

The Effects of Climate Change on the Growth and Spawning Phenology of Fishes in Aquatic
Boreal Environments

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Brenden David Slongo

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THESIS ABSTRACT

Global climate change is occurring and observed warming patterns have had significant impacts on aquatic environments as trends in water temperature are closely related to trends in air temperature. In ectothermic organisms such as fishes, temperature is relevant to the maturation and deposition of gametes during spawning, and lifetime growth potential. By using historical spawning and size at age datasets spanning 43 years, I estimated more than 100 peak spawning dates for White Sucker (*Catostomus commersonii*) and Lake Trout (*Salvelinus namaycush*) and described changes in growth of White Sucker to summarize the observed effects that local climate warming over the past 50 years has had on two economically and culturally important fishes in Northwestern Ontario. I show how spawning events are dependent on annual variation in seasonal thermal conditions, and how long-term increases in average fall surface water temperatures by 1.4°C and decreases to thermal cooling by $87^{\circ}\text{C}\cdot\text{days}$ in lakes have shifted the peak spawning date of Lake Trout by 5 days over the past 4 decades. Additionally, I show how changes in population density, likely as a result from increased survival and recruitment of juvenile White Suckers have worked to dramatically reduce the body size of White Sucker by over 90% in weight and 50% in length in some populations. Finally, I discovered that declining White Sucker body size appears to be a common pattern across an expansive geographic range. These results fill knowledge gaps in the current literature by providing observational accounts of climatic impacts to inland fish populations for a highly studied culturally significant species, and for a lesser considered, but ecologically important species.

LAY SUMMARY

Global climate change over the past 150 years as a result from human activity has and will continue to cause rapid temperature warming across the planet. Temperature is a vitally important metric in the environment, capable of governing many different processes in living and non-living things. For living creatures such as fish, their body temperatures are determined by the temperature of their environment and climate warming may have a large negative impact on their ability to survive and thrive in the environment. Fish carry important economic and cultural values in human society, thus understanding how they respond to the effects of climate change is critically important. I discovered that seasonal thermal conditions of a given year were highly important in the timing of spawning to White Sucker in the spring and Lake Trout in the fall; warmer fall seasons have changed the average time at peak spawn in Lake Trout by 5 days over the past 40 years. I also found that White Sucker over the past 4 decades are much smaller than they used to be, where some populations are more than 90% lighter today than in the 1980's. The reason for smaller fish seems to be a result of higher population sizes. Additionally, smaller White Sucker over time were found in several other lakes across Northwestern Ontario, suggesting this pattern may be representative of a regionally occurring pattern.

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Chapter 1 General Introduction

Over the next several decades, climate change is expected to become the greatest threat to global biodiversity at all levels of biological organization (Bellard et al. 2012). Indeed, the global climate has changed dramatically over the past century; global atmospheric temperature and carbon dioxide levels are two metrics of climate change that illustrate the significant changes our earth has experienced since 1880. At the time of writing, the average global temperature is 1.01°C warmer than 1880, and atmospheric carbon dioxide levels are at 418 parts per million (ppm), which is significantly higher than any recorded or predicted value across the past 800 000 years. Despite global efforts to mitigate carbon emissions, future global temperatures will continue to rise with the only uncertainty being in the magnitude of the increase (Masson-Delmotte et al. 2018).

As a consequence of a warming climate, surface water temperatures have also risen globally, as the temperature of air and surface water are closely related (Matuszek and Shuter 1996; Livingstone and Lotter 1998). Oceanic environments over the past 25 years have warmed at an average rate of 0.13°C per decade with some locations warming at 4 times this rate (Belkin 2009). On average, global summer surface water temperatures in freshwater lakes have warmed by 0.34°C per decade between 1985 – 2009, with the fastest lakes warming at an alarming 1.3°C per decade (O’ Reilly et al. 2015; Woolway et al. 2020). In northeastern North America, summer surface waters have warmed by 0.54°C per decade since 1975 (Richardson et al. 2017). A meta-analysis of 19 studies further support the notion that surface water temperatures are increasing; regional distributions of lakes are warming more intensely than global distributions, though individual lake warming trends are highly variable (Richardson et al. 2017).

Parameters describing lake habitat are also responsive to the local climate and have demonstrated changes in the face of current warming trends. Thermoclines can structurally change via faster epilimnetic warming and fluctuating dissolved organic carbon (DOC) inputs (Schindler et al. 1996; King et al. 1997; Rennie et al. 2009; Richardson et al. 2017). Where more intense epilimnetic warming occurs, stratification gradients intensify causing shallower thermoclines; alternatively, reductions in DOC inputs due to reduced precipitation can alter water clarity and therefore light penetration, causing deeper thermoclines. Lake stratification is also increasing in duration by spring and or fall warming which is promoting the development and prevalence of hypoxic lake bottoms (King et al. 1997; Poff et al. 2002; Guzzo and Blanchfield 2017). In addition, longer stratification can restrict access for certain fish species to energy rich littoral regions during the open water growing seasons (King et al. 1999; Guzzo et al. 2017).

Fish populations residing within lakes stand to be affected in several ways via changes to the quality and quantity of the lake's habitat. Spatially, volume reductions of key cold-water fish habitat will occur via reductions to hypolimnetic oxythermal habitat (Shuter and Meisner 1992; Guzzo and Blanchfield 2017). As thermoclines fluctuate from DOC inputs, which are partly governed by precipitation cycles (Schindler et al. 1996) and prolonged stratification promotes hypoxic lake bottoms, oxythermal habitat of the hypolimnion stands to shrink, potentially triggering a density-dependent response that can alter population and size structure of a species.

Temporally, changes to the timing of thermocline establishment will affect energy acquisition and timing of important biological events for fishes. Prolonged stratification can restrict access to portions of the lake for some fish species, where early development of the thermocline acts as a natural barrier, preventing movement into energy rich littoral zones and

posing strains on internal energetic demands (King et al. 1999; Guzzo et al. 2017). Accelerated warming of the shoulder seasons can also impact timing of spawning in fishes (Wedekind and Küng 2010; Farmer et al. 2015; Lyons et al. 2015). Spawning phenology is largely governed by two cues, photoperiod and temperature (Pankhurst and Porter 2003; Pankhurst and King 2010; Pankhurst and Munday 2011). While photoperiod plays a modulating role to hormones involved in gonadal development, temperature acts more acutely, aligning optimal environmental conditions with the precise timing of gamete maturation. Where photoperiod regimes will remain relatively constant for lakes, changes in surface water temperatures during spring and fall spawning seasons may impact the precise timing of spawning, potentially leading to egg deposition at suboptimal times and emergence mismatches with vital larval prey sources (Casselman 1995; Winder and Schindler 2004; Thackeray 2012).

Lastly, physiological consequences to fishes are widely expected from altered quality and quantity of aquatic habitat, but the expression of this effect is strongly debated. Undoubtedly, increased epilimnetic temperatures and prevalence of hypoxic conditions will pose metabolic strains on ectothermic fish communities, primarily expressed as a reduction in individual body size (Baudron et al. 2014; Guzzo et al. 2017; Audzijonyte et al. 2020 and others). Trends of reducing body size in conjunction with rising temperatures are well supported across many marine and freshwater taxa which has led to the proposal of the Temperature-Size Rule (TSR) as an overarching mechanism to explain the physiological response of fish (Atkinson 1994; Daufresne et al. 2009; Audzijonyte et al. 2019). While the TSR states that the individual body size of ectotherms tends to decrease with increasing temperatures (Atkinson 1994), the underlying mechanism driving this rule remains poorly understood. One explanation considers that metabolic rates of ectotherms are highly dependent on the body size, and the temperature of

their environment (Brown et al. 2004; Woodward et al. 2010). Other explanations have been based on individual oxygen demand, as oxygen solubility in water is known to scale negatively with warmer temperatures (Harvey et al. 2011). Oxygen may be a limiting factor to size and is hypothesized to occur either by “gill oxygen limitation” (GOL; Pauly 1981), “maintain aerobic scope and regulate oxygen supply” (MASROS; Pörtner et al. 2017), or “oxygen and capacity limited thermal tolerance” (OCLTT; Atkinson et al. 2006). These three mechanisms are fundamentally similar as they are based on the notion that oxygen demand outpaces the uptake ability at larger body sizes, and where dissolved oxygen content will be reduced and metabolic demand will be increased at higher temperatures, oxygen demand will outpace uptake ability more intensely, leading to asymptotic size reductions across many taxa (Audzijonyte et al. 2019). A challenge to both higher metabolic rates and oxygen limitation as a driver of TSR is the fact that when oxythermal habitat varies spatially, fish can behaviourally thermoregulate to minimize the effect on physiological function. Further, oxygen uptake can be regulated by fishes (Lefevre et al. 2018), which can also partially or fully negate the outpacing effect of demand on supply and uptake of oxygen (demand for oxygen increases, uptake ability also increases, supply is not-relevant) (Audzijonyte et al. 2019). Despite a lack of universal agreement to the underlying mechanisms of TSR, it remains a heavily cited concept to explain the physiological consequences to the body size of fish resulting from climate change.

Climate studies that attempt to predict future changes to the body size of fishes do so based on proposed underlying physiological mechanisms and complex models of ecological systems (Cheung et al. 2013; Lefort et al. 2015; Biswas et al. 2017) despite uncertainty within these mechanisms and models. This uncertainty makes them risky to use at best by resource managers (Planque 2016) and it is inherently difficult to assess the reliability of a projection

focused on changes in fish stocks even with the benefit of hindsight because of the projected period of time, and the assumptions used (Brander et al. 2013). For example, fishing mortality is reported to have an evolutionary effect on maturity in exploited stocks leading to similar size reductions (Zimmermann and Jørgensen 2015), yet this assumption is often excluded in projection models (Tu et al. 2018). Several of these projection papers have gone forward with citing climatic change alone as the sole driver of declines in fish size, despite investigating populations that support active fisheries (Cheung et al. 2013; Lefort et al. 2015; Limburg and Casini 2018). Where temperature and fishing mortality have both been considered as drivers in historically observed size declines of fish stocks, temperature driven reductions were witnessed but the majority of size reductions observed were related to fishing pressure, and the more significant climatic effect came from increased sensitivity of the populations to changes in their environment (Genner et al. 2010; Tu et al. 2018). The uncertainty stemming from these publications underlines the need for additional research regarding observed effects in unharvested populations to provide clearer evidence of the response of fishes to climate change (Lynch et al. 2016).

Two large-bodied fish species whose opposing life history qualities make them of interest for environmental monitoring programs investigating climate impacts are White Sucker (*Catostomus commersonii*) and Lake Trout (*Salvelinus namaycush*). White Sucker is a widely distributed, highly abundant, cool-water, spring spawning species (Scott and Crossman 1973). By contrast, Lake Trout is a northerly distributed, long-lived, cold-water, fall spawning species with uniquely specific oxythermal habitat requirements (Evans 2007; Guzzo and Blanchfield 2017). White Sucker rarely suffers from any significant sources of fishing mortality, meanwhile active recreational, commercial, and subsistence fisheries exist for Lake Trout throughout their

range. Finally, White Sucker has proven valuable in environmental effects monitoring, having been used as sentinels in oil sands and pulp mill effluent projects (Miller et al. 2013; McMaster et al. 2020)

The International Institute for Sustainable Development Experimental Lakes Area (IISD-ELA) is a collection of pristine boreal lakes situated east of Kenora, Ontario and is home to populations of both White Sucker and Lake Trout. For over 50 years, the ELA has functioned as a natural laboratory free of anthropogenic disturbances, making it an excellent setting in which to study the impacts of climate change on fish. Previous research has shown that the climate at ELA is changing, and numerous changes to ecosystems and the fishes they support have been observed (Schindler et al. 1990, 1996; Guzzo and Blanchfield 2017; Guzzo et al. 2017).

OBJECTIVES

The main objectives of this thesis were to evaluate White Sucker and Lake Trout for long-term trends (> 40 years) in spawning phenology and changes in historical White Sucker body size related to patterns of climate change observed at the ELA. I used in-field spawning data collected for both species to predict their peak spawning dates and assessed potential changes in peak spawning date over time in response to climate change. Additionally, I considered the linkage between spawning dates and thermal conditions of the spawning season to reveal how annual variation in thermal conditions can alter peak spawning dates.

To fulfil my second objective, I fit linear models to historical White Sucker body size data from the ELA to describe changes over time. I also fit linear models to historical body size data for populations across Northwestern Ontario and compared their response over time to the ELA White Sucker populations to evaluate the fish's utility as a sentinel species. For ELA populations of White Sucker, I sought to understand whether climate change affected body size

directly or indirectly using hierarchical partitioning on a collection of variables to predict the most likely causal factor to explain size at a given age.

Chapter 2 Shifts in spawning phenology of fishes associated with climate variation

ABSTRACT

Spawning phenology in fishes is a process heavily governed by environmental conditions. While photoperiod is the primary environmental cue, temperature is the secondary cue that aligns the final stages of maturation with optimal environmental conditions to ensure that deposited eggs have the best chance at survival. Given the importance of temperature in synchronizing active spawning, seasonal climate change may affect fish spawning schedules, and ultimately the survival of early life stages of fish. I estimated > 100 peak spawning dates for both White Sucker and Lake Trout across 8 populations from ELA lakes over 40+ years and evaluated changes to their spawning phenology over time. Additionally, I evaluated the impact of variability in surface water temperature, and seasonal cumulative growing (spring) and cooling (fall) degree days on peak spawning. I discovered a subtle but significant delay in Lake Trout peak spawning events by about 1 day/decade from 1978 to 2019, along with an increase in average fall temperature (1.4°C) and decrease in cumulative cooling degree days ($86.7^{\circ}\text{C}\cdot\text{days}$). While no temporal changes in spring conditions or peak spawning of White Sucker were observed, White Sucker spawned earlier in warmer springs when greater cumulative growing degree days $> 5^{\circ}\text{C}$ were experienced. Similarly, Lake Trout reached peak spawning later in warmer falls with fewer cumulative cooling degree days $< 20^{\circ}\text{C}$. These results demonstrate the importance of water temperature to spawning in fishes and suggest that this important life history event is susceptible to further manipulation from a continued warming climate.

Keywords: Boreal, Catostomidae, Climate Change, Fitness, Life History, Reproduction, Salmonidae

INTRODUCTION

The most recent climate evaluations suggest that earth's global temperature and atmospheric CO₂ content are at the highest levels seen in over 800 000 years, suggesting that future climate warming is inevitable despite society's future best efforts to mitigate carbon emissions in the near-term (Masson-Delmotte et al. 2018). Climate warming is a global phenomenon that often leads to warmer surface water temperatures of lakes (O' Reilly et al. 2015), but lake warming may occur heterogeneously both spatially and temporally (Guzzo and Blanchfield 2017), and may be more intense than global patterns regionally (Richardson et al. 2017). Due to the close association between atmospheric and surface water temperatures (Livingstone and Lotter 1998), important life history events in fishes cued by thermal conditions stand to be impacted with an evolving consensus of negative outcomes for fitness and recruitment (Pankhurst and Porter 2003; Pankhurst and Munday 2011).

Spawning is an important phenological event in the life cycle of fishes that is inextricably linked to environmental conditions. (Pankhurst and Porter 2003; Rogers and Dougherty 2019). Fish use two main environmental cues (photoperiod and water temperature) to initiate complex internal processes that stimulate gonadal development and incite behavioural changes that signify the start or end of the spawning season (Pankhurst and Porter 2003; Maitra and Hasan 2016). These cues are used in tandem and operate on different time scales. Where changes to baseline environmental conditions induced by climate change have already begun to significantly disrupt annual patterns, many species of fish of different life histories and ecosystems have been observed to shift their spawning schedules in accordance to the environmental change experienced (Warren et al. 2012; Lyons et al. 2015; McQueen and Marshall 2017). Such changes to this important life cycle event may negatively impact the development of embryos, as the egg

stage in fish is thought to be the most thermally sensitive life stage (Pankhurst and Munday 2011).

Photoperiod is regarded as the principle cue which dictates the initiation and broader seasonal phasing of reproductive development (Pankhurst and King 2010). The production and inhibition of melatonin, a hormone thought to be central in the control and regulation of spawning activity in fish (Maitra and Hasan 2016), is directly associated with light and dark cycles, providing fish with a physiological understanding of daylength and time of year (Pankhurst and Porter 2003). As daylength gradually rises and falls throughout the year, the secretion of melatonin inversely follows this trend, further triggering a reproductive response in fishes. Lab studies strongly suggest that significant manipulations to photoperiod regimes can shift timing of spawning much sooner or later than expected, however the effect of temperature has been poorly separated from these studies (Bromage et al. 2001). Under natural settings, photoperiod acts to gradually entrain populations to initiate reproductive development and further promotes maturation for a spawning event, but it does not explicitly control when gametes are deposited.

Temperature is regarded as the secondary cue that controls the precise timing of gamete maturation and deposition into the environment (Pankhurst and King 2010). Specifically, temperature controls the reaction rates of hormones where increases to temperature will promote hormone synthesis and activity to a point, after which further increases to temperature negatively affects activity of these hormones (Pankhurst and Munday 2011). In addition, higher temperatures can change protein shape and make steroids more water-soluble, reducing their ability to pass through cell membranes and increasing their potential for filtration through the kidneys (Pankhurst and Munday 2011). Through hormonal sensitivity, temperature can

synchronize the final stages of maturation to the ideal environmental conditions, ensuring gametes are deposited with the best chance for survival.

Laboratory studies investigating the effects that temperature has on fish physiology during spawning has discovered that reproductive hormones are sensitive to changes in thermal environment (Pankhurst and Munday 2011). These studies have demonstrated that deviations from optimal spawning temperatures produce an inhibitory effect on the spawning of fishes, whereby spawning is first promoted in spring spawners as water temperature rises to within a species-specific optimum spawning range, and then is terminated once a thermal threshold is exceeded. For fall spawners, the relationship is similar but inverted, where elevated water temperatures delays activity until the temperature declines below a specified threshold, at which point spawning is promoted and deposition of gametes can begin. As temperatures get colder and pass beyond a species optimum, spawning behaviours are again terminated.

Given that location-specific annual photoperiods are generally stable over time, changes in temperature brought about by climate change are the most likely contributor to the exact timing of the peak spawning window in fishes, and annual variability in thermal conditions are likely to be reflected in spawning patterns (Wedekind and Küng 2010; Pankhurst and Munday 2011; McQueen and Marshall 2017). It is expected that gradual increases to mean seasonal temperatures will shift spawning times earlier in spring spawning species or later in fall spawning species (Pankhurst and Munday 2011; McQueen and Marshall 2017; Rogers and Dougherty 2019). For example, a species such as Lake Trout which prefer to spawn at water temperatures approximately 10°C (Casselman 1995; Fitzsimons 1995), in theory, where warmer years cause delays to lake cooling and optimal spawning temperatures are achieved later in the season, spawning events may be delayed (Guzzo and Blanchfield 2017).

Climate-related change to the spawning phenology of fishes may lead to a cascade of fitness impairments at the population level (Zettlemoyer and DeMarche 2021). Elevated water temperatures and unfavourable environmental conditions may result in reduced reproductive success (Pankhurst and King 2010). Though warmer water temperatures during incubation expedite developmental rates (Pankhurst and Munday 2011), greater amounts of cumulative thermal exposure largely driven by more thermal exposure during the fall season has been shown to significantly reduce successful hatch rates of Lake Trout eggs to the larval fry stage (Casselman 1995). Warmer conditions during egg development can lead to the earlier emergence of fry which may expose them to initially suboptimal conditions, such as maladaptive temperatures and increased predation (Skoglund et al. 2011). Alternatively for a spring spawning species, incubation at temperatures just 2°C greater than optimal White Sucker egg development temperatures can significantly reduce hatching success (McCormick et al. 1977). Assuming for a moment that there is no limitation in resource availability, early emergent larval fishes that survive initial conditions may be rewarded by faster spring warming as this will aid in faster growth and achievement of the next life stage (Pankhurst and Munday 2011). Later-emerging larval fishes will be disadvantaged from competitive interactions and density dependence versus the early emergent survivors (Skoglund et al. 2011).

Underpinning the potential intra-specific emergent scenarios is the dynamic between the blooms of primary producers and consumers, and how they align in relation to fry emergence. Often thought of as a temporal mismatch where different environmental cues initiate blooms of phytoplankton or zooplankton (Winder and Schindler 2004; Vadadi-Fülöp et al. 2012), the mismatch is actually a result of a shift in the predator-prey dynamic between producer and consumer, where peak abundances are a function of time-lags and biomass transfer from one

trophic level to the next (Thackeray 2012). Further, the effects of climate change and increasing temperature can exacerbate time-lags in this dynamic by affecting overwinter survival, community/ size structure, egg emergence phenology, and other life history traits (Winder and Schindler 2004; Vadadi-Fülöp et al. 2012; Thackeray 2012; Hébert et al. 2021). An increase or decrease to the time-lag between phytoplankton and zooplankton may desynchronize the timing of blooms of prey from emergence of fry, and/or create scarcity of biomass resources, leading to increased competition, starvation, and ultimately reduced recruitment success of the fry (Pankhurst and Munday 2011)

Boreal shield lakes in Northwestern Ontario support abundant large and small bodied fish communities of various species, including the White Sucker and Lake Trout. White Sucker is a widespread, cool-water, spring-spawning species, whereas Lake Trout is a more northerly distributed, cold-water, fall-spawning species (Scott and Crossman 1973). Both species have been monitored in designated research lakes for decades, providing an opportunity to explore long-term effects of climate change on the timing of peak spawning events in these two species with differing spawning strategies. The average seasonal air temperature in Northwestern Ontario between September to November has increased by nearly 1.7°C since 1970, but no significant change in March to May temperatures has been observed (Guzzo and Blanchfield 2017), indicating that climatic effects temporally have occurred heterogeneously. The principal objective of this chapter was to assess shifts in the spawning phenology of White Sucker and Lake Trout. Given that spawning events in shallow waters of lakes are more likely to be determined by temperature than photoperiod, I would expect to see spawning events being driven by changes in water temperature. Further, due to unequal climate warming between spring and fall seasons in Northwestern Ontario, I hypothesize that Lake Trout spawning phenology may

have shifted but White Sucker spawning phenology may not have, compared to historic spawning schedules.

METHODS

Study Site

This study used long-term data from eight lakes over 43 years (1977-2019) from the International Institute for Sustainable Development Experimental Lakes Area (ELA) network of fifty-eight lakes pristine boreal lakes located East of Kenora Ontario, Canada (Table 2.1; Appendix 1 Figure A). Lakes 223, 224, 260, 373, 375, 382, 442 and 626 were used to evaluate the spawning phenology of White Sucker. For Lake Trout, the same collection of lakes was used except for Lake 373 due to lack of adequate data (see below). Lakes 224, 373 and 442 belong to the Long-Term Ecological Monitoring (LTER) program. These LTER lakes are intentionally left unmanipulated to reflect the natural variability and baseline ecological conditions of lakes in the region. Lakes 223, 260, 375, and 626 have all undergone ecosystem manipulations (Table 2.1). Spawning data for White Sucker and Lake Trout was first collected in 1977 and remains ongoing, though data ranges vary among individual lakes (Table 2.1). The ELA is an ideal location to evaluate peak spawning as a response to climate change, because previous research has observed other changes in the region in response to a warming climate (Schindler et al. 1990, 1996; Guzzo and Blanchfield 2017; Guzzo et al. 2017).

