to be used in this study estimated as peak catch through catch curves based on gear type.

Gear type	Lower threshold
Gill nets	301mm
Trap nets	381mm
Creel surveys (public)	421mm
Minnesota Department of Natural Resources (mixed methods)	231mm

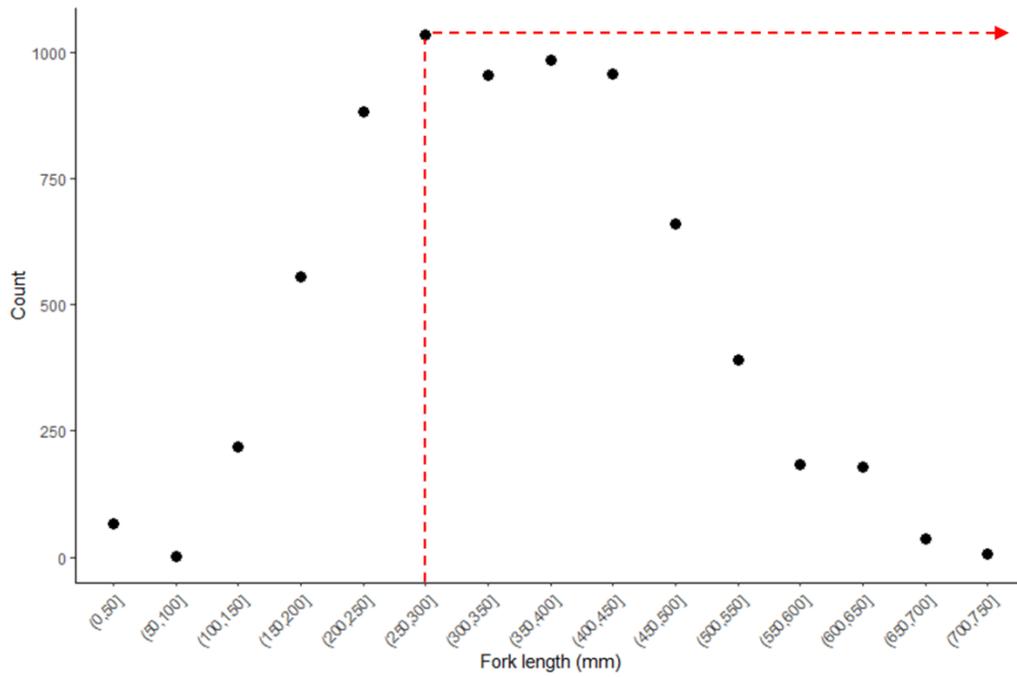


Figure A1. Frequency distribution of walleye caught during the Ontario Fall Walleye Index Netting program in various lakes within Quetico Provincial Park, ON. The size greater than peak catch signifies the lower threshold of walleye fully recruited to the sampling gear included in this study and is indicated by dashed line and arrow which in this example is a fork length of 301mm.

Appendix B.

I determined the number of samples required to accurately back-calculate the size-at-age and growth rate for a certain year. To do this, I back-calculated size-at-age 1 for the walleye in a randomly selected lake (Lac la Croix) and determined the coefficient of variation (CV) within the mean fork length at various sample sizes. I found that a minimum sample size of 6 fish per year class achieves a coefficient of variation $\leq 5\%$ in my back-calculations (Fig. 2.7). Therefore, a lake or survey was excluded from this study if there were fewer than 6 individual walleye ageing structures available for any year class.

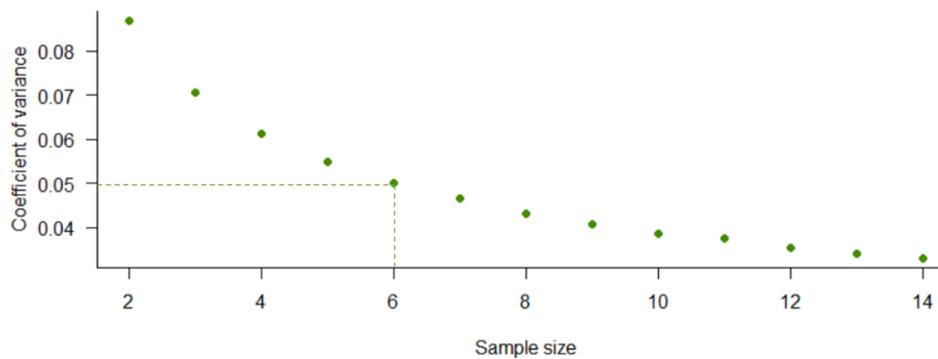


Fig. B1 Coefficient of variation for various sample sizes of mean back-calculated size-at-age 1 for walleye from Lac la Croix, Ontario. A relative error of $<5\%$ can be achieved by using a sample size of 6 or more.

Appendix C.

Data acquired from the Minnesota Department of Natural Resources (MDNR) included fish total length, whereas I used fork length. I created a Model I regression between fork length (FL) and total length (TL) using existing data from Quetico/Ontario to predict the fork length for each fish sample acquired from the MDNR. Examinations of diagnostic plots indicated that residuals were normally distributed, and that variance of error terms was homogenous. Total length had a significant effect on fork length (linear regression, $F_{1,10146} = 3.18e+06$, $R^2 = 0.997$, $p < 0.0001$), and I can therefore use the resulting regression (equation A.5) as a predictive model for fork length (Fig. C1).

$$FL = -4.61 + 0.951 * TL \quad (A.5)$$

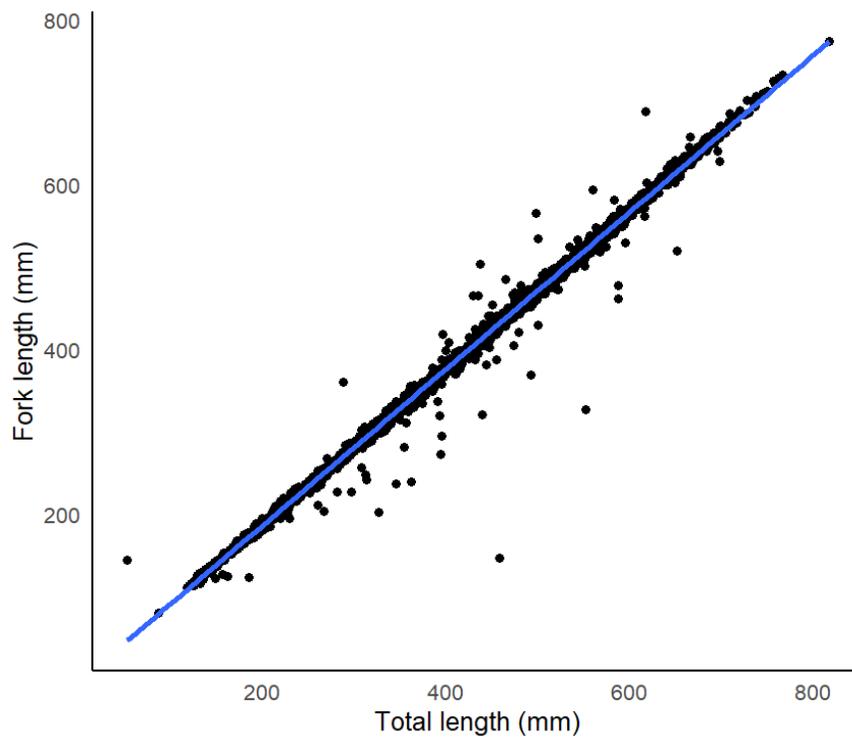


Fig. C1 Predictive linear model between fork length and total length of walleye.