Water Temperature Modelling

Given the documented importance of water temperature on spawning, daily surface water temperatures were estimated between April 4th to November 30th for every year on every lake. The ELA weather station has recorded hourly air temperature data since the summer of 1969,

such that a mean daily air temperature can be calculated. Surface water temperature data exists for all 8 study lakes, collected at varying intervals through time (ranging from hourly to bi-weekly to monthly). Air and water temperature data were used in conjunction to predict surface water temperatures for every day of the open water season, and were estimated by using the “Enhanced Multiyear Model” equation described in Matuszek and Shuter (1996):

$$(1) \quad WTEMP = C_0 + C_1 (ATEMP1) + C_2(YDAY) + C_3(YDAY)^2 + C_4(INVADYD) + C_5(ATEMP2)$$

where WTEMP is water temperature, ATEMP1 is the 15-day moving average of daily mean air temperature, YDAY is the day of the year, INVADYD is the inverse of YDAY adjusted so that ice-out is standardized as YDAY= 100, ATEMP2 is the 5-day moving average of daily mean air temperature, and C₀-C₅ are coefficients estimated from the model fit. ATEMP2 was introduced to account for water temperature variation caused by very recent air temperatures (Matuszek and Shuter 1996). The model term INVADYD in Matuszek and Shuter (1996) was set 2 days prior to earliest ice out in their data; I adopted a similar approach, setting the new standardized ice out day to YDAY 94 in my models to reflect the ELA’s earliest ice out date of Julian day 96 (April 6th, 2012). This approach ensured that there would be no gap between the ice off dates and the predicted water temperature values. All years of data with both water temperature and air temperatures were used to estimate model coefficients for each lake separately (Appendix 2 Table A).

Prior to running models for all lakes, data from Lake 442 was used to test the predictive efficacy of the model. Lake 442 was used because it had many years and observations of daily surface water temperature data available (33 years, 3367 daily observations), allowing me to test

whether the model was sufficiently robust to capture annual variation. I ran the model using 75% of the years where water temperature data was present ($N = 25$ of 33 available years for Lake 442, 2791 daily observations) and then fitted the resulting predicted water temperatures to the 25% of the remaining data that was excluded but had observed water temperatures for comparison ($N = 8$ of 33 years, 575 daily observations). A cross validation R^2 value was estimated from the match between model predictions with the observed 25% of data excluded from model generation, as per Rennie et al. (2005):

$$(2) \quad R^2 = 1 - (\sum [y_{\text{obs}} - y_{\text{predicted}}]^2 / SS_T)$$

Where y_{obs} is the observed water temperature value from the 25% of data excluded from model generation, $y_{\text{predicted}}$ is the model-estimated water temperature value from the 75% of data included for model generation, and SS_T is the total sum of squares times $N - 1$, where N is the number of observations of water temperature in the 25% of data excluded from the model.

Estimating Peak Spawning Date

Peak spawning date was estimated using similar methods for both White Sucker and Lake Trout by using the raw catch data from sampling events during their respective spawning seasons. These data contained daily catch totals of adult fish for each sex and assessed spawning condition of females (male spawning status does not vary during the 3-4-week period during which they are captured on spawning shoals; M. Rennie, Pers. Comm.). Female spawning condition was categorized as either being tight, loose/ripe, ripe & running, or spawned out (Table 2.2). Female fish typically arrive in greater numbers to the spawning shoals later than males, and they also leave the shoals sooner than males (Martin and Olver 1980; MacLean et al. 1981). For this reason, emphasis when predicting the peak spawn date was placed on the data collected from

female fish as the window of time during which females deposit their gametes is much narrower than the window for males.

Given the time constraints on field crews and the need to survey several lakes each year, no lake was sampled every day consecutively throughout the spawn within a given year, and furthermore, no lake was sampled every year across the study period. For these reasons, a peak spawning date was assessed considering the range of sampling events for each lake within a given year, using information on numbers of females observed and their spawning status to interpolate peak spawning.

The general pattern in female spawning data used to determine peak spawning required evidence of an increase, peak, and decrease of spawning activity. Increasing activity was associated with a rise in the number of females caught on the spawning shoals and greater numbers and proportions of tight fish compared to loose/ripe or ripe/running fish. Peaking windows of activity were typically associated with higher female catches along with greater numbers and proportions of females in spawning conditions favouring the ripe/running condition. Finally, decreasing spawning activity was noted by falling daily catch totals and female conditions showing a diminishing number of ripe/running individuals eventually giving way to fish in a spawned-out condition.

To determine a peak spawning date, I would objectively select a spawning start date and spawning end date from the recorded sampling events based on the criteria outlined above, which created a spawning window. Peak spawning was then estimated as the midpoint between these dates. Estimated peak spawn dates ending in 0.5 were rounded down, as 0.5 was interpreted to be the midpoint of the day (ex. Day 287.5 is still day 287). Occasionally, sampling

of a lake in a season would finish prior to the spawning window being fully captured, or data on the final sample event would resemble a peak spawning date. When this occurred, the final sample date was selected as the peak spawning date for that year; only 19% of Lake Trout spawning dates and 15% of White Sucker spawning dates were estimated in this fashion.

To account for inconsistent sampling efforts between years (e.g., many visits vs few visits to a lake), and variable catch and spawning condition information between years (e.g., few to many females, few to many spawning conditions assigned), confidence levels from 1 (low) – 10 (high) were associated with each estimated spawning date (Table 2.3). With each date and confidence value, I provided a description of what I saw in the data that detailed why I selected my chosen start and end dates and how that estimated date aligns in relation to the data present for that year. Only spawning dates with a confidence value of 6 or greater were considered for analysis. Across all sampling periods on 8 lakes for White Sucker and all 7 lakes for Lake Trout, 109 of 137 (80%) and 110 of 170 (65%) predicted peak spawning dates were included in the analysis, respectively. Lake 373 was excluded entirely from the Lake Trout analysis due to overall low confidence values assigned to the estimated peak spawning dates (20 predicted dates, only 3 of which were assigned a confidence value of 6 or greater).

To provide confidence in the application of the described method, estimated peak dates of both species from 2014-2019 were compared against the ELA field crew's in-field peak spawn estimations (made during spawning, integrating behavioural observations from visits every 2-3 days to lakes, and arguably a 'best' estimate of spawning dates made at the time observations are being taken). A total of 20 spawning dates were compared for White Sucker and 23 spawning dates were compared for Lake Trout. These estimates were compared by correlation, and through

calculation of the mean difference between methods and 95% confidence intervals (CI) of between-method differences were estimated.

Evaluating Temporal Changes in Estimated Peak Spawning Date

Changes in peak spawn dates across the 43-year study period for both White Sucker and Lake Trout were analyzed using an Analysis of Covariance (ANCOVA; Quinn and Keough 2002) approach, using the statistical program R Version 4.1.2 (R Core Team 2021). Individual spawning date observations included in the analysis were weighted by their assigned confidence level (as described above). For each test, ANCOVA was only attempted after verifying that a test for heterogeneity of slopes was non-significant ($p > 0.05$). For Lake Trout, a mixed effects model was also employed, and the value of the common slope was compared against the ANCOVA model. The categorical variable ‘lakes’ under the ANCOVA approach was a fixed effect but modelled as a random additive effect in the mixed effects modelling framework. The two models provided nearly identical results for the value of the common slope; as such, I retained lake as a fixed effect and proceeded with ANCOVA for all subsequent analyses. A t -test on planned comparisons was employed to compare adjusted means following the result of a significant ANCOVA. When no significant ANCOVA was discovered, a Tukey’s HSD was employed to compare group means.

Seasonal Climate Trend Analysis

Climatic trends relevant to the spawning season in all 8 study lakes were assessed. A mean spring or fall temperature was estimated to provide a general assessment of the conditions experienced each year (e.g., hotter, colder, typical). Mean water temperatures for the spring and fall season were calculated using the daily predicted water temperature values from April 4th to

May 31st and September 1st to October 31st respectively, for every year since 1970, the first full season in which air temperatures were recorded daily.

In addition to average seasonal water temperatures, a total value of thermal accumulation or loss measured by the cumulative of Growing Degree Days above 5°C (GDD₅) in spring and the cumulative of Cooling Degree Days below 20°C (CDD₂₀) in fall was calculated. These quantities were calculated to provide a better sense to how temperatures changed across the spring or fall season (e.g., Faster/slower warm up or cool down).

The time frame used for cumulative climate metrics were standardized so that for every year, calculations would begin April 4th and end on June 5th for GDD₅, whereas CDD₂₀ began August 1st and ended October 18th. April 4th was selected as two days prior to the earliest observed ice out in ELA lakes (which was April 6th, 2012; Guzzo and Blanchfield 2017). Selecting August 1st as the threshold to begin CDD₂₀ calculation from was chosen because this date is typically just past peak summer temperatures in ELA lakes (Scott Higgins, Pers. Comm.), thus representing the period at which lakes begin to cool. The application of base temperatures of 5°C for GDD and 20°C for CDD were used to describe the warming and cooling period leading up to the peak spawning events for both species under investigation, and to standardize the approach (Chezik et al. 2014). The end dates of June 5th and October 18th were selected as the dates at which 95% of estimated peak spawn dates had occurred for White Sucker and Lake Trout respectively, thus characterizing the conditions leading up to and including the spawning period under investigation. Both cumulative thermal metrics were calculated every year beginning in 1970 based on available meteorological data. Like spawning phenology, these variables were evaluated for temporal changes over the duration of the study period using ANCOVA to control for among-lake differences (Quinn and Keough 2002).

Evaluating Relationships between Spawning Phenology and Climate

To determine the effects of seasonal climate variability on the spawning phenology of my study species, ANCOVA was used to examine the effect of spring water temperature and GDD₅ on estimated peak spawning dates for White Sucker, and the effect of fall water temperature and CDD₂₀ on the estimated peak spawning dates for Lake Trout (Quinn and Keough 2002). In each case, the categorical variable ‘lake’ was included as a grouping variable and spawning observations were again weighted based on their assigned confidence values.

Comparing Temperatures at Peak Spawning Among Lakes

To test whether peak spawning in White Sucker and Lake Trout occurred at similar temperatures across years in all study lakes, I determined the water temperature on the estimated date of peak spawn. When both the observed and predicted water temperature was listed in the data for a given spawning date, the observed value was selected over the predicted value. One-Way Analysis of Variance (ANOVA) tests were applied to spawning water temperatures for each species, and Tukey’s HSD tests were performed to determine significant differences among lakes, when applicable (Quinn and Keough 2002).

Correlation between Adjusted Mean Spawning Dates with Lake Characteristics

I investigated whether the physical characteristics of the lakes influence the different timing of spawning for both Lake Trout and White Sucker among lakes and also the different average seasonal temperatures and heating/cooling schedules using correlation. The adjusted mean spawning dates for each species (derived from Year+Lake ANCOVA models) were examined against lake total volume, surface area, maximum depth, average depth, and Secchi depth.

In all statistical analyses, the data were examined to ensure the assumptions of the statistical models were satisfied. Results from testing the heterogeneity of slopes from each ANCOVA analysis can be found in Appendix 2 Tables B – K. Residuals of the models were assessed for normality and heterogeneity using Anderson-Darling’s Test for Normality, Levene’s Test for Homogeneity, and examination of residual plots (Quinn and Keough 2002). Any instances where data failed at least one of these tests prompted the application of data transformations to satisfy the assumptions of the model. Unless otherwise specified in the results, all data were found to be homogeneous and normal. ANOVA tests were conducted on the covariate to assess for differences in the predictor variable among the covariate levels. In cases where there were differences in the predictor among the covariate, the results were still accepted as the ANCOVA model is robust to deviations of this assumption (Quinn and Keough 2002).

RESULTS

Validation of Estimated Peak Spawn Date Method

The method employed here for estimating the peak spawning date of Lake Trout was not significantly different from estimates made in the field at the time of spawning by ELA staff for estimates during 2014–2019 (mean difference = 0.74 days later than in field estimates, 95% CI of mean differences = -0.55 to + 2.02 days), and the two estimation methods were significantly correlated ($r = 0.83$, $t_{21} = 6.83$, $p < 0.001$; Figure 2.1A). On average, the same estimation method applied to White Sucker peak spawning dates yielded estimates only slightly earlier than those determined in the field (mean difference = -1.70 days, 95% CI -3.17 to -0.23 days), and like Lake Trout, the two methods were significantly correlated ($r = 0.65$, $t_{18} = 3.64$, $p = 0.002$; Figure 2.1B). The close agreement between my method and in-field estimates provided confidence that

this approach could be applied to all years of data to yield accurate and meaningful peak spawning dates.

Evaluating Temporal Changes in Estimated Peak Spawning Date

To determine whether a temporal change in peak spawning date occurred for Lake Trout, the relationship between the peak spawning date and year was tested and found to be consistent across lakes (Year*Lake interaction: $F_{6,96} = 2.01, p = 0.072$). A significant increase in Lake Trout peak spawning date with time over all lakes during the study period was detected (ANCOVA, Year effect: $F_{1,102} = 13.57 p < 0.001$), with a common delay in Lake Trout spawning among lakes of 5 days over the entire period of study, or a rate of 1 day per decade, (Figure 2.2A; Table 2.4). The ANCOVA also revealed significant differences in the timing of spawning among lakes, controlling for the temporal effect (Lake effect: $F_{6,102} = 18.95 p < 0.001$). An ANOVA on the covariate (Year) was significant ($F_{6,103} = 4.44 p < 0.001$), which reflected different years of study among lakes, but observations over time overlapped among most lakes in the dataset, suggesting this had little influence on the results (Figure 2.2A). Planned comparison *t*-tests on the adjusted lake means of Lake Trout spawning from the ANCOVA indicated that Lake Trout in Lake 260 and 382 spawn the earliest (~day 279 or October 6th), Lakes 223, 224, 442 and 626 spawn the latest (~day 287 or October 14th) and Lake 375 spawns in between these dates (~day 284 or October 11th).

To determine whether a temporal change in peak spawning date occurred for White Sucker, the relationship between the peak spawning date and year was found to be consistent across lakes (Year*Lake interaction: $F_{7,93} = 0.81 p = 0.58$), and ANCOVA revealed no significant effect of year on peak spawning dates across lakes during the study period ($F_{1,100} = 0.51, p = 0.49$; Figure 2.2B). However, it did reveal a significant difference in spawning date

among lakes ($F_{7,101} = 5.87, p < 0.001$), indicating that White Sucker in different lakes operate on different spawning schedules. A Tukey's HSD follow up test identified Lake 442 as the first lake to spawn (~day 140 or May 20th), followed by Lakes 375, 382 and 626 (~day 146 or May 26th), and finally Lakes 223, 224, 260, and 373 as the latest spawning lakes (~day 149 or May 29th).

Estimation of Water Temperatures

To evaluate the predictive efficacy of the surface water temperature model, the predicted independent observations of water temperature from Lake 442 yielded a cross validation R^2 of 0.99. The average absolute difference between the observed surface water temperature values left out of the model and the predicted values generated from the Matuszek & Shuter (1996) model was 0.8°C, indicating good agreement between observed and predicted values (Table 2.5). Based on these results, individual lake models were generated to provide surface water temperatures for the open water season across all years (Appendix 2 Table A)

Seasonal Climate Trend Analysis

To determine whether the thermal conditions of the aquatic environment during fall were changing, the relationship between average water temperature of the fall season and CDD₂₀ over time was evaluated among all 7 Lake Trout lakes and was found to be consistent (Year*Lake interaction in both models: Fall water temperature: $F_{6,336} = 0.03, p = 1.00$; CDD₂₀: $F_{6,336} = 0.08, p = 1.00$). An ANCOVA revealed a significant and common shift towards higher average fall water temperatures and fewer cumulative CDD₂₀ over the study period across all lakes (fall water temperature: $F_{1,342} = 82.6, p < 0.001$; CDD₂₀: $F_{1,342} = 111.32, p < 0.001$; Figure 2.3). The common slopes estimated from the models (Table 2.4) indicate that since 1970, the average fall surface water temperature has increased by 1.4°C and the cumulative thermal loss during the fall

period has been reduced by $86.7^{\circ}\text{C}\cdot\text{days}$ (Figure 2.3). Residuals of the ANCOVA models failed normality tests and the application of data transformations did not improve results; histograms of the residuals appeared reasonably approximate of normal distributions in the fall water temperature model and showed some minor left skew in the CDD₂₀ model (Appendix 3 Figure A), and ANCOVA is generally robust to minor deviations from this assumption (Quinn and Keough 2002). No visible trends were detected in the residual vs fitted plots of either model.

To test whether the thermal conditions of the aquatic environment during spring were changing, the relationship between average spring water temperatures and GDD₅ with time were evaluated among all 8 White Sucker lakes and found to be consistent (Year*Lake interaction in both models: spring water temperature: $F_{7,384} = 0.0004, p = 1.00$; GDD₅: $F_{7,384} = 0.0006, p = 1.00$). Neither the average spring water temperature nor cumulative GDD₅ changed significantly over the study period (ANCOVA: spring water temperature: $F_{1,391} = 0.13, p = 0.72$; GDD₅: $F_{1,391} = 0.54, p = 0.46$; Figure 2.4). Residuals of the ANCOVA models failed the normality test only for the average spring water temperature model, and the application of data transformations did not improve results enough to pass the test. Examination of the residual vs fitted plot and residuals histogram showed a reasonable approximation of normality and only minor left skew (Appendix 3 Figure A) but was not so dramatic as to discount the model results (Quinn and Keough 2002).

Evaluating the Relationship between Spawning Date and Climate Variability

To determine whether annual variability in fall thermal conditions influenced the date of spawn, the relationship between Lake Trout estimated peak spawning date and either average fall water temperature or CDD₂₀ was evaluated and found to be consistent across all 7 lakes (fall

water temperature*Lake: $F_{6,96} = 0.96, p = 0.46$; CDD₂₀*Lake: $F_{6,96} = 0.90, p = 0.5$). The ANCOVAs indicated that estimated peak spawning date was influenced by both average fall water temperature and CDD₂₀ (fall water temperature: $F_{1,102} = 5.48, p = 0.02$; CDD₂₀: $F_{1,102} = 10.93, p = 0.001$). The common slopes estimated from the model (Table 2.4) suggested that a 1°C increase in the average fall water temperature or a total decrease of 37°C·days during the fall season was sufficient to shift spawning later by 1 day (Figure 2.5). An ANOVA of the covariate was significant for both models (fall water temperature: $F_{6,103} = 8.00, p < 0.001$; CDD₂₀: $F_{6,103} = 8.95, p < 0.001$) reflecting differences among lakes in average fall water temperatures and cooling schedules, however, the general relationship was consistent across lakes for both models as evidenced by an insignificant interaction between lakes and fall water temperature or CDD₂₀. Residuals of the ANCOVA model using fall water temperature as the response variable narrowly failed the test for normality, but a histogram of the residuals showed a near-normal distribution (Appendix 3 Figure A).

To determine whether annual variability in spring thermal conditions influenced the date of spawn, the relationship between White Sucker estimated peak spawning date and either average spring water temperature or GDD₅ was evaluated and found to be consistent across all 9 lakes (spring water temperature*Lake: $F_{7,93} = 0.83, p = 0.57$; GDD₅*Lake: $F_{7,93} = 0.23, p = 0.98$). The ANCOVA models indicated that estimated peak spawning date was influenced by both average spring water temperature and GDD₅ (log spring water temperature: $F_{1,100} = 54.1, p < 0.001$; GDD₅: $F_{1,100} = 72.03, p < 0.001$). The common slopes estimated from the model (Table 2.4) predict that a 1°C increase in spring water temperature should advance White Sucker peak spawning date by 2.4 days. Similarly, an increase of 17°C·days was enough to shift spawning sooner by 1 day (Figure 2.6). An ANOVA of the covariate was significant for both models

(spring water temperature: $F_{7,101} = 6.29 p < 0.001$; GDD₅: $F_{7,101} = 2.403 p = 0.03$) reflecting differences among lakes in average spring water temperatures and warming schedules, however, the general relationship was consistent across lakes for both models as evidenced by an insignificant interaction between lakes and spring water temperature or GDD₅.

Differences in Temperature at Peak Spawn Date Among Lakes

To assess whether peak spawning among lakes occurred at different temperatures for both species, Lake Trout appeared to have no significant difference in the estimated temperature on the day of peak spawning among the 7 lakes (ANOVA, $F_{6,103} = 1.75 p = 0.12$; Figure 2.7), where peak spawning occurred at an average of 10.9°C (St. Dev: +/- 1.8, SE: +/-0.2; Figure 2.8) across all lakes. In contrast, White Sucker showed a significant difference in the log values of temperature at peak spawning date among the 8 study lakes ($F_{7,101} = 3.33 p = 0.003$). A Tukey's HSD post-hoc test revealed that spawning temperatures for the lakes were divided into 3 main groups: those that spawn at warmer temperatures (Lakes 224 and 260; 16.8°C) those that spawn at mid-range temperatures (Lakes 223, 373, 375, 382, and 626; 15.3°C) and those that spawn at cooler temperatures (Lake 442; 14.0°C, Figure 2.7).

Correlation between Adjusted Means and Lake Characteristics

To evaluate for correlations between adjusted means from Year + Lake spawning ANCOVA's, among all lake characteristics evaluated, only surface area was significantly correlated with the adjusted mean spawning date for Lake Trout ($r = -0.76, t_5 = 2.65, p = 0.045$; Figure 2.9) and was nearly significantly correlated with the mean spawning date for White Sucker ($r = 0.65, t_6 = 2.09, p = 0.08$; Figure 2.9). Plots of the non-significant correlation tests can be found in Appendix 3 Figure B - E. Surface area was not found to be further correlated with any adjusted means from spring or fall surface water temperatures, GDD₅ or CDD₂₀, however,

Secchi depth was shown to be strongly negatively correlated with adjusted means of fall water temperature ($r = -0.9$, $t_5 = -4.73$, $p = 0.005$) and positively correlated with CDD₂₀ ($r = 0.87$, $t_5 = 3.98$, $p = 0.01$; Figure 2.10).

DISCUSSION

Environmental conditions during spawning, and specifically the average temperature and cumulative thermal environment during the shoulder seasons experienced by both Lake Trout and White Sucker appear to be important drivers in spawning phenology for these species. A 1.4°C increase to the average fall water temperature was observed over the 50-year period examined, and Lake Trout spawning events now occur 5 days later on average in 2019 than 1978; no such seasonal trend was observed in spring water temperature, and White Sucker spawning events occur at the same time on average as historical spawning schedules. However, given significant relationships for both species with mean annual temperatures in spring and fall, annual increases to average water temperatures by 1°C would be expected to delay Lake Trout peak spawning by 1 day in the fall, or advance White Sucker spawning by 2.4 days in the spring. Alternatively, in units of thermal accumulation, my study suggests that annual increases to thermal retention during the fall of 37°C·days can delay peak Lake Trout spawning by 1 day, and annual increases to thermal gain of 17°C·days can advance White Sucker spawning by one day. These relationships between temperature metrics and peak spawning dates in both species, as well as directional changes to annual thermal conditions in the fall demonstrate important links between spawning phenology and climate in both species.

My observations of delays in Lake Trout spawning are consistent with the expectation that rising temperatures driven by climate change will alter the timing of spawning in fishes

(Pankhurst and Munday 2011; Warren et al. 2012; Lyons et al. 2015). Previous work investigating phenological changes to Lake Trout habitat availability at ELA indicated that the onset of the fall period shifted roughly one week later in 2013 than what was expected through the 1970s, though the length of the fall season was stable (Guzzo and Blanchfield 2017). Changes in fall climatic conditions and spawning phenology of Lake Trout observed in my study are consistent with the one-week shift in the onset of the fall period specific to Lake Trout previously reported (Guzzo and Blanchfield 2017). As the initiation of summer's end gradually delays, elevated water temperatures persist longer into the fall season which delays the onset of cooling for lakes. The result of this shift is an increase in both above average fall temperatures and thermal retention during the spawning season for Lake Trout, ultimately delaying the commencement of spawning.

My findings are also consistent in magnitude with the only other study that has evaluated changes in phenological timing of Lake Trout spawning, but this study was over a shorter time period. Lyons et al. (2015) reported that a population of Lake Michigan Lake Trout was spawning as much as 5 days later in 2006 than previously expected in 1983. The same study also examined the Lake Trout population at the Apostle Islands of Lake Superior but found no significant trend in spawning between 1988–2012. Overall, the total adjustment in spawning date between ELA Lake Trout and Lake Michigan Lake Trout was similar, though the decadal rate of change in Lake Michigan Trout was nearly double the decadal rate of change among ELA populations. Interestingly, the analysis by Lyons et al (2015) of Lake Michigan water temperatures at the time indicated no significant temporal changes during the open water season, however more recent research has shown this to be an artefact of the time frame under investigation (Mason et al. 2016; Zhong et al. 2019). Only 13 years of water temperature data

were analyzed despite evaluating spawning trends over 24 years. Furthermore, October in Lake Michigan appears to be the month with the greatest warming rate compared to all other months of the year over the past 25 years (1995-2019; Anderson et al. 2021).

The peak spawning date of Lake Trout observed in ELA populations appears to be outpacing the expected shift that might be expected due to temperature alone (Appendix 3 Figure F), suggesting that spawning phenology may be influenced by factors beyond seasonal thermal conditions (Lyons et al. 2015, this study). Factors that could affect gonadal development in the lead-up to spawning such as oxy-thermal habitat and food availability may also be relevant contributors to spawning phenology (Lyons et al. 2015). A phenomenon known as skipped spawning is based upon the premise of suboptimal growth and gonadal developmental conditions (either by poor food resources or surviving in harsh, energy demanding environments; Rideout and Tomkiewicz 2011). This pattern has also been observed directly in Lake Trout (Morbey and Shuter 2013; Goetz et al. 2021). Based on relationships observed from annual variation to thermal conditions, spawning should occur one day later by either an increase of 1°C to the average fall water temperature or decrease of 37°C CDD₂₀, which over the study period would predict a delay in spawning by 1 – 3 days, less than the observed 5-day delay. In a closely related species, Brook Trout (*Salvelinus fontinalis*) delayed spawning activity by 7 days for every 1°C increase in summer maximum air temperatures, likely due to metabolic disruption diverting energy away from gonadal development (Warren et al. 2012). In small shield lakes like those found at the ELA, optimal oxy-thermal habitat during the summer is becoming increasingly rare (Guzzo and Blanchfield 2017), which may ultimately impact metabolic rates leading to reduced growth and reproductive impairment (Evans 2007). Additionally, a reduction in the duration of the spring period/lengthening of summer has been shown to limit the ability of

Lake Trout to access key littoral resources (Guzzo et al. 2017). Reduced access to important energy sources and occupation of sub-optimal oxy-thermal habitat are both likely to place significant metabolic strain on Lake Trout, potentially further exacerbating climate-related delays in spawning.

Though no shift in White Sucker peak spawning dates or spring thermal conditions were observed over time, White Sucker peak spawning was significantly related to spring thermal conditions; based on the relationships reported here, a 1°C increase in mean spring water temperature would be expected to advance White Sucker spawning by approximately 2.5 days, indicating that a directional shift towards warmer springs (a predicted outcome of climate change; Bush and Lemmen 2019) would likely advance White Sucker spawning phenology in our region. In other regions where spring warming has been observed, other spring spawning species have typically advanced their dates of spawn to keep pace with a changing climate. For example, Yellow perch (*Perca flavescens*) in Lake Michigan have shifted their peak spawning dates between 1.8 and 6.2 days per decade earlier to keep pace with optimal thermal temperatures (Lyons et al. 2015). Spring spawning European Grayling (*Thymallus thymallus*) are now engaging in reproductive activity as much as 3-4 weeks earlier in a season across a 62-year period as their critical spawning temperature of 6°C continually advanced over the years (Wedekind and Küng 2010). Additionally, Walleye (*Sander vitreus*) spawning phenology was shown to be significantly advanced with earlier ice off dates in Minnesota lakes (Schneider et al. 2010).

The mean temperature at peak spawning date for ELA Lake Trout was not significantly different among lakes and occurred on average at 11°C every year. This value is similar to other reports of observed Lake Trout spawning temperatures which have ranged from 6.6°C – 11.5°C

across the Great Lakes and various inland waterbodies (Scott and Crossman 1973; MacLean et al. 1981; Casselman 1995; Fitzsimons 1995; Lyons et al. 2015). Lake Trout were seldom observed spawning at higher water temperatures across the study period (only 8% of spawning events observed at 13°C or higher), but the vast majority of spawning events occurred near or below the ~11°C temperature mark, indicating 11°C was a critical threshold temperature important to inciting spawning activity.

The timing of spawning in White Sucker has also previously been characterized as an event based on the attainment of a critical threshold temperature, rather than the attainment of a cumulative threshold temperature (Hamel et al. 1997). Hamel et al. (1997) suggests 13°C is an important spawning cue to White Sucker, as cessations to spawning were observed when water temperatures fluctuated below 13°C and resumed as they fluctuated above 13°C. While not studied at this fine scale in the current study, my findings suggest that thermal thresholds of White Sucker populations at ELA appear to be population specific. However, my results also indicate that the timing of spawning in White Sucker are strongly related to the conditions experienced in a given spring season, as spawning phenology scaled negatively with both average spring water temperature and GDD₅ across all lakes. Additionally, my results align well with the literature of reported spawning temperatures for White Sucker. Unlike Hamel et al. (1997), where five of six distinct populations spread across a large spatial range in Quebec were observed to begin spawning at a common temperature of 13°C, peak spawning of White Sucker at ELA ranged nearly 3°C (14–17°C). Literature reporting spawning temperatures of White Sucker indicates a range between 9.4°C and 17°C (Hamel et al. 1997; Catalano and Bozek 2015), and an optimal spawning temperature of 15.5°C (McCormick et al. 1977; Hasnain et al. 2010) which agrees well with our observed spawning temperatures.

Heating and cooling in temperate lakes are driven by atmospheric temperature, morphology, and DOC content (Livingstone and Lotter 1998; Richardson et al. 2017; Craig et al. 2017). Both Lake Trout and White Sucker spawning events showed relationships with environmental conditions, and both species experienced among-lake differences. Lake surface area appeared to be the only lake-morphometric feature to provide insight as to why spawning in ELA lakes occurs at slightly different times from one another; on average, Lake Trout spawning occurred sooner in lakes with larger surface area than lakes with smaller surface area, and the opposite was true for White Sucker. Presumably, with more surface area to release heat, the larger lakes should release more surface heat than the smaller lakes in the fall, and in spring, with less surface area to heat up, the smaller lakes should warm quicker, causing the fish occupying these lakes to spawn sooner than the fish in the larger lakes. However, this hypothesis was not supported by further examination into surface area's relationship with seasonal surface water temperatures and GDD₅/CDD₂₀ among lakes, indicating that surface area could not fully describe why some lakes heated or cooled more than others. Interestingly, Secchi depth (a measure of water clarity) provided some insight into among lake thermal differences, in that lakes with the greatest water clarity were the warmest and cooled the least, and the shallowest Secchi belonged to the coldest lakes that incurred the greatest amount of cooling; no similar effect was discovered in spring temperatures and GDD₅. Dissolved organic carbon (DOC) inputs are largely responsible for water clarity as it is known to play a role in the thermal structure of lakes (Schindler et al. 1996; King et al. 1997; Richardson et al. 2017). This result supports the notion that DOC inputs are an important factor in thermal structure, and that lake cooling in the fall may be influenced by DOC inputs accrued over the open water season.

An observed pattern over the course of any given spawning season for some populations of Lake Trout and White Sucker is a tendency for younger, smaller fish to migrate and potentially spawn sooner than the older, larger fish (Bond and Machniak 1979; Martin and Olver 1980; Casselman 1995). Repeated evidence shows that fish populations globally will experience body size reductions induced by climate change (Daufresne et al. 2009), suggesting the potential for size-based skews to drive changes in spawning phenology. However, for several reasons, I do not believe that potential changes in mean size over time are contributing to the shifts in phenology observed here. First, concerning Lake Trout, evidence shows that when access to littoral resources becomes restricted due to warming water temperatures, growth and condition of Lake Trout suffer (Guzzo et al. 2017). While the size of spawning individuals was not assessed in this study, if access to littoral energy sources became increasingly restricted over time, size shifts of Lake Trout populations at ELA would likely skew towards smaller individuals as growth rates and condition decline, leading to smaller size at maturity. This shift to smaller mature Lake Trout would be expected to skew spawning events sooner (Martin and Olver 1980; Casselman 1995), rather than later as I demonstrated. Similarly, size trends of spawning White Sucker were not explicitly considered for this chapter, though other research shows marked declines in size at age of populations from lakes that I have examined for spawning phenology (Chapter 3). Maturity is related to age for these suckers, and slower immature growth may be leading to smaller sizes at maturity in this population (Chapter 3). However, despite marked declines in size, there is no tendency for the timing of spawning to begin sooner than historical records as demonstrated here, again suggesting that environmental factors are a more prominent driver of spawning phenology than population size structure.

Without a well-timed successful spawn, a cascade of fitness impairments may be expected for both Lake Trout and White Sucker. As shown here, water temperature directly affects timing of spawning and egg deposition into the environment, which if deposited at suboptimal egg incubation conditions, can lead to hatching at a suboptimal time in relation to larval food sources, causing reduced early life stage survival (Casselman 1995; Asch et al. 2019). For larval fish that do survive hatching from potentially suboptimal incubation conditions, emergence too early exposes fry to a greater risk of predation, and emergence too late disadvantages fry by density dependence limitations (Skoglund et al. 2011). The first year of growth is vitally important to determining the asymptotic size a fish can achieve (Sibly et al. 2015) and also over winter survival (Biro et al. 2004, 2005), so if first year growth rates and lipid stores are not optimized, increased winter mortality and reduced body size may result. For the survivors, reduced fecundity is to be expected at smaller sizes (Ahti et al. 2020), and combined with a phenological alteration, this may begin a negative feedback loop that promotes lower survival, smaller, and less fecund fish, ultimately challenging the reproductive resilience of a species (Lowerre-Barbieri et al. 2017). Further impacting fitness is a tendency for many fish species to participate in skipped spawning (Trippel and Harvey 1990; Rideout and Tomkiewicz 2011; Morbey and Shuter 2013; Goetz et al. 2021), an event usually determined by poor nutritional or environmental conditions (Rideout and Tomkiewicz 2011), and both are conditions that have been increasingly observed at the ELA (Guzzo and Blanchfield 2017; next chapter). A successful spawn is vitally important to the continuation and fitness of a species, such that adapting one's spawning phenology to environmental change becomes critical to long-term success of the population (Zettlemoyer and DeMarche 2021).

While a change in spawning phenology can undoubtedly impact the next generation's ability to recruit to the adult population, it is unlikely spawning phenology has contributed to fitness impairments in the two species considered here. Firstly, as the average fall thermal conditions track warmer, I discovered a shift in Lake Trout spawning greater than would be expected based on the interannual variation patterns discovered. Lake Trout that spawn in warmer fall conditions subject their eggs to greater accumulated thermal units, which is associated with increased early developmental rates and greater proportions of mortality within a cohort (Casselman 1995). That Lake Trout are spawning later than would be expected based on relationships with temperature alone may suggest spawning delays are a result of greater metabolic demand throughout the summer (Evans 2007; Guzzo et al. 2017). Alternatively, from an egg's perspective, a greater delay in spawning than otherwise predicted by temperature might provide protection from excessive accumulated thermal units (Casselman 1995). A shift to a later spawning date, coupled with evidence that the length of fall seasons are not changing in this region (Guzzo and Blanchfield 2017), suggests that Lake Trout are responding to the temperature signal and providing their eggs the best chance to incubate and hatch next spring.

Similarly for White Sucker, the absence of a change in spring thermal conditions and spawning dates suggest optimal spawning and recruitment conditions remain for this spring spawner. While there is evidence for a longer spring, this mostly is a result of an earlier ice off combined with an onset of summer (defined as development of a 15°C isotherm) that has been consistent over time on average (Guzzo and Blanchfield 2017). Lab tests investigating the effects of early-life temperatures to White Sucker show that optimum egg hatching occurred at an incubation temperature of 15.2°C and widespread mortality occurred at eggs incubated at 24.1°C (McCormick et al. 1977). Larval growth rates were optimized at ~26.9°C and were deleterious at

> 30.0°C, but thermoregulating behaviours were observed, showing adaptive capacity to lethal temperatures (McCormick et al. 1977). This suggests that in addition to demonstrating relative stability in mean spawning dates over time, larval White Sucker during spring and summer are likely adaptable to the current degree of warming conditions, though as with Lake Trout, again relays the importance of spawning at the right thermal conditions to maximize recruitment potential.

Based on my findings, if a change in fitness or recruitment success were to occur in these populations, it would likely be due to an effect of altered food webs or altered juvenile survival rates independent from shifts in spawning phenology exclusively. Phytoplankton and zooplankton predator-prey dynamics can be affected in numerous ways in response to rising temperatures (Vadadi-Fülöp et al. 2012), which may affect time-lags between the peak abundance of prey and consumers and reduce the total biomass transferred to the zooplankton level (Thackeray 2012). Shorter winters can also contribute through the suppression of spring chlorophyll *a* due to increased survival of (and grazing by) overwinter-adapted zooplankton species under the ice (Hébert et al. 2021). This can influence top-down effects on the first significant primary productivity bloom of the season, potentially cascading into impacts for juvenile fish (Hébert et al. 2021). Both White Sucker and Lake Trout feed intensively on zooplankton during their age-0 life stages (Siefert 1972; Borgmann and Ralph 1985; Ellen Marsden et al. 2022). If juvenile fish do not achieve somatic growth thresholds or if lipid stores are not adequately stockpiled for the winter, predation and overwinter starvation are likely to increase mortality (Biro et al. 2004, 2005; Mogensen and Post 2012). The increases in mortality can be a result from food resources limiting growth rates, mid summer temperatures pausing feeding activity, or some combination of the two that force juveniles to engage in riskier energy

acquisition behaviour leaving them more susceptible to predators (Biro et al. 2005; Mogensen and Post 2012). However, if food resources are plentiful, and overwinter mortality is limited, better juvenile recruitment may be expected, thus greater levels of competition and density-dependent factors may influence overall population fitness. Chapter 3 presents evidence for instability of zooplankton food resources and greater White Sucker abundances in several study lakes from this chapter, further supporting the notion that to date, fitness and recruitment changes of my species have likely been a result of a changing food web and age-0 survival that are otherwise independent to the spawning phenology of Lake Trout and White Sucker.

CONCLUSION

This study is the first to evaluate long-term phenological responses in reproductive events for White Sucker and for inland populations of Lake Trout. My findings agree with previous research that suggests phenological changes to the spawning of fishes are expected in a warming climate. Through this research I have demonstrated the importance of temperature trends on the peak spawning dates of two lake-spawning species with differing life history strategies, and so, these results may be applicable to many populations of White Sucker and Lake Trout. Lake-spawning White Sucker typically do so in the shallows of lakes which may explain why surface water temperatures can shift peak spawning dates so significantly by up to 2.5 days. Across a Lake Trout's range, these findings would be applicable to inland Lake Trout populations that experience full destratification during the fall turnover, or shallow-spawning Lake Trout occupying much larger lakes that do not fully turn-over. Overall, this study further highlights the importance of successful spawning to population fitness and recruitment, and managers should continue to advance strategies that protect spawning and nursery habitats that facilitate early survival of fish.

TABLES

1 Table 2.1. Description of lakes used, years of data included in the spawning analyses, historical lake usage and physical morphological
 2 properties

Lake	Used in White Sucker Analysis	White Sucker Data Range (# Years in Model)	Used in Lake Trout Analysis	Lake Trout Data Range (# Years in Model)	Other Experiments Conducted During Used Data Ranges	Ref. To Paper	Surface Area (m ²)	Max Depth(m)	Volume (m ³ *10 ⁶)	Secchi Depth (m)
223	Yes	1977 – 2019 (20)	Yes	1977 – 2019 (15)	Yes (Acidification; 1976 – 1990)	Mills et al. 1987	27.3	14.4	1.89	5.4
224	Yes	1987 – 2018 (16)	Yes	1978 – 2019 (22)	No (LTER)	N/A	25.9	27.4	3.07	6.5
260	Yes	1989 – 2019 (13)	Yes	1984 – 2019 (20)	Yes (Estrogen; 2001 - 2003)	Kidd et al. 2014	32.8	14.2	1.98	4.5
373	Yes	1989 – 2019 (22)	No	N/A	No (LTER)	N/A	27.3	20.7	3.11	6.1
375	Yes	1989 – 2010 (7)	Yes	1989 – 2019 (18)	Yes (Aquaculture; 2003 – 2007)	Rennie et al. 2019	23.2	26.8	2.70	4.5
382	Yes	1985 – 2005 (14)	Yes	1984 – 2008 (13)	No (NORDIC Netted in 2003)	N/A	36.9	13.1	2.13	4.0
442	Yes	1991 – 2019 (9)	Yes	1990 – 2018 (13)	No (LTER)	N/A	16.0	17.8	1.36	4.4
626	Yes	2008 – 2019 (8)	Yes	2008 – 2018 (9)	Yes (Diversion; 2011 – Ongoing)	N/A	27.9	11.2	1.90	5.4

3

4

Table 2.2. Type and description of spawning conditions

Spawning Condition	Description of the spawning condition
Tight	Females are full of eggs but do not release many when pressure is applied to the belly. Presence of tight females indicates time to spawn is nearing but has not arrived yet.
Loose/Ripe	Females almost ready to spawn and release some eggs when pressure is applied to the belly. Loose/Ripe females indicate that spawning is about to begin
Ripe & Running	Females are ready to spawn. Eggs are being freely released without much added pressure. Ripe and Running females indicate that fish are actively spawning.
Spawned out (Spent)	Females have concluded spawning and have no eggs left to release. Spent females indicate that the height of the spawn has passed.

Table 2.3. General description of the spawning patterns associated with confidence values assigned in the catch and condition data collected by ELA crews from 1977 – 2019

Confidence Value	General Description of The Data That Would Be Associated with The Confidence Value
1 – 5	Insufficient Data. Either too few visits (e.g., 1-3), too spaced-out sample events (e.g., 4+ days in between visits), not enough females caught, little to no conditions reported on, or some combination of all 4. Unable to assess spawning trends with any degree of certainty. Confidence of 5 can potentially infer spawn but significantly lacking in supporting data.
6	Sample events are more frequent (e.g., 3+ visits) and female catch numbers can assess a spawning period (enough to see a rising, peaking, falling trend), but condition data may be sparsely assigned in relation to overall female catch or not totally consistent with trends (e.g., 1-2 conditions assigned each day). Could also be where a final sample date shows good evidence of a peak (e.g., 10+ females, 3-4 assigned ripe condition). Determining a spawn range is manageable, but peak date is only somewhat supported by data, or peak date lands on a final sample date.
7	Progression of spawn is evident with good female data that shows a rise, peak, and decline in catch. Sample event spacing is reasonable (e.g., max 3 days between visits), and condition data is plentiful enough to support the strong trends in female catch numbers (e.g., 4+ conditions assigned each day). Occasionally a 7 was given to final sample dates, but only when data was strong (e.g., 12+ females, 6+ ripe/running). Determining a range is overall easy and peak date is fairly supported by the data
8 – 9	Progression of spawn very evident. Many females caught and plentiful condition data that together, support the rise, peak, and decline of spawning. Determining range is easy and peak date supported by data (where peaks are easily visible in catch data)

Table 2.4. Summary table of the equations of the common slope derived from the ANCOVA models

ANCOVA Model	Slope	Intercept	Significant? Y/N
LT_spawn ~ Lake + Year	0.11196	63.1763	Y
WS_spawn ~ Lake + Year	-0.0381	225.315	N
CDD20 ~ Lake + Year	-1.7661	3769.83	Y
FallWtemp ~ Lake + Year	0.02819	-42.571	Y
GDD5 ~ Lake + Year	-0.1612	650.392	Y
SpringWtemp ~ Lake + Year	0.00181	5.13633	N
LT_spawn ~ Lake + CDD20	-0.0272	292.86	Y
LT_spawn ~ Lake + FallWtemp	0.9895	272.918	Y
WS_spawn ~ Lake + GDD5	-0.059	168.746	Y
WS_spawn ~ Lake + SpringWtemp	-2.405	170.306	Y

Table 2.5. Validation of Matuszek & Shuter (1996) Enhanced Multi-year water temperature model; predictive efficacy of the model developed using 75% of years from Lake 442

Year Left Out of Model	Cross-Validation R ² Value	Avg Absolute Difference (°C)	Number of Observations
1987	0.9982	0.7°C	13
1990	0.9891	1.2°C	14
1991	0.9968	1.3°C	14
1998	0.9955	1.0°C	13
2004	0.9996	0.8°C	147
2014	0.9988	0.9°C	71
2016	0.9987	0.8°C	119
2017	0.9998	0.8°C	184
All Years	0.9999	0.8°C	575

FIGURES

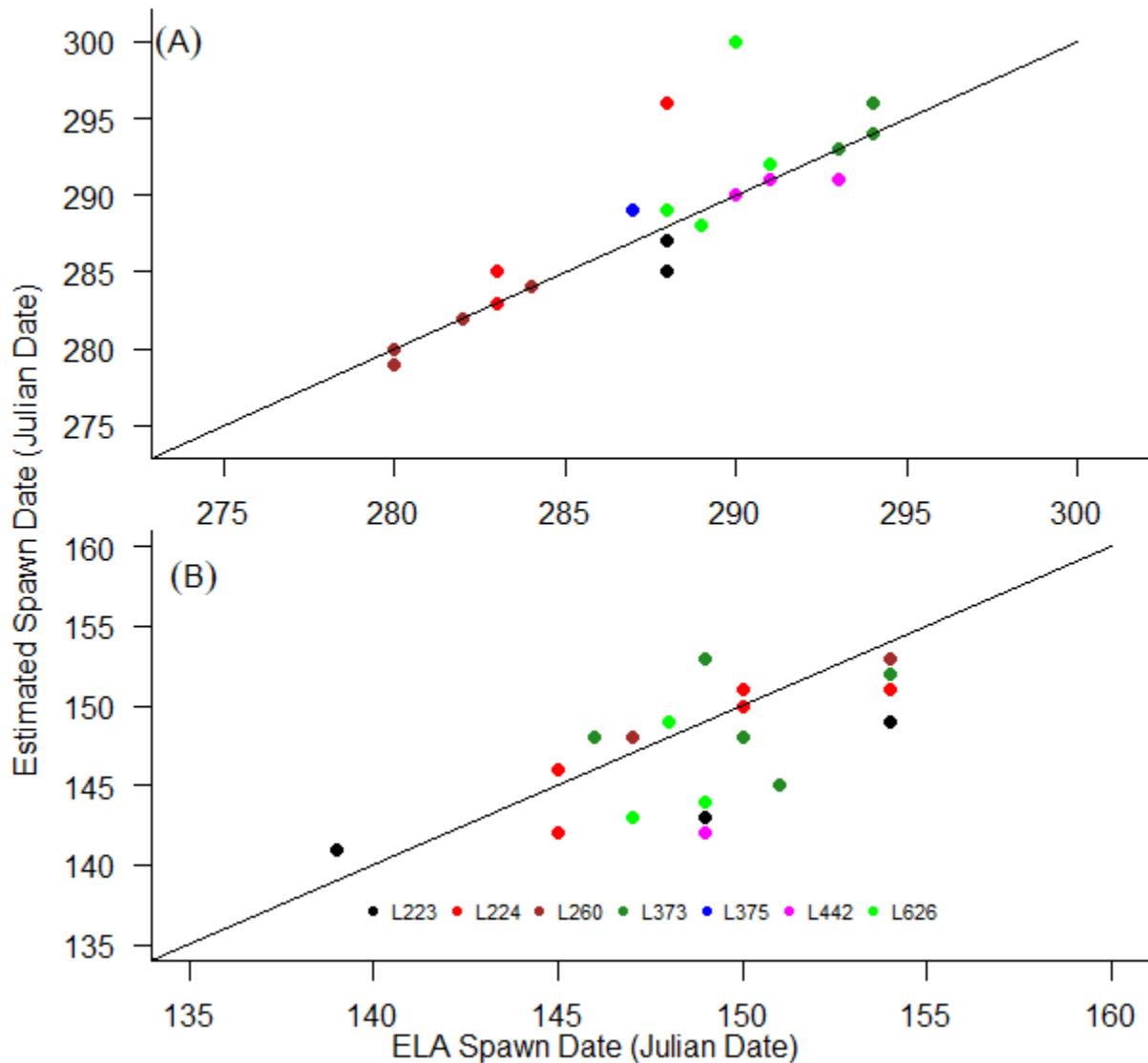


Figure 2.1. Correlation plots of estimated peak spawning date created via methods described in this paper versus ELA staff's selected spawn date based on infield estimation during 2014–2019. (A) shows Lake Trout estimates ($r = 0.83$), (B) shows White Sucker estimates ($r = 0.65$). Black line in both plots indicates 1:1 agreement line for comparison.

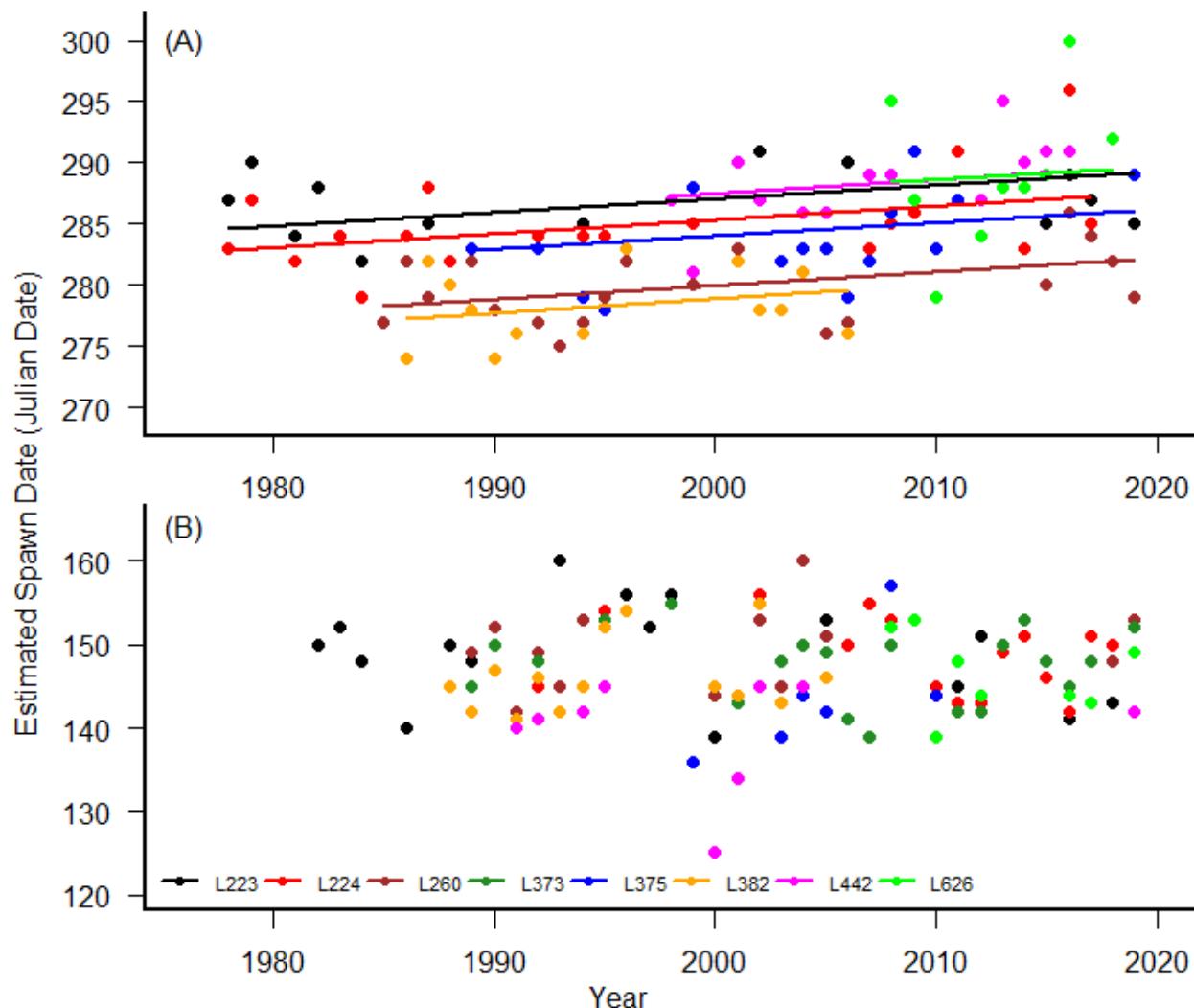


Figure 2.2. Estimated peak spawning date of Lake Trout (A) and White Sucker (B) over time. For Lake Trout, date of spawn is shifting by 0.1 days each year, or 1 day per decade ($y = 0.1x + 63.2$). R^2 value indicates this model describes 56% of the variation experienced by spawn dates over time.

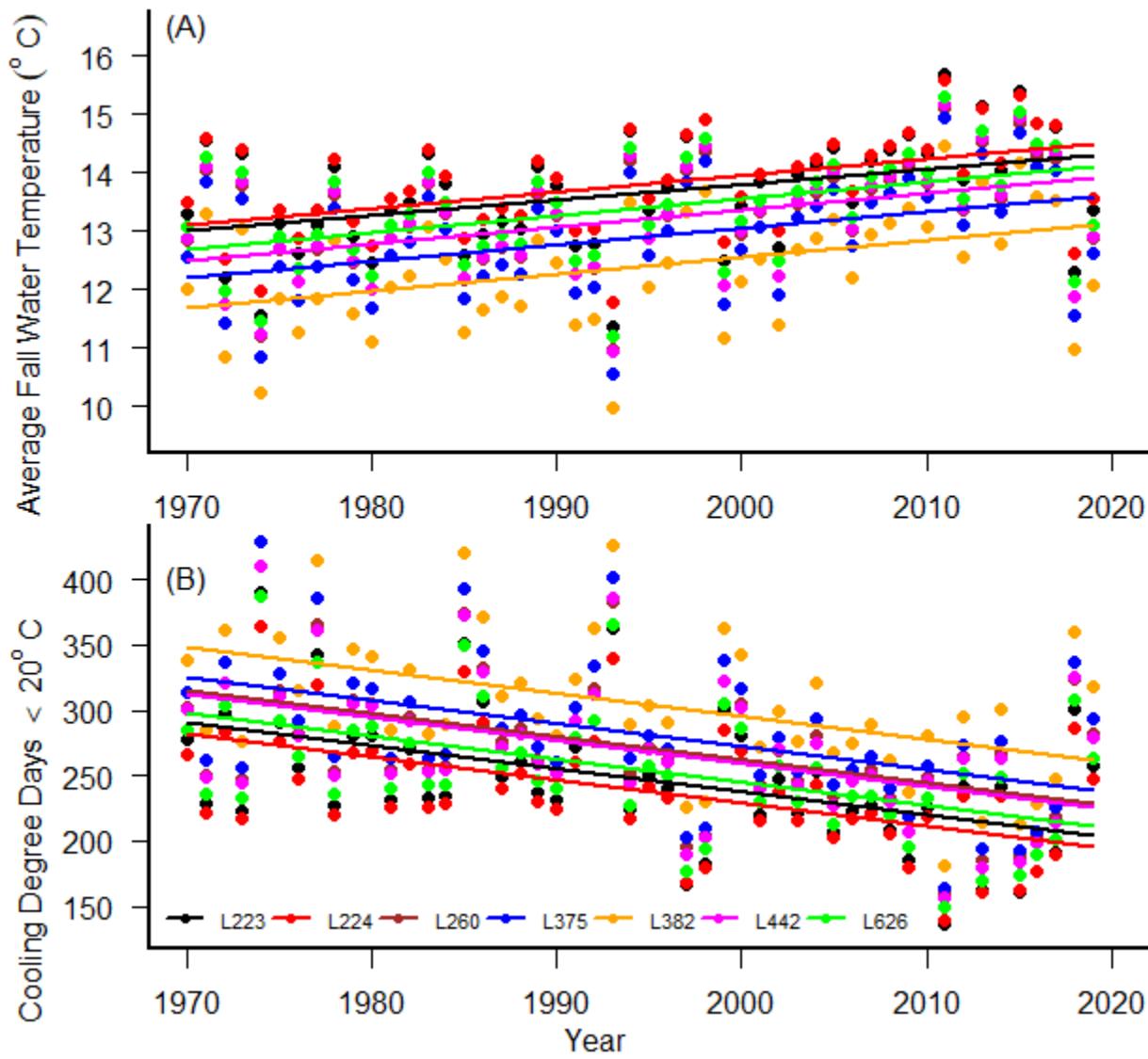


Figure 2.3. Seasonal fall climatic trends of mean fall water temperatures through time (A), and cumulative cooling degree days through time (B). Average fall water temperature is increasing by $0.03^{\circ}\text{C}/\text{year}$ ($y = 0.03x + -42.4$) and CDD₂₀ is decreasing by $1.9^{\circ}\text{C}/\text{year}$ ($y = -1.9x + 4090$). R² values suggest the model explains 36% and 35% of the variance in (A) and (B) respectively. Some lines and points may not be visible due to the closeness of the data.

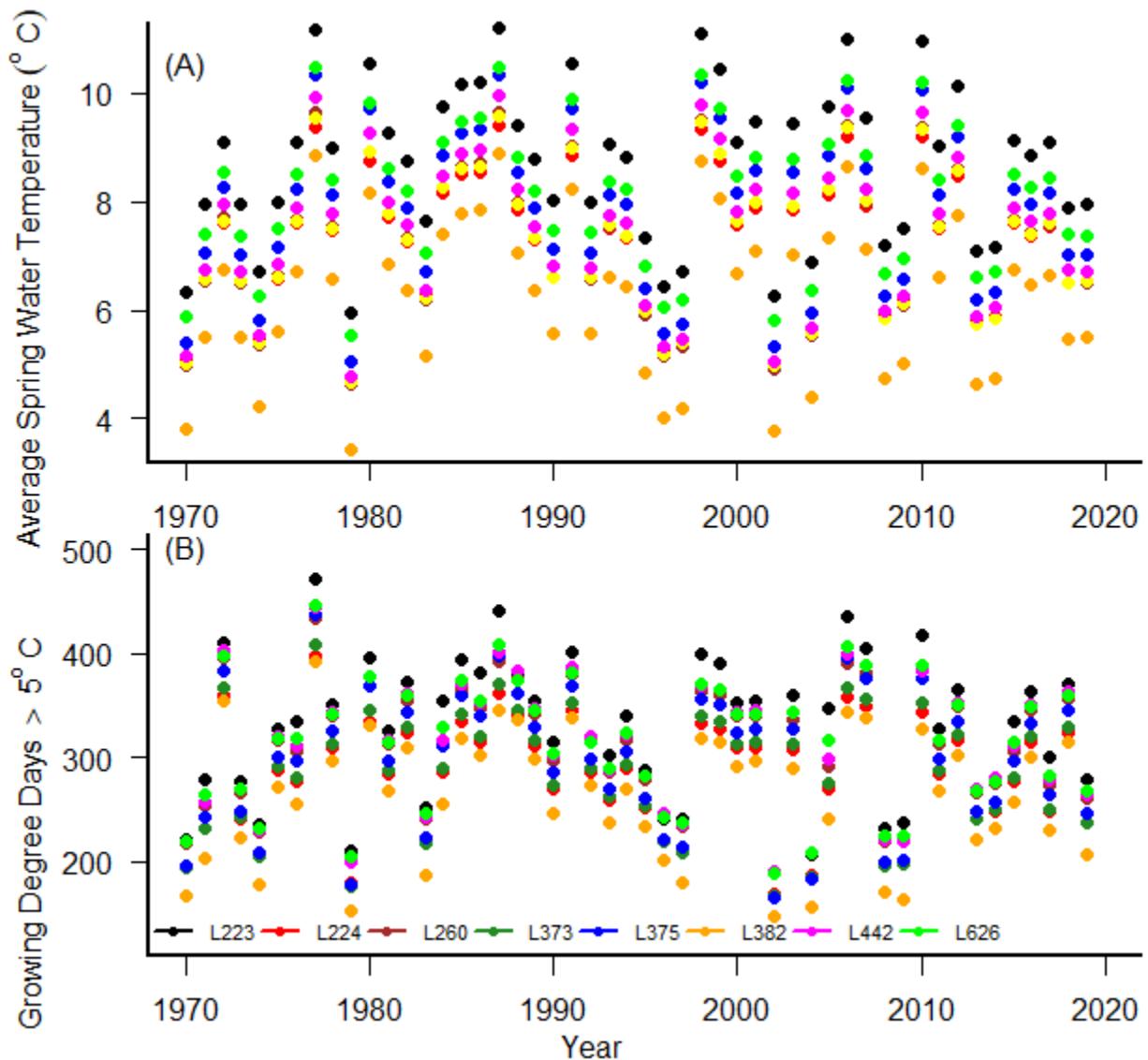


Figure 2.4. Seasonal spring climatic trends of mean spring water temperatures through time (A), and cumulative growing degree days through time (B). Average spring water temperature and GDD₅ are not significantly changing over time. Some datapoints may not be visible due to the closeness of the points.

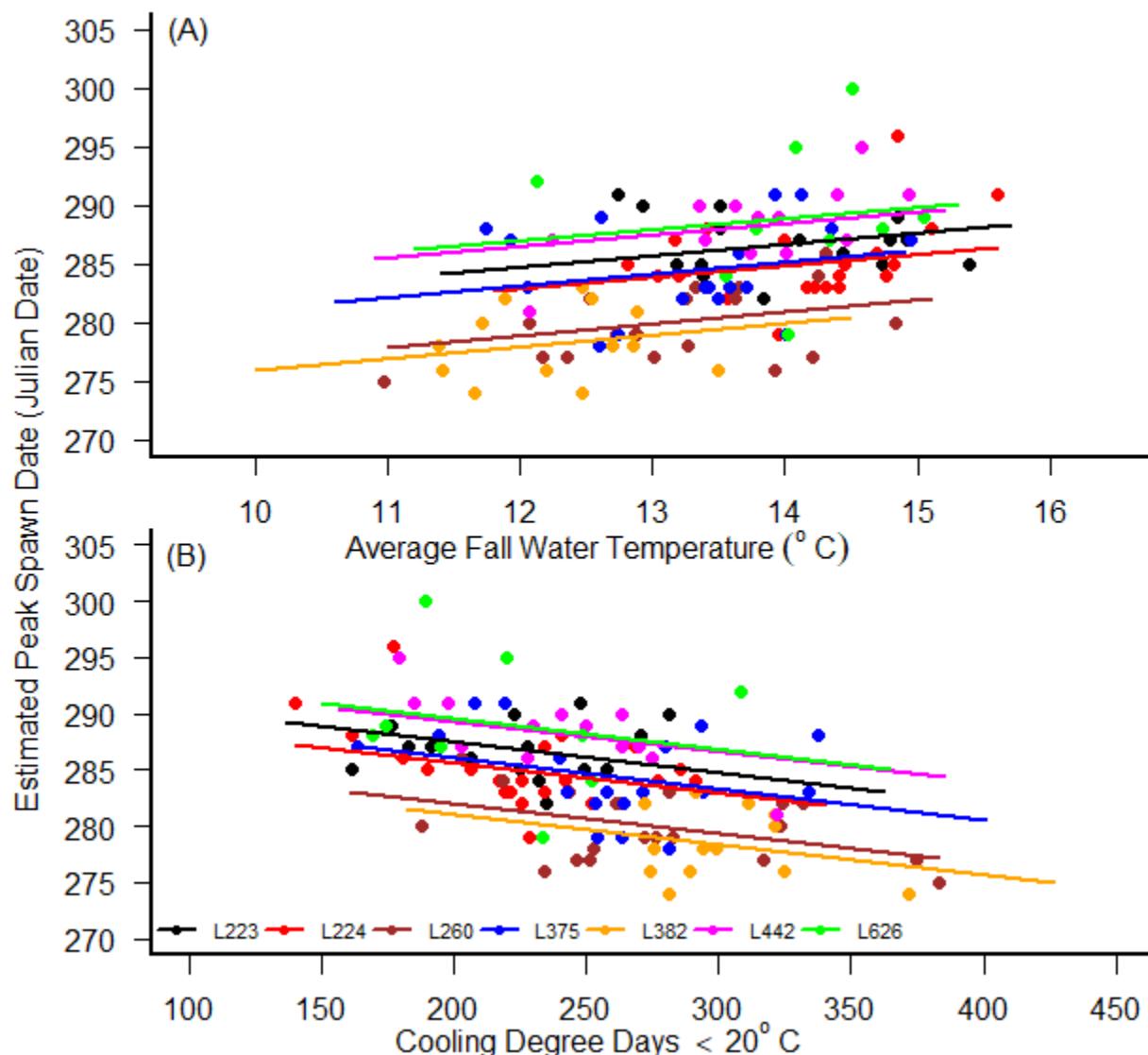


Figure 2.5. Estimated peak spawning date of Lake Trout in relation to (A) average fall water temperature and (B) cumulative cooling degree days. A 1°C increase to fall water temperature ($y = 1x + 272.9$) or 37°C day decrease in CDD₂₀ ($y = -0.03x + 292.9$) is needed to shift the spawning date later by 1 day. R² values suggest the model explains 52% and 54% of the variance in (A) and (B) respectively.

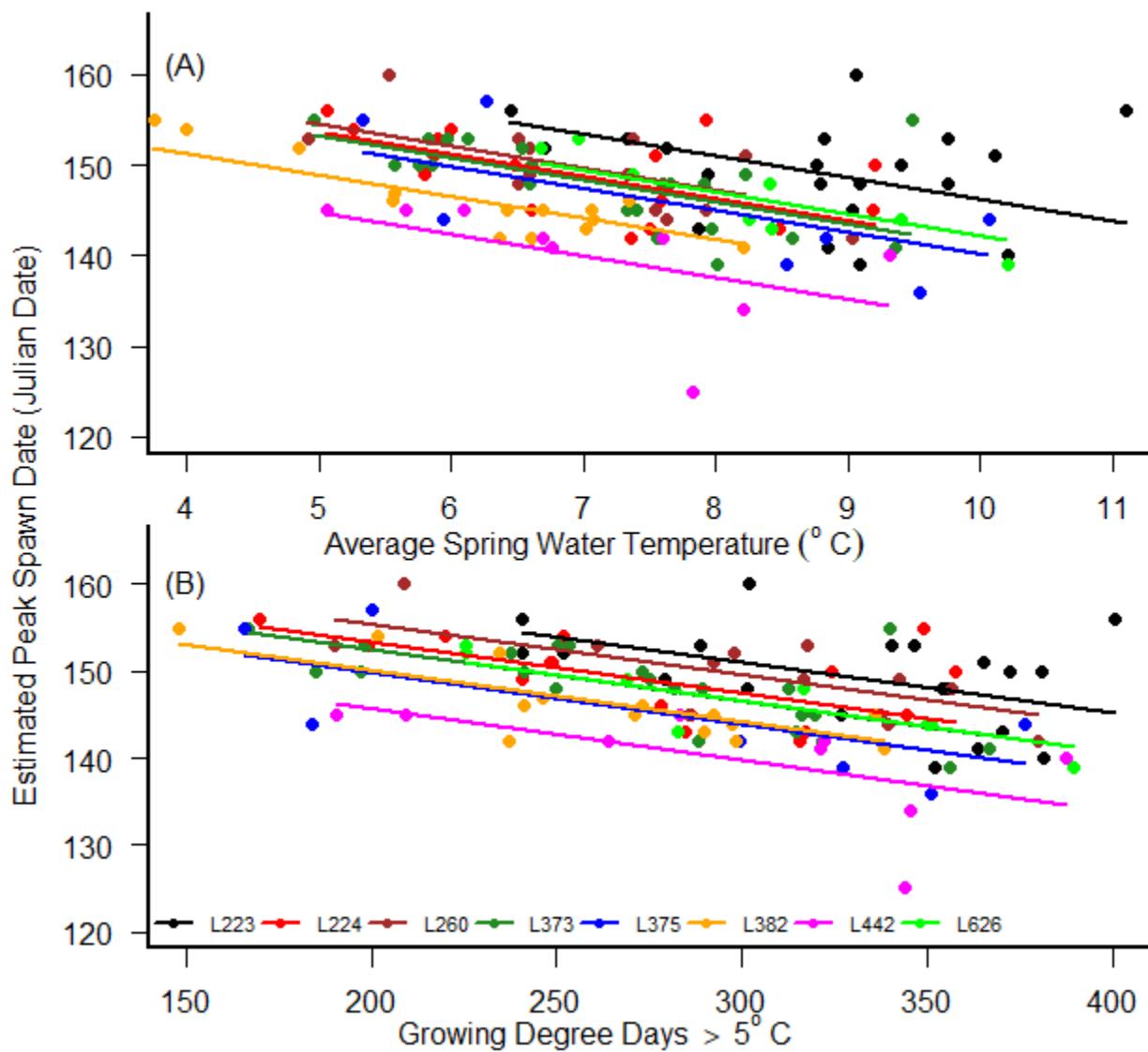


Figure 2.6. Estimated peak spawning date of White Sucker in relation to (A) average spring water temperature and (B) cumulative growing degree days. Approximately a 1°C increase to spring water temperature ($y = -2.4x + 170.5$) or 17°C day increase in GDD_5 ($y = -0.06x + 168.7$) is needed to shift the spawning date sooner by 1 day. R^2 values suggest the model explains 48% and 53% of the variance in (A) and (B) respectively.

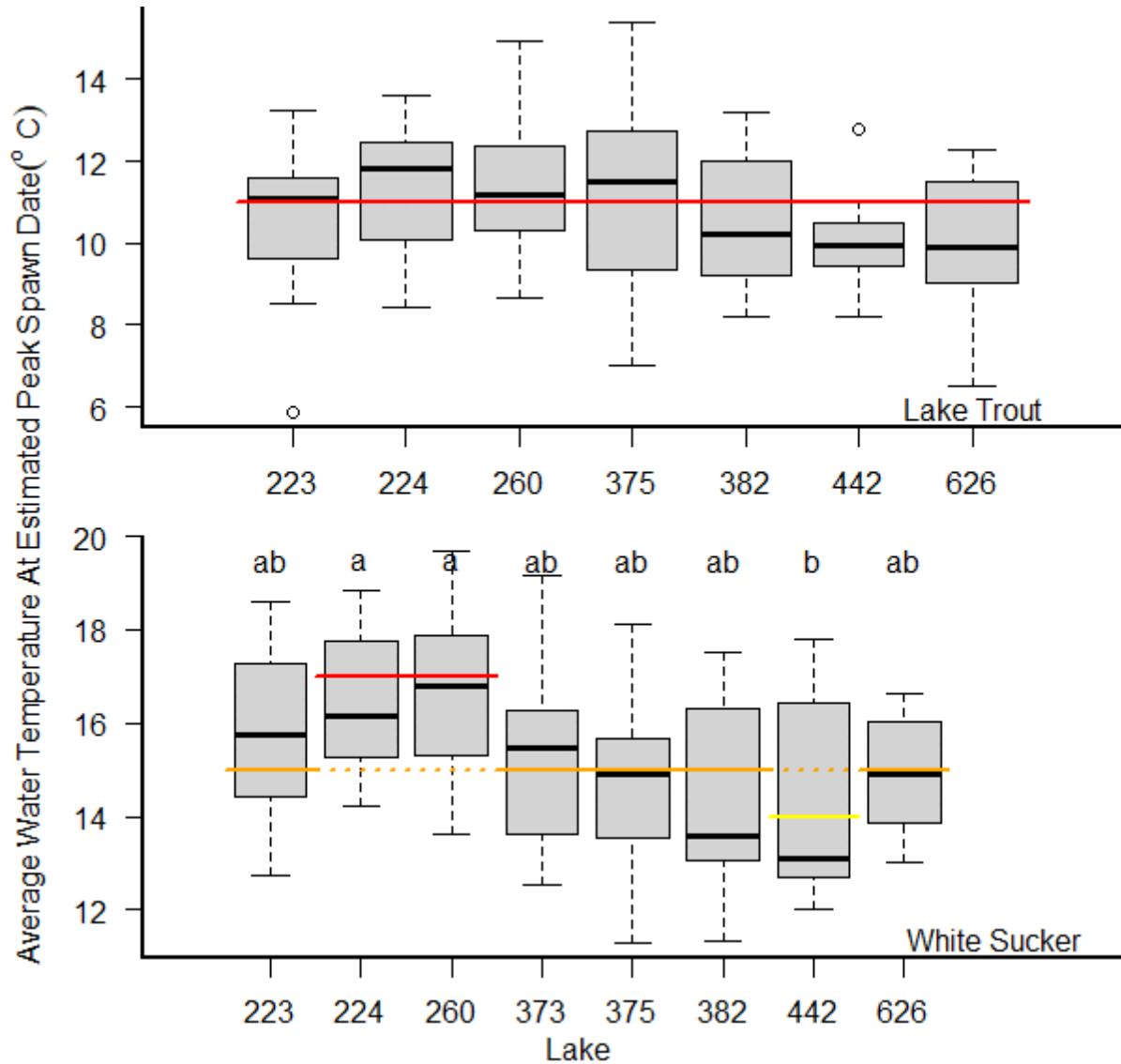


Figure 2.7. Average temperature at peak spawn date for Lake Trout (top) and White Sucker (bottom) among lakes studied. The lettering atop the White Sucker figure indicate results from post-hoc tests where differences among lakes were revealed. Lake Trout tend to spawn at a consistent temperature of 11°C across all lakes. White Sucker tend to have different thermal preferences at peak spawning across lakes and are separated by warm (16.8°C), medium (15.3°C) and cold (14.0°C) spawning temperatures. Mean spawning temperatures of lakes are represented by the solid horizontal lines.

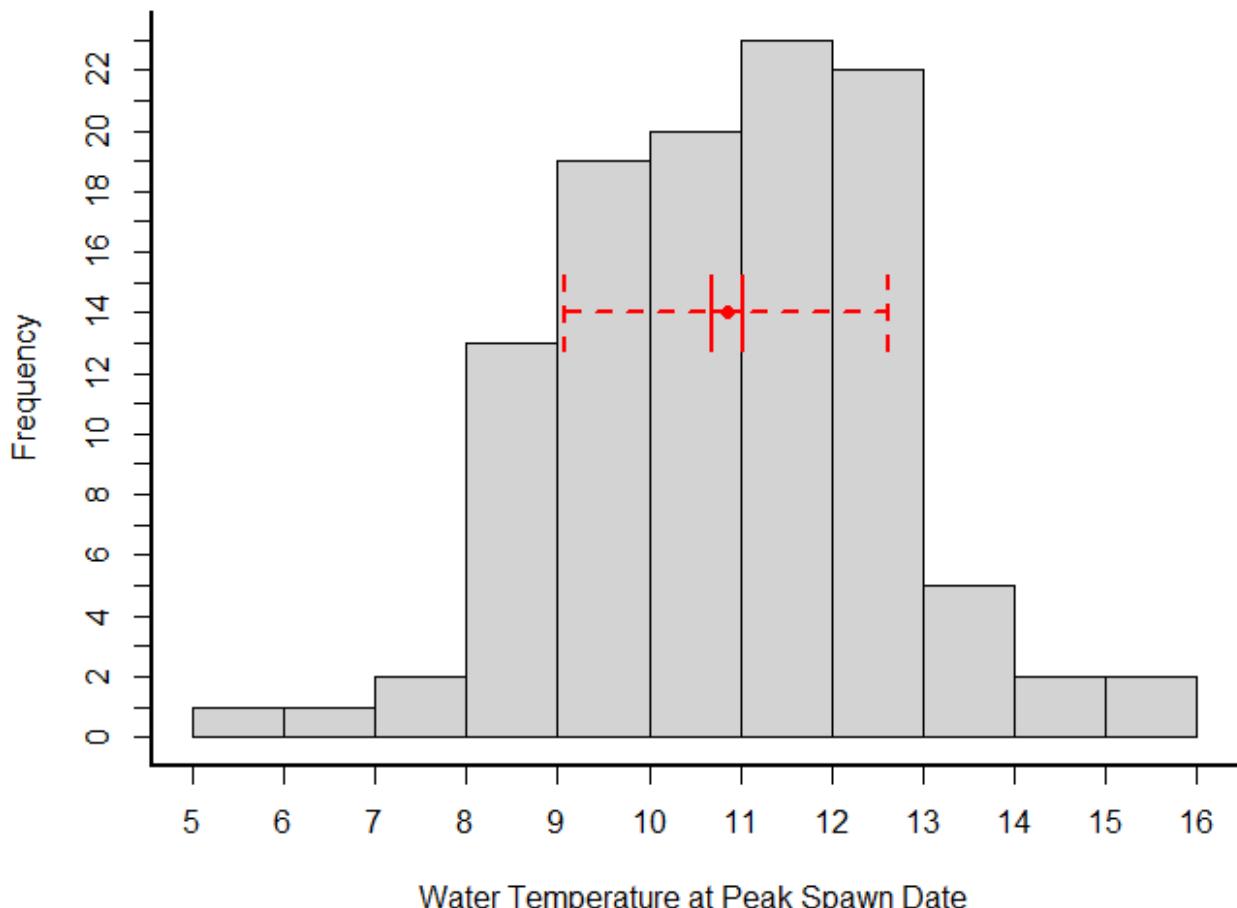


Figure 2.8. Frequency histogram of water temperatures recorded on date of peak spawn for Lake Trout. Water temperatures are a mix of observed values when data was present on the peak spawning date, and predicted values when no observed data was recorded on the date. Red dot represents mean temperature of 10.9°C. solid error bars represent +/- 1 standard error of the mean (0.17) and dashed error bars represent +/- 1 standard deviation of the mean (1.77).

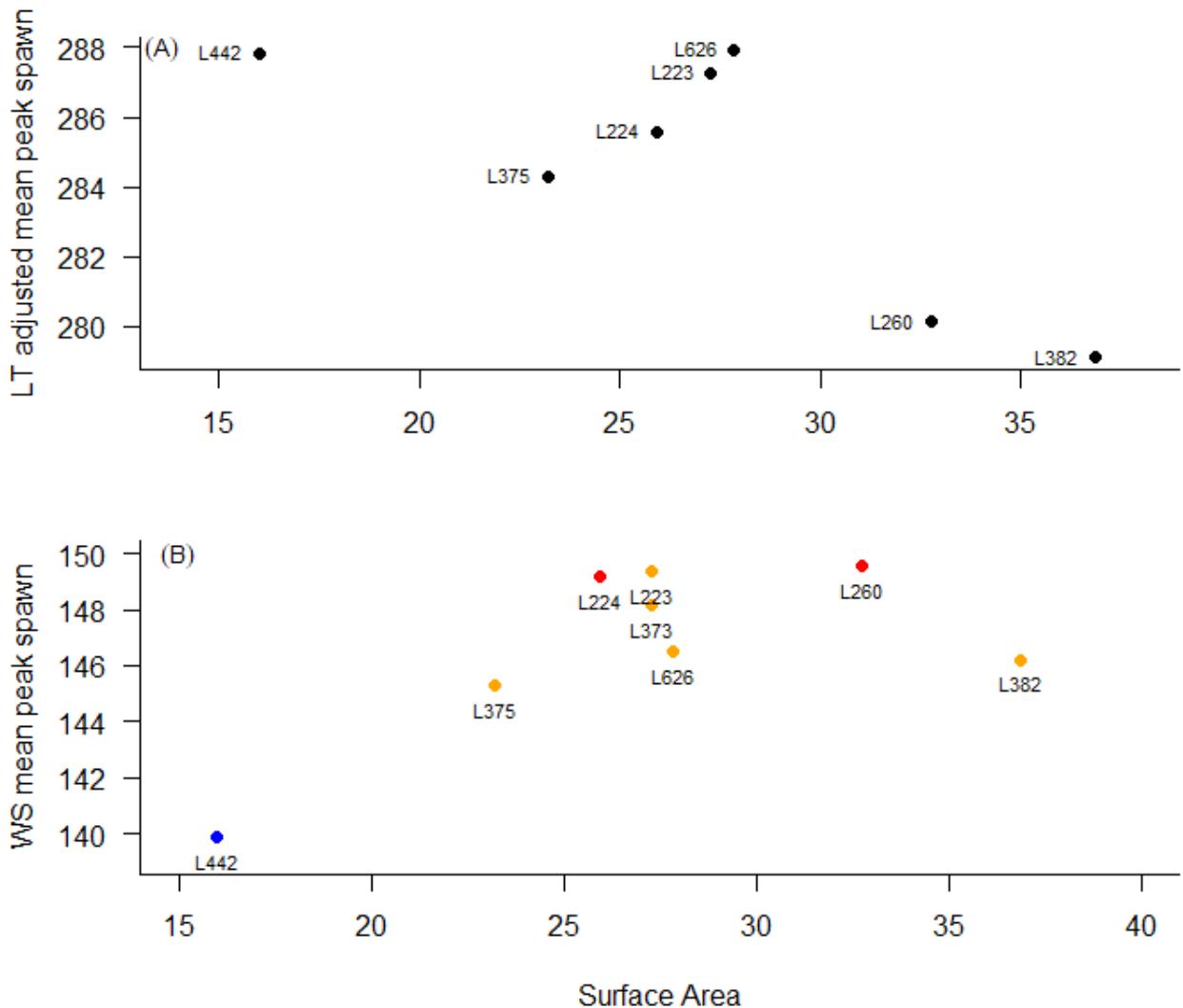


Figure 2.9. Correlation plot between estimated peak spawning date of Lake Trout (A) and White Sucker (B) versus the physical lake characteristic surface area. The Lake Trout plot was significant and the White Sucker plot was nearly significant. Correlation coefficients (r) indicate strong negative agreement in Lake Trout ($r = -0.76$) and moderate-strong positive agreement in White Sucker ($r = 0.65$). Colour differences in the White Sucker plot represent different critical spawning temperatures among the lakes as seen in Figure 2.7; Blue = cold lake (14°C), Orange = mid-temp lakes (15.3°C) and Red = warm lakes (16.8°C).

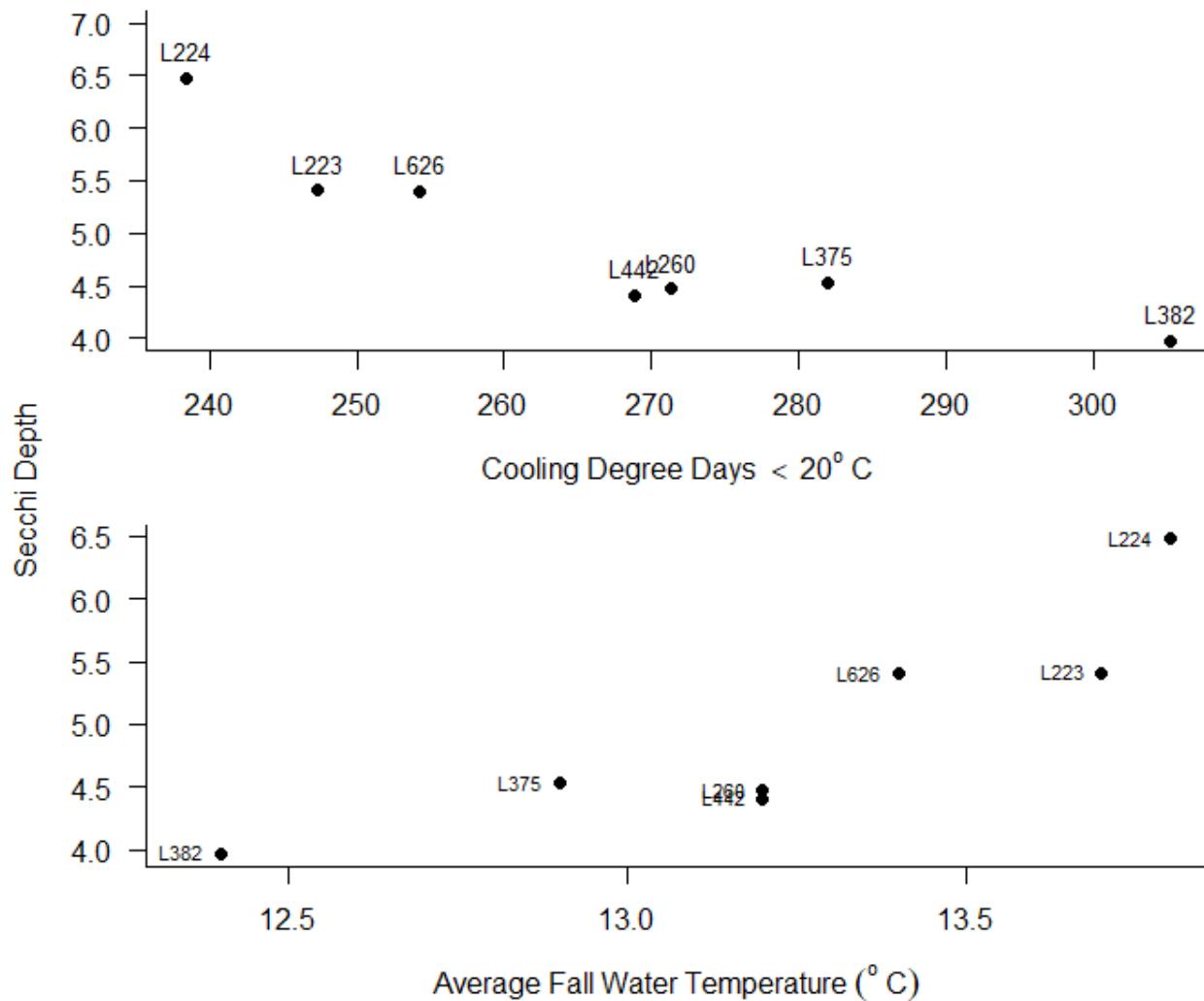


Figure 2.10. Correlation plot of depth of Secchi readings as a measure of water clarity between sum cooling degree days (A) and average fall surface water temperature (B). Both plots were significant and highly correlated (plot A $r = -0.9$; plot B $r = 0.87$)

Chapter 3 Mechanisms of climate-related growth declines of White Sucker

ABSTRACT

Climate change is expected to disrupt aquatic communities globally and research suggests declining fish body size is an expected outcome. White Sucker (*Catostomus commersonii*) are an environmentally tolerant, non-game species with a North American-wide distribution that may prove useful as a sentinel species for climate effects monitoring. I evaluated long-term (20–40 year) datasets for potential climate-induced size reductions of White Sucker in 3 Northwestern Ontario lakes with extensive data on abundance, climate, and food availability (ELA lakes), and 4 other lakes in the region lacking detailed ecosystem-level data (Northern Development, Mines, Natural Resources and Forestry; NDMNRF lakes). White Sucker of representative age classes from ELA lakes declined in size by 25 – 95% in weight, 17 – 64% in length, and 11 – 26% in length-based body condition. Examination of growth drivers identified growing degree days, food availability, and abundance all as negative contributors to growth declines at various ages, though the most likely affect was via increased abundance. Within the four NDMNRF lakes, fewer and lesser growth declines were observed across age classes, yet there were observed weight and length declines of ~ 50% and 20% respectively, indicating some level of effect on these populations as well. These results demonstrate how a warming climate may improve survival and cause a population level response in species via density dependence to alter size distributions of populations. This research further advances the knowledge of climate change research by describing observed trends in a widely distributed non-game species and provides evidence for its potential utility as a sentinel species for climate monitoring projects.

Keywords: body size, *Catostomidae*, hierarchical partitioning, juvenile, metabolism, size at age, survival

INTRODUCTION

There is growing evidence that climate change directly affects the body size of fishes, both in marine and freshwater environments (Lefort et al. 2015; Lynch et al. 2016; Lema et al. 2019). As ectotherms, the asymptotic body size of fish is partly governed by the Temperature Size Rule (TSR; Atkinson 1994). While there is debate regarding the exact mechanism by which TSR operates (Pauly 1981; Atkinson et al. 2006; Pörtner et al. 2017), and whether these mechanisms are valid descriptors of the pattern or not (Lefevre et al. 2018; Pauly and Cheung 2018; Audzijonyte et al. 2019), this rule describes the otherwise widely observed phenomenon that higher temperatures beget fish of smaller body sizes (Kolding et al. 2008; Daufresne et al. 2009; Pauli et al. 2017). However, a common criticism of such observations made in populations experiencing active fisheries is that harvest has a similar effect on body size (Zimmermann and Jørgensen 2015; Ahti et al. 2020). Thus, potential fisheries effects must either be accounted for in statistical models (e.g., Tu et al. 2018) or investigated in populations not subject to fishing pressure.

Climate change may also affect fish body size indirectly. Food availability is well correlated with growth potential and survival in fishes (Borgmann and Ralph 1985; Anderson and Sabado 1995; Biro et al. 2004; Rennie et al. 2009), and changes to primary production are known to result in similar changes in overall fish production (Downing et al. 1990; Downing and Plante 1993; Blanchard et al. 2012; Hecky and DePinto 2020). The impacts of climate change on planktonic communities have been well documented, where variable responses to phenology, abundance, distribution, size, and community structure have been observed, with many suggesting zooplankton communities may be more variable year to year (Winder and Schindler 2004; Vadadi-Fülöp et al. 2012; Hébert et al. 2021). A significant concern regarding

phenological changes has been the potential effect of a warmer temperature on important predator-prey dynamics of phytoplankton and zooplankton, leading to longer time-lags between peak abundances and greater discrepancies in biomass transfer to zooplankton, which may ultimately reduce resources available to fishes of all life stages (Winder and Schindler 2004; Thackeray 2012). Climate may also limit fish growth indirectly through limiting population size; fish growth is density dependent (e.g., Chen and Harvey, 1995; Pierce et al., 2003), and climate-induced changes may affect habitat space (e.g., total volume or thermal suitability; Shuter and Meisner, 1992), or by a net change in recruitment success and mortality, both of which directly impact abundance (Lynch et al. 2016).

Given these potential impacts of climate on fishes, certain attributes may make some species good sentinels for understanding impacts of climate on fisheries. Sentinel species are generally useful in identifying the status of a community, habitat, or ecosystem, and have been widely adopted in environmental monitoring programs (Beeby 2001; Zacharias and Roff 2001). Good sentinel species are generally defined as ubiquitous in distribution, abundant, easy to identify, tolerant to (but manifests a change in) a wide range of environmental conditions, and large enough to provide materials for analysis (Beeby 2001). Sentinel species previously proposed to quantify climate change impacts include Gentoo Penguins (*Pygoscelis papua*; Carpenter-Kling et al., 2019), Pacific Oysters (*Crassostrea gigas*; Thomas et al., 2018), western North American stoneflies (genus *Lednia*; Green et al., 2022), and various apex marine predators globally (Hazen et al. 2019), but few freshwater fish examples currently exist.

The biology of the White Sucker (*Catostomus commersonii*) lends itself well to their potential use as a species for evaluating climate change impacts. White Sucker are an easily identifiable, relatively longer lived large-bodied fish with a broad North American distribution

and are typically highly abundant in the waterbodies they inhabit (Scott and Crossman 1973). Additionally, they are poorly regarded as a species for commercial, recreational or sustenance fisheries, and thus rarely experience significant fishing mortality compared to other targeted species (Scott and Crossman 1973). White Sucker are a cool water species with a broad thermal tolerance (Scott and Crossman 1973; Bond and Machniak 1979; Wakefield and Beckman 2005; Hasnain et al. 2010), and occupy environments known to be experiencing climate change (Guzzo and Blanchfield, 2017, this study). Indeed, the use of White Sucker as a sentinel species for the evaluation of environmental impacts in both lake and river environments has been validated through its use in environmental effects monitoring projects Canada-wide, from the Alberta oil sands to Northern Ontario pulp mills (Doherty et al. 2010; Miller et al. 2013; McMaster et al. 2020).

Growth of White Sucker can be highly variable among populations (Scott and Crossman 1973; Chen and Harvey 1995), and correlated with several factors; growth of younger age classes are heavily dependent upon food availability, where higher densities of benthos, specifically chironomids, are associated with increased growth rates (Trippel and Harvey 1987; Chen and Harvey 1995). White Sucker can reflect bi-modal feeding distributions, favouring either benthivory or zooplanktivory (Saint-Jacques et al. 2000). Larger asymptotic sizes of White Sucker are generally correlated with less abundant populations (Trippel and Harvey 1987; Chen and Harvey 1995). The presence of piscivorous fish (via increased mortality and competitive release) can also improve growth of immature suckers (Bertolo and Magnan 2005). Finally, environmental temperatures can also influence growth trajectories of White Sucker via metabolism, where increased temperature results in greater oxygen consumption (Beamish

1964), though behavioural thermoregulation in this species is also known to occur (Trippel and Harvey 1987).

Given that the optimal temperature for adult White Sucker growth is 25.5°C (Hasnain et al. 2010), growth in the northern portion of their range might be predicted to increase with a warming climate. However, negative impacts are possible if a warming climate impacts variables known to alter growth such as reducing food availability, increasing population density, or increasing metabolic function beyond an optimal rate. The objectives of this study were therefore to 1) assess whether changes in White Sucker growth were occurring in unharvested, unmanipulated lakes over a 41 year time series in a region of Northwestern Ontario where climate change has been well-documented (Guzzo and Blanchfield 2017), 2) evaluate variables important in explaining growth variation in these populations, and 3) assess the generality of these findings when applied to other White Sucker populations not subject to intense targeted fishing harvest in Northwestern Ontario.

METHODS

Study Site

To evaluate long-term changes in growth and growth correlates in White Sucker, I used data from three lakes within the IISD Experimental Lakes Area (ELA) located East of Kenora Ontario, Canada, from 1976 to 2019 (Appendix 1 Figure A). Specifically, Lakes 224, 373 and 442 were selected, all of which are part of the Long-Term Ecological Monitoring program, which are closed to fishing and not manipulated, thus reflecting only natural variability of the region.

Collections of White Sucker biological information has occurred on a near-annual frequency during the period of study. Sampling began on Lake 224 in 1976, followed by Lake 442 and 373 in the mid 1980's. Lake 442 was last sampled in 2008 and only recently resumed spring sampling in 2019; due to the large gap between sampling events, the 2019 data were not assessed in this study (Table 3.1). Field sampling efforts occurred during the spring and fall. Beamish-style trap nets (Beamish 1972) were used to catch White Sucker congregating near spawning shoals in spring and through random encounters during the fall. Captured fish were temporarily held in large tubs of lake water for transport from nets to the sampling site onshore.

Morphometric data of fork length (FLEN; nose to inside fork of caudal fin), total length (TLEN; nose to farthest point of caudal fin) and round weight (RWT; weight on capture) were measured and recorded, and the leading 1-3 rays from pectoral or pelvic fin were clipped and taken for age analysis. Sex and spawning condition of an individual were determined in spring by the expression of gametes from gently applying pressure down the abdomen of the fish towards the anus. To facilitate population estimates, fish were tagged via seasonal batch marks on the dorsal fin to quickly identify the capture years of the individual and identify fish captured previously in the current sampling period. Prior to 2017, a subset of White Sucker larger than 200 mm were targeted for application of a 4-digit, externally sutured Carlin tag each spring to provide individual-level information. Starting in 2017, all White Sucker larger than 200 mm encountered were also implanted with a unique 15-digit passive integrated transponder (PIT) tag. Morphometric data from fall sampling efforts were excluded from size analyses as fall data can lead to ageing and size at age biases. However, estimates of population size from the fall were used in conjunction with spring population estimates to provide a yearly average population

estimate. To fill in gaps where estimates for one or both time periods were absent, linear interpolation was used.

To evaluate the generality of findings from ELA lakes to other Northwestern Ontario lakes, additional White Sucker populations were investigated through data provided by biologists from the Ontario Northern Development, Mines, Natural Resources and Forestry (NDMNRF) for Lac des Milles Lacs (LDML), Lake of the Woods (LOTW), Lake Nipigon, and Whitefish Lake (hereafter collectively referred to as NDMNRF lakes; Appendix 1 Figure B). These lakes were selected because they have historical datasets comparable in length to those evaluated from ELA lakes; LOTW data began collection in 1986, followed by Whitefish in 1989, and LDML and Nipigon both began generating consistent sampling programs in 1999 (Table 3.1). In proximity to the ELA field station, Whitefish Bay of LOTW is the closest, lying only ~ 30km southwest in a straight-line distance. The remaining 3 lakes are to the east or southeast of ELA, ranging from 230km – 330km away. All four lakes are larger than the study lakes at ELA, with LOTW and Lake Nipigon being two of the largest inland lakes in all of Ontario by surface area. These lakes also tend to support more diverse ecosystems, and all are subject to varying degrees of anthropogenic disturbance in the form of fishing (recreational, commercial, or subsistence), pollution, eutrophication, and the introduction of invasive species. Sampling of these lakes has been performed via fish community index netting (FCIN; (Salmon and Livingston 1997, 1998; Mosindy 2011), fall walleye index netting (FWIN; Morgan, 2002) and broadscale monitoring (BSM; Sandstrom et al., 2013) programs during the time period under investigation. These programs employed gillnets set overnight (16+ hours) at randomly selected sites and destructive biological sampling was performed on the catch, where morphometrics, sex, and ageing structures were all collected. Sampling occurred during the summer and fall months for these

programs, which contrasts with the ELA's emphasis on the spring period for size and age data, however the sampling frame has been consistent over years for each waterbody, thus minimizing bias arising from variable catch periods. White Sucker were not of primary focus during much of the sampling on LOTW and Nipigon, therefore sex data in these datasets were sparse and investigations of changes in size at age over time are based on pooled samples that do not differentiate based on sex. Due to the large size of LOTW and Nipigon, data collected through the BSM program (2008 – Present) was conducted regionally, where a full sampling of the lakes occurred over two sampling seasons. This sampling effort should not affect size at age estimates over time as the sections of these lakes are not physically obstructed from one-another, and White Sucker in these lakes are free to move throughout the entire lake.

Ageing Structure Preparation and Interpretation

White Sucker fin rays are regarded as the most accurate and accessible ageing structure, making them the preferred option to age populations for several organizations including the ELA and Ontario NDMNRF (MacCrimmon 1979; Chalanchuk 1984; Sandstrom et al. 2013). The pectoral fin ray method is a proven and validated technique for ageing White Sucker, and is a reliable method for ageing older fish as well (Chalanchuk 1984). Pectoral fin rays can be attained from fish through non-lethal sampling which lends itself well to mark/recapture studies and tracking longer term trends in age over time (MacCrimmon 1979; Chalanchuk 1984).

Slide preparation of 2014 – 2019 ageing structures were performed as described in Pritchard et al. (2019). Briefly, fins were cured in epoxy using a 2:1 mixture of resin to hardener and set to dry under a fume hood for 24 hrs. Once dried, cross-sectional cuts were made using a Buehler low speed jeweler saw. The first cut was made close to the edge of the sample to remove the frayed edge caused by sampling tools used during field collection and to establish a

perpendicular axis across the fin ray. After the initial cut, 4 cross-sectional pieces were taken from the fin, with a target thickness of 80 – 90mm. Each piece was then rinsed in water to remove dust and placed on a slide from left to right in order of the cuts performed, where consideration was given to the orientation of the placed cross-section so that each cross-section showed annuli of a different cut. Shandon mounting media was applied using a plastic pipette which secured the cross sections in place, and were set to dry under a fume hood for 24 hrs. Fin ray cross sections of both recent and historical data were viewed using a LaxcoTM LMC 4000 Trinoc Microscope, and age estimation was performed using the marginal increment analysis method (Campana 2001). NDMNRF biologists used the same preparation and ageing methods.

Confirmation of Historically Assigned Ages

To ensure standardization in age determinations in our datasets over the time series among different readers, a comparison of age assignment between readers was undertaken. From 1973 to 2013, two different biologists were responsible for the ageing of ELA White Sucker, where the second biologist began age interpretation in the early 1990's (Ager 1: Pre 1995, Ager 2: Post 1995). The ability of the post-1995 reader (Ager 2) to accurately assign ages using the pectoral fin ray for these populations had been previously confirmed (Chalanchuk 1984). Due to the inherent subjectivity required in assigning age estimates, the potential for interpretation error can be high among different readers, justifying the need for an independent evaluation (Campana 2001). To do so, I independently re-aged White Sucker fin rays collected pre- and post- 1995. Comparison and confirmation of ages from the two periods were performed using percent agreement. Slide boxes of White Sucker slides were randomly selected from the available collection of ageing samples, and slides were aged blindly (i.e., without prior knowledge of the previously assigned age for any given specimen) to remove potential bias.

Updating Ageing Records

Age determination for White Sucker collected from 2014 to 2019 was required for the study. To ensure good characterization of ages from across the size distribution of available fish, fork length data were sorted into size bins by increments of 50mm. Up to 20 fish per 50 mm size bin per year in each lake were randomly selected, and where possible, were split equally between sexes (10 males and 10 females). Confidence values on a scale of 1 – 10 (low – high) were assigned with each estimated age. Once ages were assigned and entered into a computer database, the age for individuals with prior or later detections (based on their individual tag number) were assigned by addition or subtraction from the year of observation compared to the year of capture when fish were aged. In total, I aged 326 samples from Lake 224 and 313 samples from Lake 373.

Additionally, a small collection of fish ($N = 36$) were captured during the fall of 2020 in Lake 224 to assess and confirm my ability to produce accurate ages. Only fish that had previously been captured, tagged, and had an ageing structure taken were selected in 2020, allowing for the assignment of two ages to the same individual fish (based on tag number) over a known passage of time. In total, 72 slides of fin ray cross-sections were viewed from 36 fish ($N = 36$ fish \times 2 fins/fish = 72 slides).

Temporal Size at Age Analysis- ELA lakes

This study evaluated changes to White Sucker size at age as a proxy for changes to growth rates (and hereafter referred to as growth; Ahti et al., 2020) over time for three morphometric variables: fork length (FLEN), round weight (RWT) and body condition (BCD). Body condition was assessed using a length-based method, and calculated using a standard weight equation for this species (Bister et al. 2000):

$$(1) \quad \text{Body condition} = \text{Round weight} / 10^{-4.755+\log_{10}(\text{Fork length}) * 2.94}$$

The standard weight equation generates an indexed measure of mass relative to the 75th percentile of weight for a given length for the species and can be applied to fish with a fork length of 100mm or greater in length.

Based on an assessment of age-at-maturity (determination of the 20% quantile of all male or female data for a given lake; Appendix 4 Figure A; M. Rennie Pers. Comm.), male and female White Sucker begin to mature in ELA lakes between 3–5 years of age. Based on this, populations were separated into an immature dataset (consisting of ages 1 – 4), and a mature dataset (consisting of ages 5 – 10). The immature dataset used only White Sucker for which sex was undetermined to exclude early maturing fish. Conversely, the mature dataset used only sexed individuals, separating for males and females due to known size dimorphism among sexes within this species (Scott and Crossman 1973). Age 10 was selected as the final age class to include in the analysis, as initial analyses indicated that asymptotic size for females was achieved by age 10 and few males older than age 10 occurred in the dataset.

To analyse changes over time in average FLEN, RWT, and BCD at age of immature and mature White Suckers, linear models were fit for each dataset using Lake, Age, Sex, and Year as predictor variables (Quinn and Keough 2002). Models were fit beginning with a 4-way interaction term; non-significant interactions were progressively removed until the simplest model with only significant interactions was determined. Both datasets used Lake and Age as categorical variables and Year as a continuous variable. The dataset of mature fish also included Sex as a categorical variable. Age class 1 was not evaluated for BCD analysis because few fish in this age class were greater than 100mm (Bister et al. 2000).

Temporal Size at Age Analysis- NDMNRF Lakes

Similar to ELA lakes, changes to growth (from size at age data) of White Sucker in populations of other Northwestern Ontario lakes were evaluated based on the change in average FLEN, RWT and BCD over time and linear models were fit to the data in the same fashion as performed in the ELA populations (Quinn and Keough 2002). Maturity and maximum age class breakpoints of 4 and 10 respectively were similarly applied to these datasets. Mature fish in LOTW and Lake Nipigon were assessed without sex as a categorical predictor variable (see above).

Comparison of Growth Changes among White Sucker Populations

In order to help interpret complex lake-specific interactions in my models, comparisons of changes in growth were made between all ELA and NDMNRF study lakes by estimating a rate of change (slope of linear decline or annual percent change) for representative age classes and also the total size decline over each lake's study period, calculated from the equations predicted by fitted linear models.

Evaluation of Potential Drivers of Size at Age

To understand variables associated with observed changes in the growth of White Sucker, three variables were examined related to climate variability, resource availability and intra-specific competition: climate variability was assessed as cumulative Growing Degree Days of surface water temperature above 5°C during of the open water season (GDD₅; Neuheimer and Taggart, 2007; Venturelli et al., 2010); food availability was measured as average annual zooplankton biomass (ug/L dry weight), and population density, measured as annual average abundance estimate. GDD₅ was calculated from predicted daily water temperatures (Chapter 2) and population estimates were derived by using a Schnabel census based on the numbers of

marked and unmarked fish within a sampling period and estimated over multiple capture events in each lake. While benthic invertebrate data are largely unavailable from ELA lakes, Kidd et al. (2014) showed that emergence patterns of invertebrates from Lake 442 during 1999-2003 mirror trends in peak zooplankton biomass within a season, suggesting that zooplankton biomass is an accurate representation of the temporal trends in food available to White Sucker generally. Further, limited diet analysis of White Sucker from ELA lakes indicates a high degree of zooplanktivory (Rennie et al., unpublished data) and is supported by observations in other small Ontario lakes that report high rates of zooplanktivory (Saint-Jacques et al. 2000). Moving averages from 1 – 10 years were calculated and offset by 1 year so that the value of the predictor variable matched the age class under evaluation to better reflect the conditions experienced during the cumulative lifespan by a given age class. For example, to represent the average food availability over the lifespan for spring captured age class 4 White Suckers of 1994, a 4-year average of zooplankton biomass during 1990-1993 was chosen. The cumulative growth of the fish in 1994 has not realized the effect of the current year's food availability but is rather a function of the prior conditions experienced over the lifetime of the fish. Years where food availability and population estimates were missing were interpolated linearly from the preceding and succeeding year's estimates.

Analysis of Growth Drivers: Hierarchical Partitioning

Hierarchical partitioning (HP) was employed to determine the joint and independent contributions of climate variability, food availability and population density on White Sucker growth (Mac Nally 2002). This method does not seek to develop a single ‘best’ model to explain growth, but rather evaluates all possible models in a multiple regression setting to identify the most likely causal factors (Mac Nally 2000, 2002). The HP method accomplishes this by

considering the average influence one variable provides over all models in which it appears (Mac Nally 2000). Additionally, the averaging method employed is thought to reduce multicollinearity, a significant problem for multiple regression models when present (Mac Nally 2000, 2002). To determine the statistical significance of the predictor variables, the data matrix was randomized 999 times and the distribution of independent variable contributions were computed. Extreme independent values relative to the randomized distribution were expressed as Z-scores, where Z-scores equal to or greater than +/- 1.65 (upper 95% CI) were considered to be statistically significant explanatory variables in the analysis (Mac Nally 2002). If the Z-score for a variable was nearly significant, the data matrix was re-randomized, this time with 9999 iterations to better determine whether the variable was significant or not.

For the sake of simplicity, HP was applied to only representative age classes for each of mature and immature White Sucker datasets. Consideration as to which age classes to use were dependent upon 3 criteria: (1) model output: e.g., if the model was additive, one age class in the mature or immature dataset was selected as representative of all the other age classes. (2) Rate of change: e.g., if the model in a dataset was not multiplicative, and two or more subgroups of age classes were similar amongst themselves yet different between subgroups, one age from each subgroup would be selected. (3) Available data: e.g., the age class with the most data available across the time series was selected, all else being equal. From this selective process, age classes 4, 6, and 8 from Lake 224, age classes 2, 3, and 5 from Lake 373, and age classes 4 and 5 from Lake 442 were selected. All mature age classes were analyzed using female data, though patterns in female size at age should be representative of males as sex was additive in all models (see results). Lake 442 did not have a second mature age class evaluated for HP due to sparse data in older age classes, exacerbated by the shorter sampling frame available (and these two factors

leading to misalignment of the size at age data with the moving average estimates of predictor variables).

Tests of linear model assumptions

Assumptions of the statistical models were evaluated to ensure residuals of the models were normal and evenly distributed. In cases where residuals failed normality testing using Anderson-Darling's Test for Normality, \log_{10} and square root transformations were first applied to the response variable, and continuous predictor variable if necessary. If normality was not satisfied after transforming both variables using \log_{10} , the results were still accepted though interpreted with caution. Cases where transformations were required, and whether normality was successfully resolved or not by transformations are noted in the results.

RESULTS

Age Validation

Pre-1995 (Ager 1), a total of 282 fins were re-examined. Of the 282 fins, 234 were aged the same as the previously recorded age (83% exact agreement). 48 of these fins were aged one year apart, and no fins had age differences of 2 years or greater (100% within 1-year agreement between the previous age and my determination; Table 3.2, Figure 3.1). Post-1995 (Ager 2), I re-examined 274 fins. Of these, 260 fins had exact agreement between the previous age and my age (95% exact agreement; Figure 3.2), 13 fins were aged 1 year apart, and only 1 fin was aged 2 years apart. Thus, there was nearly 100% agreement within one year of samples re-examined, similar to the pre-1995 assessment (Table 3.2). Overall, 556 fins were examined between both eras and 555 of these fins were assessed to within 1 year of each other, suggesting that the

historical ageing data for White Sucker was robust between both eras and is consistent with determinations made for 2014-19.

Of the 72 fins selected for confirmation of interpretation of ages on the same individual fish, I was unable to confidently assign an age to three fish, which were thus excluded from the analysis. Blind evaluation of the remaining 33 fish (66 fins) yielded a 100% exact agreement between ages (Table 3.2); in all cases, the difference in assigned age between the initial capture and the 2020 capture was equal to the number of years difference between capture events for all fins evaluated. The maximum years difference between capture of fishes was 3 years (2017-2020), the youngest and oldest fish aged in this exercise was 5 and 17 years old respectively, and only 9% of ages were assigned 12 or greater (6 of 66), indicating determinations were largely made over age classes known to be reliably interpreted by pectoral fin rays.

Temporal Size at Age Analysis – ELA Lakes

Initial linear models attempting to describe growth revealed significant interaction terms between Year with the predictor variable Lake, indicating that changes in growth with time were different among lakes. To interpret results more easily, a lake-specific approach to data analyses was adopted (model equations and coefficients for all ELA lakes can be found in Appendix 5). When modelling size at age of the immature and mature data on a lake-specific basis, the predictor variable Year was significant (either as a main effect or as part of a significant interaction) in all lakes for all size variables except for Lake 442 BCD (Mature data), and in nearly all cases had a negative coefficient value, indicating declines in growth have occurred in ELA lakes. In the mature fish models, Sex was found to be a significant additive term in all cases (no interaction with other variables), such that females were always larger than males, reflecting sexual size dimorphism in this species, but rates of change over time were similar between males

and females. All models except for Lake 224 FLEN, and Lake 442 BCD (Mature datasets) required \log_{10} transformations on both the continuous response (size, as either FLEN, RWT or BCD) and predictor variable (Year) to satisfy the assumption of normality of residuals. For several models (indicated below), \log_{10} transformations of both the response and predictor did not satisfy normality. These results were accepted but interpreted with caution, as histograms of the residuals appeared generally normal with slight skews (Appendix 4 Figure B), and residual plots indicated that observed rates of change were more rapid than could be modeled with \log_{10} transformations, indicating models based on \log_{10} -transformed data are a conservative description of growth declines over time in these lakes.

Lake 224

Linear models for Lake 224 revealed negative relationships across time for both immature and mature White Sucker for all three size variables (Figure 3.3). Models describing immature fish were additive, indicating a similar growth decline among age classes over the period of study (ages 1-4; $\log_{10}\text{RWT}$ $\log_{10}\text{Yr}$: $F_{1,60} = 60.55, p < 0.001$; $\log_{10}\text{FLEN}$ $\log_{10}\text{Yr}$: $F_{1,60} = 53.01, p < 0.001$; $\log_{10}\text{BCD}$ $\log_{10}\text{Yr}$: $F_{1,51} = 37.93, p < 0.001$). Conversely, models on the mature datasets revealed Year*Age differences, suggesting that declines in growth rates of White Sucker were age-specific (ages 5-10: $\log_{10}\text{RWT}$ $\log_{10}\text{Yr}^*\text{Age}$: $F_{5,234} = 8.23, p < 0.001$; FLEN Year*Age: $F_{5,234} = 4.86, p < 0.001$; $\log_{10}\text{BCD}$ $\log_{10}\text{Yr}^*\text{Age}$: $F_{5,234} = 3.63, p = 0.004$). In Lake 224, immature age classes 1-4 declined annually by -7.6% in round weight, -2.4% in fork length, and -0.9% in body condition (Table 3.3). Mature age classes 5-10 declined annually by a range of values, most steeply in age class 6 for weight, length, and condition (-9.3%, -8.6mm, -0.8% respectively; Table 3.3). Age 8 fish declined by the slowest rates for all three variables (RWT: -

4.6%, FLEN: -5.3mm, BCD: -0.4%; Table 3.3). After transformations, normality was not satisfied for body condition in either mature or immature datasets, nor for mature RWT data.

Lake 373

The linear models for Lake 373 revealed negative relationships across time in the immature and mature fish for all three size variables (Figure 3.4). Immature fish revealed significant Year*Age differences for weight and length but were additive for condition, suggesting weight and length growth declines were occurring at different rates among immature age classes 1-4 but were consistent among ages for body condition (ages 1-4: \log_{10} RWT \log_{10} Yr*Age: $F_{3,81} = 4.53, p < 0.005$; \log_{10} FLEN \log_{10} Yr*Age: $F_{3,82} = 3.09, p = 0.03$; \log_{10} BCD \log_{10} Yr: $F_{1,67} = 32.29, p < 0.001$). The models produced from mature White Sucker were all additive, indicating that growth and condition of age classes 5-10 were declining at the same rate over time (ages 5-10: \log_{10} RWT \log_{10} Yr: $F_{1,168} = 36.34, p < 0.001$; \log_{10} FLEN \log_{10} Yr: $F_{1,169} = 33.28, p < 0.001$; BCD Year: $F_{1,168} = 23.9, p < 0.001$). Declines to growth among immature fish were greater in older age classes, where on an annual basis, age 2 weight and length declines were -3% and -0.9% respectively, age class 3 weight and length declines were nearly twice than those observed in age 2 (-6.2% and -1.9% respectively; Table 3.3). Body condition across all immature age classes declined slightly but significantly by -0.01 units annually (Table 3.3). Growth of mature males and females from age classes 5-10 declined annually by -3.8% in weight, -1.2% in length, and -0.5% in condition (Table 3.3). After transformations, normality was not satisfied for the mature models and body condition of the immature data.

Lake 442

Linear models describing growth changes in Lake 442 were unlike Lake 224 and 373 as the directional change in growth was not consistent across age classes (Figure 3.5). Immature

White Sucker growth models revealed additive relationships where declines to growth were occurring for all variables (ages 1-4: $\log_{10}\text{RWT}$ $\log_{10}\text{Yr}$: $F_{1,45} = 64.64, p < 0.001$; $\log_{10}\text{FLEN}$ $\log_{10}\text{Yr}$: $F_{1,45} = 63.84, p < 0.001$; $\log_{10}\text{BCD}$ $\log_{10}\text{Yr}$: $F_{1,42} = 22.5, p < 0.001$), whereas the mature White Sucker models produced significant Year*Age relationships indicating that each age class had a unique rate of change, and this change in growth was not uniform directionally (age 5-10: RWT Year*Age: $F_{5,76} = 4.36, p < 0.001$; $\log_{10}\text{FLEN}$ $\log_{10}\text{Yr}$ *Age: $F_{5,76} = 3.08, p = 0.01$). Unlike Lakes 373 and 224, condition of mature fish did not change significantly over time, but differences among age classes and sexes were present (age 5-10: $\log_{10}\text{BCD}$ Age: $F_{5,82} = 4.48, p = 0.001$, Sex: $F_{1,82} = 13.35, p < 0.001$). Annual growth declines of weight, length and condition in immature fish were -8.9%, -2.9%, and -0.6% respectively (Table 3.3). Mature fish experienced the widest range of growth changes, where age classes 5, 6 and 7 declined in weight and length by as much as -8.2g and -0.4% respectively, versus age classes 8, 9 and 10 where weight and length increased annually by as much as 37.5g and 0.7% respectively (Table 3.3). However, it is important to note that declines in growth of younger age classes all occurred after 2000, whereas observations of fish from these older age classes after 2000 were sparse, making evaluations of growth declines during this period of time impossible (Figure 3.5). After transformations, normality was not satisfied for length and condition in the mature dataset.

Temporal Size at Age Analysis- NDMNRF Lakes

Initial linear models attempting to describe growth discovered significant Year*Lake interaction terms, indicating lake-specific modelling was required. Lake-specific modelling of NDMNRF populations revealed significant positive, negative, and no trends over time, depending on the lake (model equations and coefficients for all NDMNRF lakes can be found in Appendix 6). In all mature lake-specific models, Sex in White Sucker models was only an

additive term, indicating that size differences exist between males and females, though the relationship with growth over time was consistent between sexes (as observed in ELA lakes). Normality of the residuals did not always pass the Anderson-Darling Normality test even after \log_{10} or square root transformations. When transformations caused residuals to deviate even greater from normality (e.g., indicated by an increase to the test statistic of the AD test), the untransformed data were retained. These results were similarly interpreted with caution, but this often arose in non-significant models, or in models without Year as a significant effect. Histograms of the residuals were evaluated for the models that violated normality assumptions when Year had a significant effect, and the distributions appeared generally normal (Appendix 4 Figure C).

Immature data for NDMNRF lakes revealed several different patterns of changes in growth, with most directional changes being negative over time. Annual changes to weight were experienced in 3 of 4 populations, and were described by additive models except for LOTW, which was described by a Year*Age model. The immature White Sucker in LDML declined by -21.2g (LDML age 1-4: RWT Year: $F_{1,7} = 10.87, p = 0.01$; Table 3.4, Figure 3.6), immature LOTW sucker ranged from -0.97% to +5.97% on average (LOTW age 1-4: sqrt-RWT Year*Age: $F_{3,110} = 3.35, p = 0.02$, Table 3.4, Figure 3.7), and Lake Nipigon suckers declined by -3.78% (Nipigon age 1-4: \log_{10} RWT Year: $F_{1,27} = 5.59, p = 0.03$; Table 3.4, Figure 3.8). Immature White Sucker from Whitefish Lake did not weigh less over time (Table 3.4, Figure 3.9). Fork length in all immature populations and age classes were shown to change over time annually and were described by additive models, except for LOTW. Immature LDML White Sucker declined by -3.7mm (LDML age 1-4: FLEN Year: $F_{1,8} = 6.69, p = 0.03$), LOTW suckers ranged from -0.2mm to +3.2mm (LOTW age 1-4: FLEN Year*Age: $F_{3,110} = 3.3, p = 0.02$), Lake

Nipigon suckers declined by -1.24% (Nipigon age 1-4: FLEN Year: $F_{1,27} = 5.57, p = 0.03$) and Whitefish Lake suckers declined by -0.86mm (Whitefish age 1-4: FLEN Year: $F_{1,15} = 16.2, p = 0.001$). Body condition remained stable across all age classes in all populations except in Lake Nipigon, where condition changes were described by a Year*Age model and ranged from -0.01 units in age class 2 to +0.01 units in age class 4 annually (BCD Year: $F_{2,25} = 4.22, p = 0.03$; Age class 1 was excluded because there was only one datapoint).

Changes to growth over time in mature fish among all external populations were largely not witnessed over time. Lake Nipigon experienced significant annual declines to weight and length in mature age classes by only -9.5g and -2.0mm (Nipigon age 5-10: RWT Year: $F_{1,59} = 5.9, p = 0.02$; FLEN Year: $F_{1,59} = 8.88, p = 0.004$; Table 3.4, Figure 3.8). Conversely, Whitefish Lake mature White Sucker experienced a small but significant annual increase to weight and length of mature age classes by +6.1g and +1.0mm (Whitefish age 5-10: RWT Year: $F_{1,65} = 21.34, p = <0.001$; FLEN Year: $F_{1,66} = 33.33, p < 0.001$; Table 3.4, Figure 3.9). Additionally, Lake of the Woods experienced a statistically significant but nearly negligible change to condition of mature fish by -0.001 units annually (LOTW age 5-10: BCD Year: $F_{1,204} = 3.9, p = 0.0495$; Table 3.4, Figure 3.7). The remainder of growth variables for these lakes and all size variables of Lacs des Milles Lacs White Suckers showed no change to growth over time evidenced by Year bearing no significance either as an interaction or when considered in additive models (Table 3.4, Figure 3.6). Of the models listed above where changes to growth were discovered, only the model for length in Lake Nipigon and condition in LOTW failed normality assumptions, and transformations in these cases did not improve model fits.

Comparison of ELA and NDMNRF Populations

Between the ELA and NDMNRF datasets, most immature White Suckers experienced growth declines. Growth declines of ELA populations were more pronounced than in NDMNRF lakes, as losses to weight, length and condition occurred exponentially (\log_{10} scale) in nearly all age classes (Table 3.3, Table 3.5). White Suckers in Lake 224 at representative age classes are on average 92% lighter, 54% smaller, and 26% poorer condition than historical sizes. A similar narrative emerges in Lake 373 where White Suckers are on average 75% lighter, 36% smaller, and 17% less proportionately sized than historical records. Lake 442 immature fish growth was reduced on par with the previous two lakes (81% lighter, 42% smaller, 11% less proportionately sized). Compared to the NDMNRF populations, no NDMNRF lake experienced as dramatic annual or total declines over time in growth (Table 3.4, Table 3.6). Declines to weight growth were a mix of linear (LDML), exponential (Nipigon), and square root (LOTW), and declines to fork length growth were mostly linear (LDML, LOTW, Whitefish) but also exponential (Nipigon). Immature weight reductions ranged from 27% in age 2 LOTW fish to 50% and 52% in LDML and Nipigon fish respectively. Similarly with fork length, a range of declines were experienced from 3% and 6% in age 2 LOTW and age 4 Whitefish, to 19% and 21% reductions in LDML and Nipigon fish. Only Lake Nipigon age 2 White Suckers experienced a body condition decline among the external lakes, and this relationship was linear. The immature Lake Nipigon White Suckers have reduced in condition by 59%, a metric greater than any body condition decline observed across all 7 study populations.

When comparing the different populations of mature White Sucker for changes to growth in representative age classes, ELA White Suckers exhibited consistent declines across all age classes and growth metrics in Lake 224, 373 and only in younger mature fish for weight and

length of Lake 442 (Table 3.3, Table 3.5). Seven of the 9 growth evaluations underwent exponential changes and the remaining two were linear (Lake 224 FLEN, Lake 442 RWT). Consistent with declines of immature fish, Lake 224 White Suckers were as much as 95% lighter, 64% shorter and 23% poorer conditioned, and Lake 373 White Suckers were 71% lighter, 32% shorter and 14% less proportionately sized. Lake 442 younger mature fish (where data length was still respectable for interpretation) experienced 26% and 17% declines to weight and length and no declines to condition. From the NDMNRF data, only mature White Sucker of Lake Nipigon declined steadily in length (Table 3.4, Table 3.6) and the decline was by a maximum of 40mm (9%) in any mature age class; the shallowest compared to any lake ELA or NDMNRF lake. Lake Nipigon White Sucker weight also declined at a steady linear rate and when compared to the younger mature representative age class in Lake 442, declines in Lake Nipigon were greater over the whole study period (Lake Nipigon: 15%, -180g; L442: 26%, -147g). LOTW body condition declined by a statistically significant but negligible amount (-0.001 units, 3% over 34 years) and was not comparable to the 10+ percent declines observed in ELA populations.

Hierarchical Partitioning

Across representative age classes from each of the 3 ELA lakes, the outcomes from hierarchical partitioning and partial regression plots showed that the selected predictor variables were all significantly responsible to varying degrees at explaining the variance in size at some point during the lifespan of White Sucker. GDD5 in all lakes have increased, and zooplankton biomass levels in lakes 224 and 442 have declined precipitously from their peak levels, however biomass in lake 373 has been variable over time (Appendix 4 Figure D, E, F). Lastly, all three lakes have experienced rapid increases to population densities (Appendix 4Figure D, E, F).

Recall that representative age classes were ages 4, 6, 8 in Lake 224, 2, 3, 5 in Lake 373, and 4, 5 in Lake 442. In Lake 224, 4-year-old White Sucker sizes (representative of immature fish in this lake) were most significantly negatively explained by zooplankton abundance (RWT 80.9%, Z = 6.7; FLEN 84.9%, Z = 6.71; BCD 75%, Z = 4.14; Table 3.7, Figure 3.10). Independent contributions from GDD₅ were significantly negatively responsible for declines in all 3 variables of 6-year-old females (representative of younger mature sucker; Cumulative GDD₅: RWT 41.5%, Z = 2.5; FLEN 47%, Z = 2.69; BCD 35.7%, Z = 2.34), and food availability was significantly negatively responsible to weight, condition, and nearly significantly negatively responsible to length (food availability: RWT 31.2%, Z = 1.65; FLEN 31.8%, Z = 1.56 @ 9999 iterations; BCD 59.8%, Z = 4.34). Finally, 8-year-old females (representative of older mature sucker) were nearly significantly negatively explained by population density for weight and length, though not for body condition (both re-tested at 9999 iterations: RWT 72.6%, Z = 1.61; FLEN 60.3%, Z = 1.45). In summary, partial regression analysis revealed the majority of relationships between growth predictor variables and size variables were negatively related (Table 3.7).

Examination of Lake 373 outcomes showed that climate was most negatively responsible for weight and length of 2-year-old fish (immature fish with a slower declining growth rate), and food availability was most positively responsible for body condition, though none of these were identified as significant (RWT 62.6%, Z = 0.27; FLEN 80.4%, Z = 0.49; BCD 83.8%, Z = 0.89; Table 3.7, Figure 3.11). Population density appeared to be the sole variable most negatively responsible for declines with all size metrics of 3-year-old fish (immature fish declining in growth more quickly; RWT 75%, Z = 4.01; FLEN 77.3%, Z = 5.53; BCD 77%, Z = 1.26). Finally, a mix of climate and population were most negatively responsible for explaining the size

of 5-year-old females (mature fish representative of all mature age classes; Cumulative GDD₅: RWT 37.4%, Z = 2.02; FLEN 29%, Z = 1.07; BCD 55.7%, Z = 2.83; Population density: RWT 56.7%, Z = 3.18; FLEN 68.9%, Z = 3.73; BCD 40.3%, Z = 1.91). Partial regression revealed negative trends between all growth metrics of all age classes with GDD₅ and population density, and nearly all positive trends with food availability (Table 3.7).

The outcomes from hierarchical partitioning in Lake 442 showed that independent contributions of population density to 4-year-old fish (representative of the immature population) were most significantly negatively explained by population density, though it was not significant for body condition (RWT 89.8%, Z = 4.04; FLEN 85.8%, Z = 4.02; BCD 93.8%, Z = 0.91; Table 3.7, Figure 3.12). Five-year-old fish (representative of mature suckers whom are declining in growth) were most negatively explained by population density and food availability for length and weight, and body condition seemed to be negatively explained most by GDD₅ and food availability, though none of these contributions were significant (Population density: RWT 51.4%, Z = 0.67; FLEN 48.4%, Z = 0.69; food availability: RWT 47.2%, Z = 0.52; FLEN 48.6%, Z = 0.65; BCD 30.5%, Z = -1.01; Cumulative GDD₅: BCD 50.9%, Z = -0.98). Partial regression analysis revealed that for age class 4, GDD₅ and food availability were positively correlated with all size variables (with exception to BCD~ food availability) and population density was negatively correlated with all variables. Among age class 5, only GDD₅ was positively correlated with weight and length; BCD~ GDD₅, and all relationships between population density and food availability were negative (Table 3.7).

DISCUSSION

Growth of White Sucker in all ELA reference populations (e.g., those not undergoing any intentional manipulation) declined significantly throughout the 33-year study period. On average, growth of White Suckers in the representative age classes across Lake 224, 373, and 442 declined between 25 – 95% in weight, 17 – 64% in length, and 11 – 26% in condition. The oldest age classes of Lake 442 were the only White Sucker from ELA lakes shown to be growing larger over time, yet this can likely be attributed to the smaller dataset (i.e., shorter period of evaluation) for this lake. Interestingly, the greatest declines across all ELA lakes appear to be in the immature ages, a pattern that held true within the NDMNRF lakes despite physical (e.g., lake size) and geographical differences.

Observed declines in White Sucker growth were associated with several environmental factors; annual growing degree days above 5°C have increased and zooplankton biomass levels have declined dramatically from peak densities experienced in Lake 224 and 442 but have been variable over the decades in Lake 373. Consistently, populations and biomass of White Sucker sharply increased in all 3 ELA lakes, but these increases to population density seemingly had no effect on zooplankton biomass levels (Appendix 4 Figure G), suggesting the significant negative relationship between food resources and White Sucker growth declines are likely an artefact of a different relationship that was not evaluated here (e.g., the potential role of DOC inputs; Tonin 2019). With no anthropogenic interference in these systems, few other possible causes exist for the changes to our growth variables besides climate change. These results demonstrate that the effects of climate change are significantly impacting the growth potential of White Sucker both directly via changes in environmental temperatures and indirectly via changes in population density.

Density dependence is a well-documented phenomenon that, via competition for shared resources is capable of altering the asymptotic body size of fishes (Chen and Harvey 1995; Pierce et al. 2003). Population size was identified as a leading or secondary contributing factor to growth declines in our oldest age classes across all lakes and was negatively associated with all size variables of all age classes. Indeed, population estimates and biomass are increasing over time at the ELA in conjunction with significant declines to size-at-age. This most likely has to do with more favourable conditions to support the survival of juvenile fishes through their first growing and overwintering seasons (Biro et al. 2004). Age-0 White Suckers have been shown to accumulate biomass at optimal rates when occupying water temperatures of 27°C (McCormick et al. 1977); the faster a juvenile fish achieves its required somatic growth target, the longer in the season it has to accumulate lipid stores for overwinter survival (Biro et al. 2004, 2005). Evidence from another study (Guzzo and Blanchfield 2017) shows that winter seasons are becoming shorter at the expense of longer, warmer growing seasons in this region, a finding corroborated here by increased annual GDD₅ in our lakes. This suggests that conditions favourable to juvenile growth and survival have likely improved for this species, and that increases in population density and biomass are likely due to higher juvenile survival.

There were clear increasing trends in GDD₅ over time in all 3 lakes, which for a species whose preferred thermal growing optima is ~25°C (Hasnain et al. 2010), more GDD should promote growth rates and sizes at a given age, yet these trends appear to be negatively contributing to White Sucker growth declines in Lake 224 and 373. Environmental temperatures control the vital rates such as metabolism and consumption of ectotherms, which can affect body size either separately or in combination (McCormick et al. 1977; Borgmann and Ralph 1985; Atkinson 1994; Brown et al. 2004; Volkoff and Rønnestad 2020). Growing degree days directly

relate the thermal energy of the environment with an organism's cumulative metabolism and has explained much of the variation in size and maturity relationships among immature fish species (Neuheimer and Taggart 2007; Venturelli et al. 2010). These studies show that fish growth and GDD are positively correlated, and lower densities may further increase growth rates predicted by GDD (Venturelli et al. 2010). In my study, under higher densities, higher environmental temperatures and metabolic processes are potential causal factors to growth declines, even after maturation. When fish become sexually mature, they begin re-allocating energetic gains from somatic growth to reproductive development which constitutes a significant energetic investment (Lester et al. 2004). This added energetic cost coupled with a greater need to compete as populations increase (Chuard et al. 2018) may be constraining energy supply in older fish, leaving less energy to contribute to weight, length, and condition gains, ultimately causing smaller sizes at ages and reduced individual fecundity. Although behavioural thermoregulation has been documented in the species (McCormick et al. 1977; Trippel and Harvey 1987), it is likely not relevant in this scenario, as the increasing amount of competition forces fish to become more active, regardless of the thermal costs involved (Chuard et al. 2018).

White Sucker has long been thought of as a benthic feeder, whose diet is primarily composed of chironomids (Trippel and Harvey 1987; Chen and Harvey 1995), though Saint-Jacques et al. (2000) showed that White Suckers are flexible in their diet and can switch their resource use when one forage base becomes exhausted. Limited gut analysis of White Sucker and the bedrock lake bottoms of the ELA suggest zooplankton may be an important forage species for White Sucker in these lakes. My study indicates food availability (zooplankton biomass) was a significant negative influence on size at age of White Sucker in Lake 224, however White Sucker abundance was not correlated with zooplankton biomass (Appendix 4

Figure G), suggesting observed relationships between zooplankton and White Sucker growth are an artefact of a different relationship unaccounted for in this study.

Recent research into the effects of varying DOC gradients across lakes on resource availability have shown that higher DOC content is associated with lower biomass of zooplankton, benthic invertebrates, and White Sucker, indicating perhaps DOC or light penetration is playing a mediating role between food availability and White Sucker abundance (Tonin 2019). Using stable isotopes, this recent study found that chironomids were identified as an important diet component of White Sucker, and that zooplankton may not be as effective at capturing patterns of resource availability as well as initially thought (Tonin 2019). Tonin (2019) found that fewer food resources support lower White Sucker biomass, i.e., fewer fish with faster growth and larger sizes occurring when fewer resources are present in the system. Tonin (2019) and my study highlight that density dependence is a critically important factor in the growth relationships in ELA lakes because these are unexploited systems that lack additive pressures.

Fewer growth declines to White Sucker populations in NDMNRF lakes were witnessed across the region, but when declines occurred, they were most notably discovered in the immature ages of these populations (when excess energy is solely directed to somatic growth). The size reductions were much less drastic than those witnessed in the ELA lakes, and only in Lake Nipigon was stunted immature growth carried through to the older ages. These lakes are all much larger and complex in habitat and biological community than the ELA lakes, which for a White Sucker, may help to insulate them from serious harmful climatic impacts, potentially explaining why growth was not as significantly reduced compared to ELA populations. Due to a lack of associated environmental data, we did not investigate the drivers of growth relationships in the NDMNRF lakes, so it is unclear which specific variables are contributing to slower

immature growth rates in these lakes. However, White Suckers in these systems are not likely to be significantly targeted by any amount of fishing effort, thus they should be reflective of the conditions in their environment. I believe the fact that I see a change in somatic growth rates to immature age classes of an environmentally tolerant, unexploited species, supports my claim that White Suckers are likely to be negatively impacted by climate change, and thus are a useful sentinel species for climate change monitoring.

The consequences of reduced body size in fishes due to driving pressures such as climate change are far-reaching and capable of impacting a species fitness in many ways. Recently summarized by Ahti et al. (2020), individual-level implications may alter juvenile and adult growth rates, behavioural changes, and fecundity. At the population level, a change in body size can change population growth, and phenotypic and genotypic expression. Finally at the ecosystem level, predator-prey dynamics may change, and trophic cascades may occur if body size changes take effect. Further complicating matters at the ecosystem level, body size may be capable of initiating positive feedback loops, where a slight change to smaller sizes may amplify predation dynamics and mortality leading to reduced overall biomass of a species (Audzijonyte et al. 2013). Ultimately the consequences of reduced body size in response to external pressures such as climate change may contribute to reduced survival of a species at all levels of biological organization.

In my study, I have identified that a population level response to a warmer climate seems to be the leading cause for size declines, as this has been paralleled by increases to GDD₅ which are presumably having positive effects to juvenile survival and negative effects to adults through increased competition. Further, there are clear negative trends in the zooplankton biomass levels of these lakes, which is likely still relevant to White Sucker growth, but at a lesser degree than

initially hypothesized to be. Spawning phenology has not been changed by population size shifts nor climate change, though Chapter 2 presents evidence that spawning events may be highly susceptible to climate change, should a trend to warmer springs occur. Finally, growing seasons and over-wintering periods have changed for the better from a juvenile fish's perspective (McCormick et al. 1977; Borgmann and Ralph 1985; Biro et al. 2004), suggesting the climatic influence on these lakes may have promoted juvenile survival and recruitment at the expense of adult body growth.

The independent evaluation of the historical ageing data showed that exact agreement between readers was strong and agreement between all readers within one year was nearly 100%. There was some evidence of age overestimation in age 3-4 fish from the pre-1995 period which could exacerbate declines if pre-1995 fish were aged one year older than supposed to be. However, of all samples determined to be age 3 or 4 by myself, only 29% (38 of 131) of these samples did not agree exactly with the previously determined age. This was the only case of any significant source of ageing bias between readers and across all age classes. Despite this potential bias in two age classes, we still observed significant declines in growth across all ages, increasing my confidence that the large depressions to size at age were not a result of inconsistent age interpretation.

CONCLUSION

A recent review paper has identified knowledge gaps of the current literature and future needs of climatic research on inland fish populations of North America (Lynch et al. 2016). They correctly identify that the current body of information focuses mostly on 1) distributional shifts,

2) projections of future effects, and 3) coastal/great lakes regions and important game species of those regions. This study addresses all three knowledge gaps, as it provides observational evidence of climatic effects to growth in a poorly regarded, non-game species across a Northwestern Ontario distribution. Further my study supplies resource managers with a potentially useful sentinel species for monitoring aquatic climate change impacts across North America. Ultimately my study shows that White Sucker populations have very likely been affected by climate change, most significantly due to increased survival and density dependent consequences. Understanding the range of potential ecological effects to a species via climate change will help better inform the survival and fitness expectations of future individuals and populations.

TABLES

Table 3.1. Breakdown of lakes used, years of data included in the growth analyses, and physical lake morphological characteristics.

Lake	Data Range (years inclusive)	# Years included in models	Surface Area (m ²)	Max depth (m)	Average Depth (m)	Water Clarity (m)
Lake 224	1979 - 2018	30	25.92	27.4	11.8	6.5
Lake 373	1987 - 2019	29	27.3	20.75	11.4	6.1
Lake 442	1990 - 2008	18	16	17.8	8.5	4.4
Lacs des Milles Lacs	1999 - 2018	8	24511	24.4	6.8	2.5
Lake of the Woods	1986 - 2019	34	434900	64	N/A	< 1 to > 3.5
Lake Nipigon	1999 - 2018	12	484800	165	55	N/A
Whitefish Lake	1989 - 2018	10	2871	6.4	2	2.5

Table 3.2. Summary of ager comparisons relaying number of samples examined and how the agers compared in the interpretation of the slides. Ager 1 was responsible for the pre-1995 era and Ager 2 was responsible for the post-1995 era. BDS was the principle ager of this study, responsible for the verification of historical data and updating records from 2014 – 2019.

Test	Exact agreement (#)	Agreement within 1 year (#)	Exact agreement (%)	Within 1-year agreement (%)	Structures examined (Total #)
Ager 1: BDS	234	282	83%	100%	282
Ager 2: BDS	260	273	95%	99.60%	274
BDS: BDS	66	66	100%	100%	66

Table 3.3. Annual rates of change to size at age of White Sucker from representative age classes in the ELA lakes. Percent decline indicates exponential relationship.

Lake	Ages	RWT	FLEN	BCD
224	1–4	-7.60%	-2.40%	-0.90%
	6	-9.30%	-8.6mm	-0.80%
	8	-4.60%	-5.3mm	-0.40%
373	2	-3.00%	-0.90%	-1.1%
	3	-6.20%	-1.90%	-1.1%
	5–10	-3.80%	-1.20%	-0.50%
442	1–4	-8.90%	-2.90%	-0.60%
	5	-8.2g	-1.00%	0
	8	+37.5g	0.70%	0

Table 3.4. Annual rates of change to size at age of White Sucker from representative age classes in the NDMNRF lakes. Percent decline indicates exponential relationship

Lake	Age	RWT	FLEN	BCD
LDML	1-4	-21g	3.7mm	0
	5-10	0	0	0
LOTW	1	5.71%	3mm	0
	2	-0.97%	0	0
	3	0.74%	1.0mm	0
	6-10	0	0	-0.001
NIP	2	-4g	-2mm	-0.01
	4	-4g	-2mm	0.01
	9	-9.5g	-2.mm	0
WFSH	1-4	0	-1mm	0
	7	+6.1g	1.0mm	0

Table 3.5. Total average decline in growth of representative age classes for White Sucker among ELA lakes over each lake's study frame (Lake 224 & Lake 373: 1987 – 2019, Lake 442: 1990 – 2008). Decline in growth is expressed as a numeric and percent value.

Lake	Age	RWT %	RWT (g)	FLEN %	FLEN #	BCD %	BCD #
224	4	-92.30%	-226g	-53.70%	-140mm	-26.00%	-0.28
	6	-95.60%	-1173g	-64.00%	-275mm	-23.00%	-0.27
	8	-78.10%	-1002g	-38.00%	-168mm	-12.30%	-0.14
373	2	-63.00%	-22g	-25.60%	-36mm	-17.40%	-0.17
	3	-87.50%	-127g	-47.00%	-105mm	-16.80%	-0.17
	5	-71.00%	-378g	-32.00%	-105mm	-14.50%	-0.17
442	4	-81.50%	-363g	-41.80%	-134mm	-11.10%	-0.11
	5	-26.00%	-147g	-17.40%	-61mm	--	--
	10	14.00%	+112g	1.60%	+6mm	--	--

Table 3.6. Total average decline in growth of representative age classes for White Sucker among NDMNRF lakes over each lake's study frame (LDML & Nipigon: 1999 – 2018, LOTW: 1986 – 2019, WFSH: 1989 – 2018). Decline in growth is expressed as a numeric and percent value.

Lake	Age	RWT	FLEN			BCD	
LDML	4	-50%	-402g	-19%	-70mm	--	--
	6	--	--	0%	--	--	--
LOTW	1	535.00%	+270g	66%	+107mm		
	2	-27.00%	-64.5g	-3%	-8mm	--	--
	3	28.00%	+90.5g	12%	+32mm	--	--
	6	--	--	--	--	-3%	-0.04
NIP	2	-52.00%	-108g	-21%	-52mm	-59%	-1.4
	4	-52.00%	-227g	-21%	-66mm	20%	0.2
	9	-15%	-180g	-9%	-39mm	--	--
WFSH	4	--	--	-6%	-25mm		
	7	18%	+176g	7%	+29mm	--	--

Table 3.7. Partial regression coefficients indicating directionality of the relationship between the predictor variables (GDD, POP, ZOOP) and response variables (RWT, FLEN, BCD). Green squares indicate significant relationships ($Z > +/- 1.65$), light green squares indicate nearly significant relationships ($Z > +/- 1.45, < +/- 1.65$) discovered in hierarchical partitioning analyses.

Lake	Age	Size Variable	GDD	POP	ZOOP
Lake 224	Age 4	RWT	-0.04	-0.16	-0.34
		FLEN	-0.03	-0.08	-0.24
		BCD	-0.000005	0.000178	-0.000249
	Age 6	RWT	-0.31	-1.06	-1.34
		FLEN	-0.11	-0.20	-0.35
		BCD	-0.0001	0.0001	-0.0004
	Age 8	RWT	0.01	-1.54	-0.16
		FLEN	-0.01	-0.29	-0.06
		BCD	0.0001	-0.0002	0.0001
Lake 373	Age 2	RWT	-0.02	-0.01	0.01
		FLEN	-0.03	-0.01	0.00
		BCD	-0.00007	-0.00001	0.00017
	Age 3	RWT	-0.05	-0.10	0.03
		FLEN	-0.04	-0.09	0.04
		BCD	-0.00004	-0.00011	0.00010
	Age 5	RWT	-0.34	-0.58	-0.48
		FLEN	-0.07	-0.15	-0.06
		BCD	-0.0001	-0.0001	0.0001
Lake 442	Age 4	RWT	0.03	-0.35	0.06
		FLEN	0.01	-0.16	0.06
		BCD	0.00001	-0.00009	-0.00002
	Age 5	RWT	0.12	-0.80	-1.53
		FLEN	0.05	-0.25	-0.47
		BCD	-0.000004	-0.000047	-0.000210

FIGURES

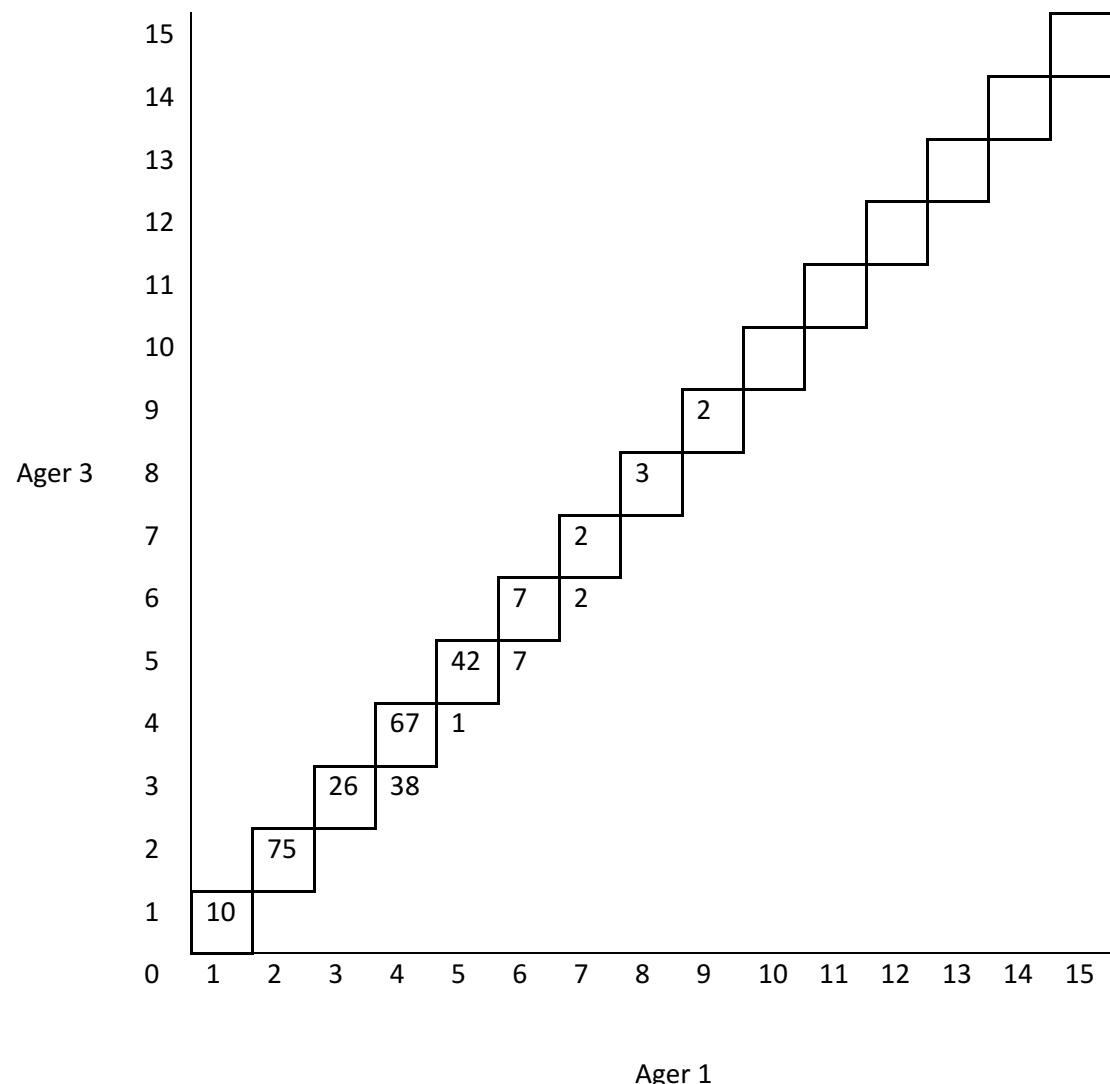


Figure 3.1. Size at age comparison plots between the ager of the current study (Ager 3) and the ager responsible for ages assigned through the 1970's, 1980's and the early 1990's (Ager 1). Values on the plot indicate the number of fins aged at a certain age. Values that fall within the boxes indicate perfect agreement between the agers.

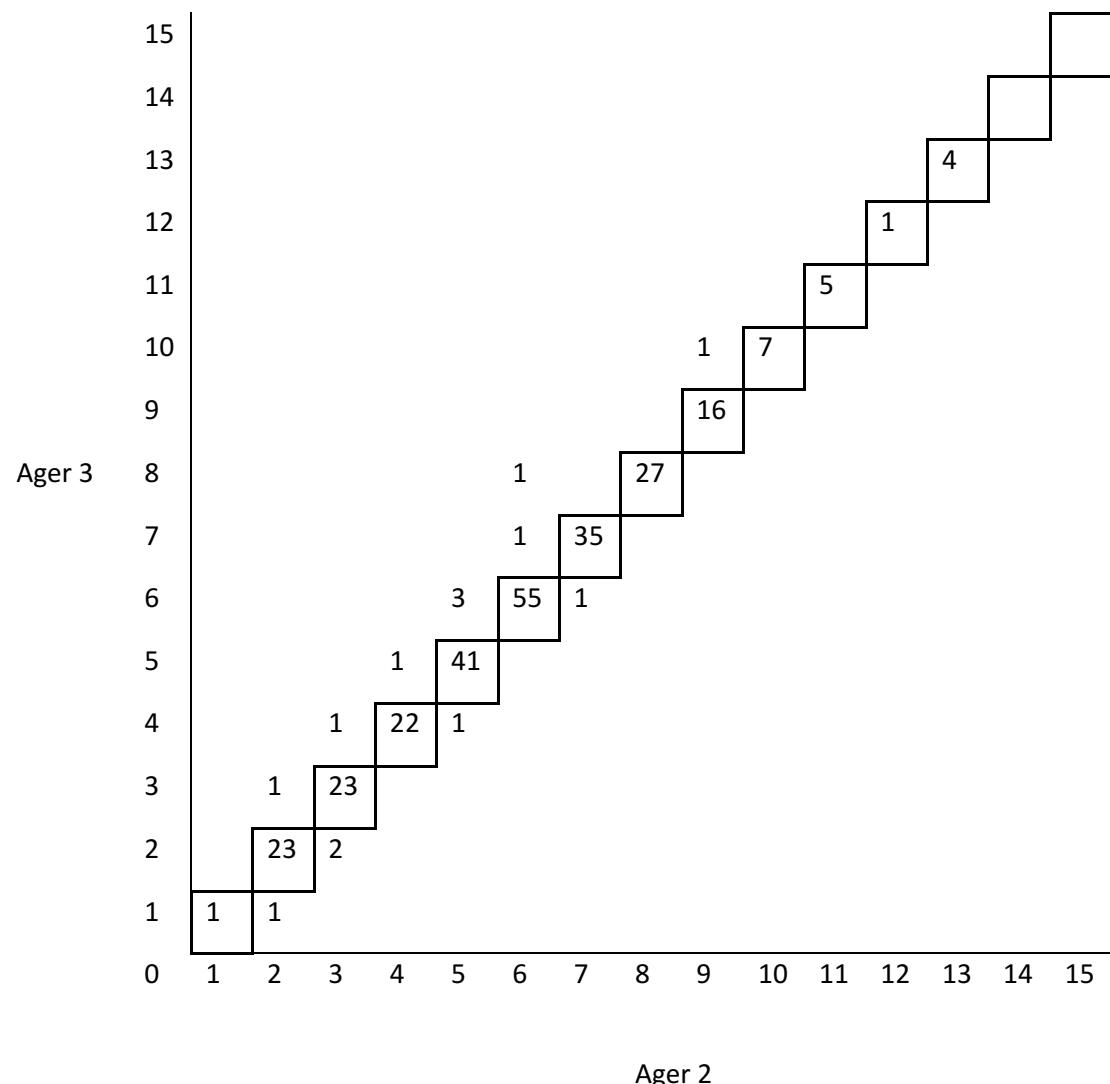


Figure 3.2. Size at age comparison plots between the ager of the current study (Ager 3) and the ager responsible for ages assigned from the mid 1990's to 2013 (Ager 2). Values on the plot indicate the number of fins aged at a certain age. Values that fall within the boxes indicate perfect agreement between the agers.

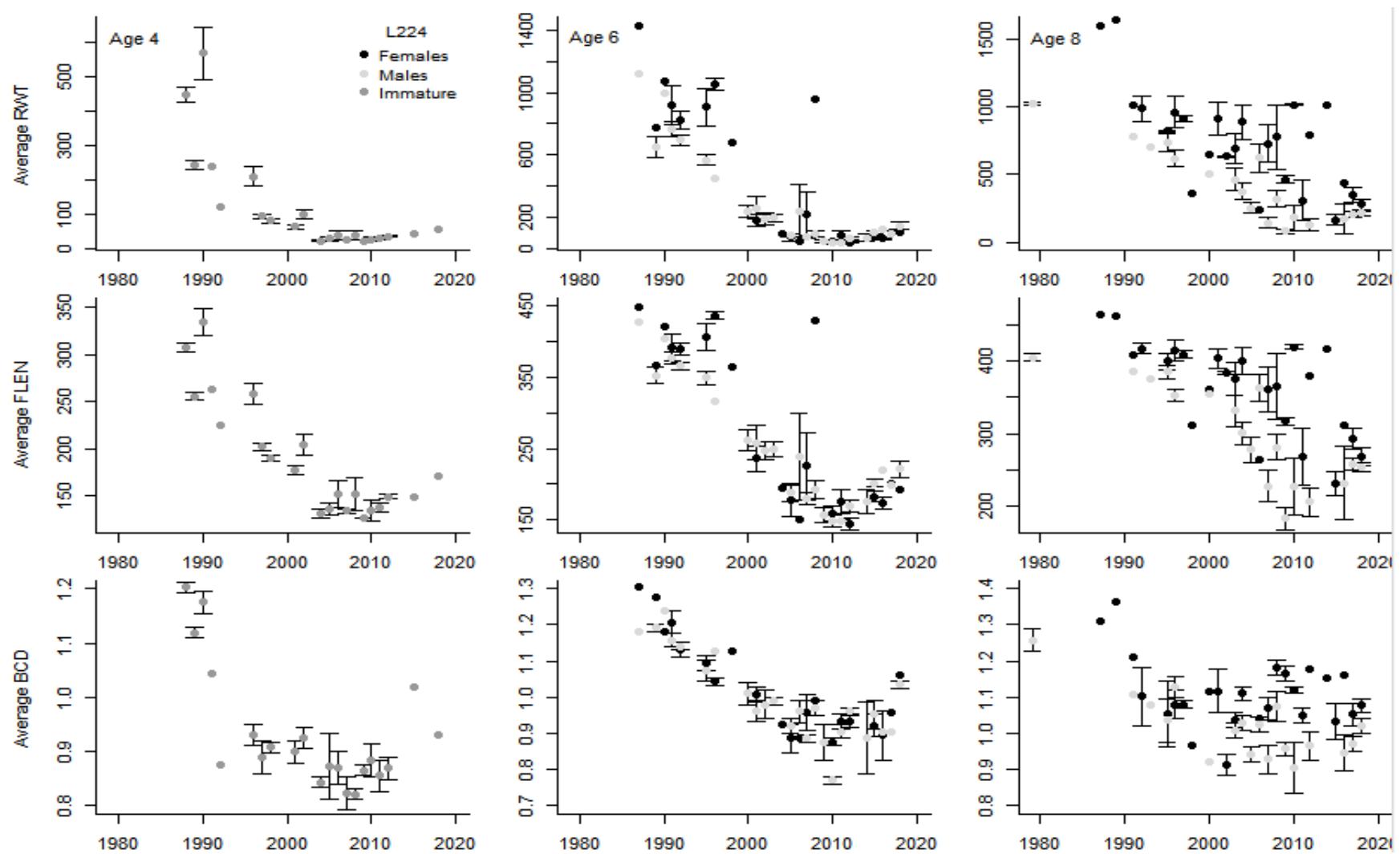


Figure 3.3. Representative age classes from Lake 224 depicting changes in size at age over time. Age classes are by column while size variables are by rows Bars represent standard error of the mean. R^2 values range from 0.50 (mature body condition) to 0.78 (mature fork length) indicating overall fair to strong model fits.

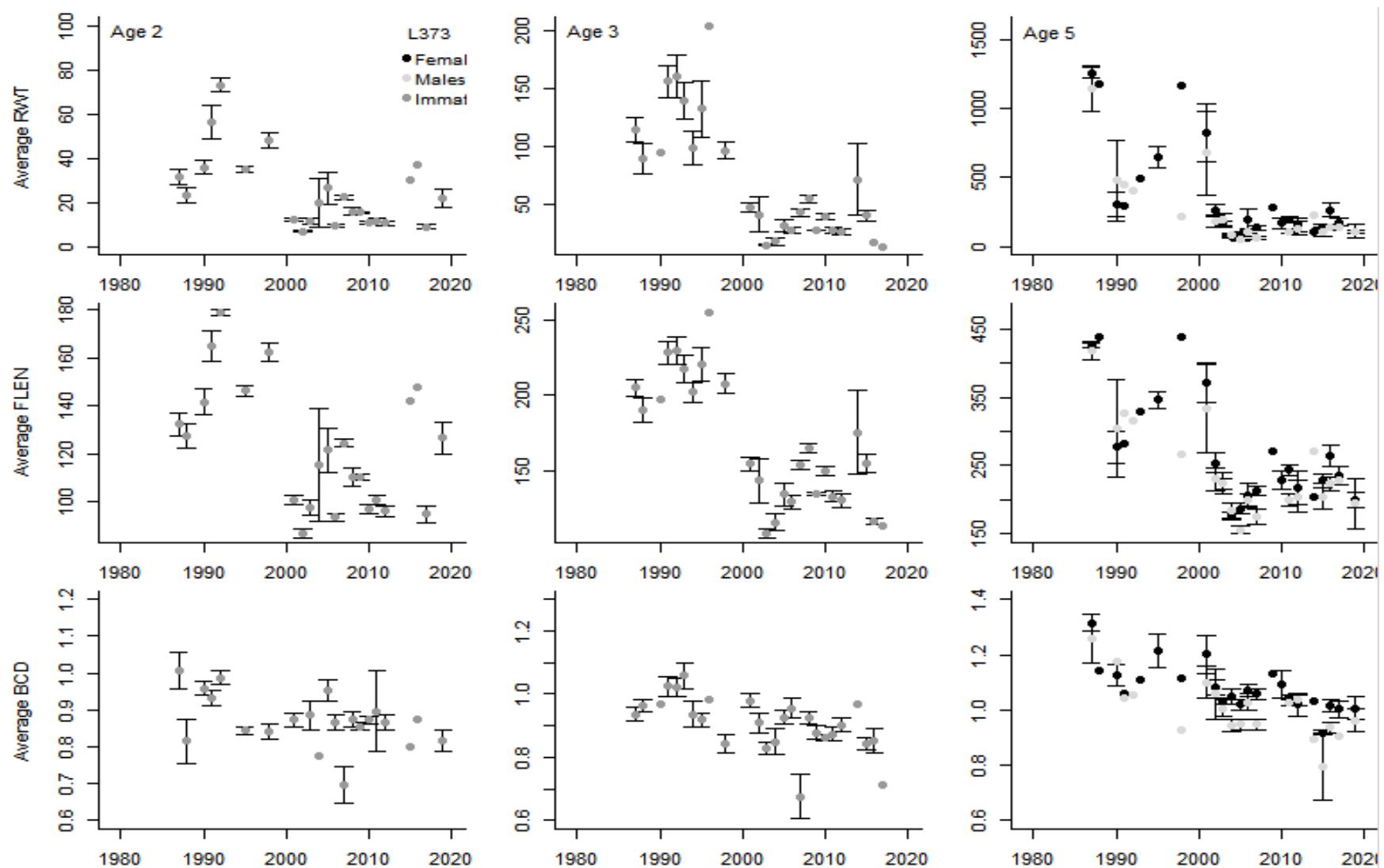


Figure 3.4. Representative age classes from Lake 373 depicting changes in size at age over time. Age classes are by column while size variables are by rows Bars represent standard error of the mean. R^2 values range from 0.42 (mature body condition) to 0.82 (immature round weight) indicating overall fair to strong model fits

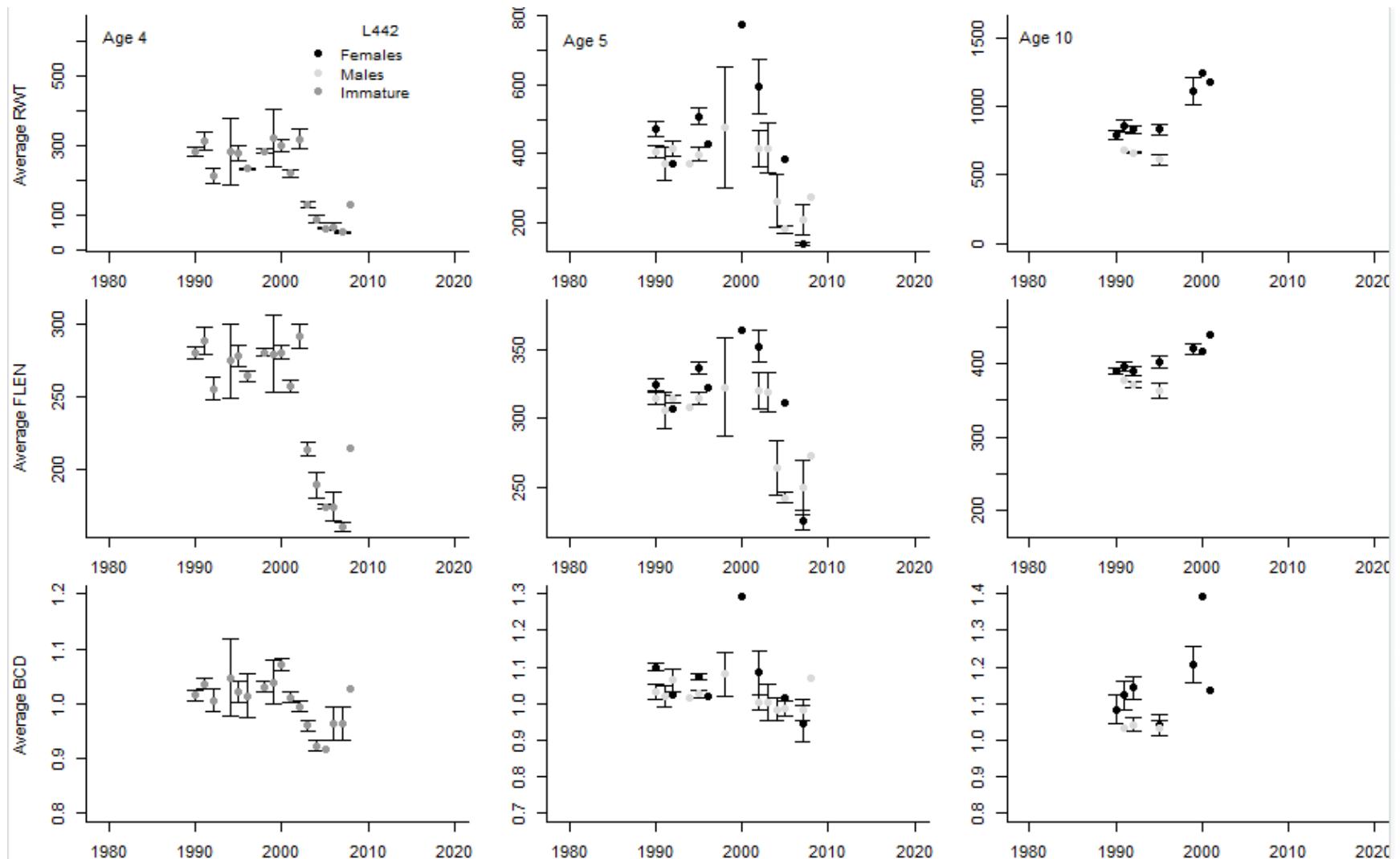


Figure 3.5. Representative age classes from Lake 442 depicting changes in size at age over time. Age classes are by column while size variables are by rows Bars represent standard error of the mean. R^2 values range from 0.3 (mature body condition, year non-significant) to 0.85 (immature weight and length) indicating certain models for size at age fit more strongly than others.

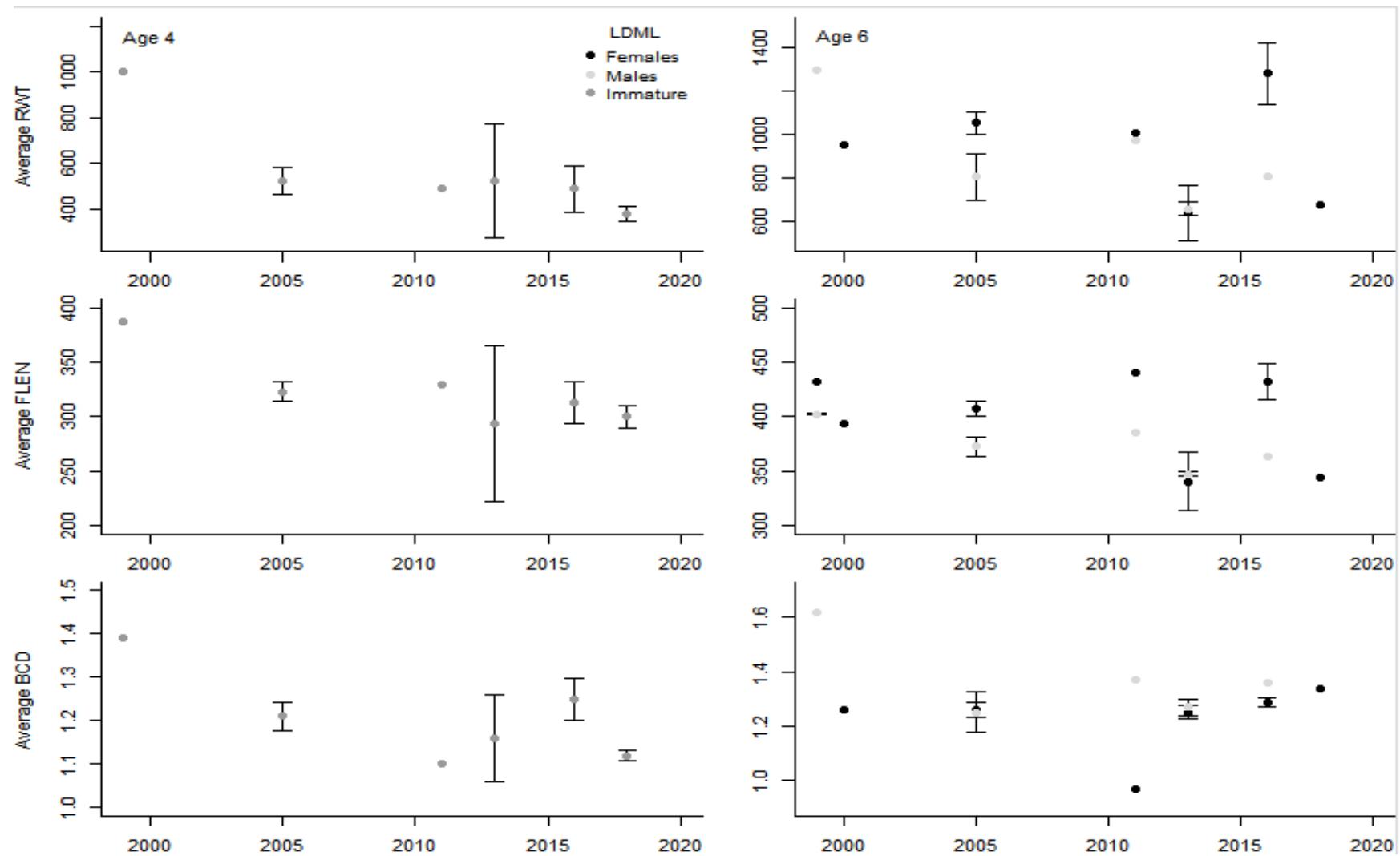


Figure 3.6. Representative age classes from Lac des Milles Lacs depicting changes in size at age over time. Age classes are by column while size variables are by rows. Bars represent standard error of the mean. With the exception of body condition, R^2 values range from 0.34 (mature weight) to 0.87 (immature length) indicating overall fair to strong model fits

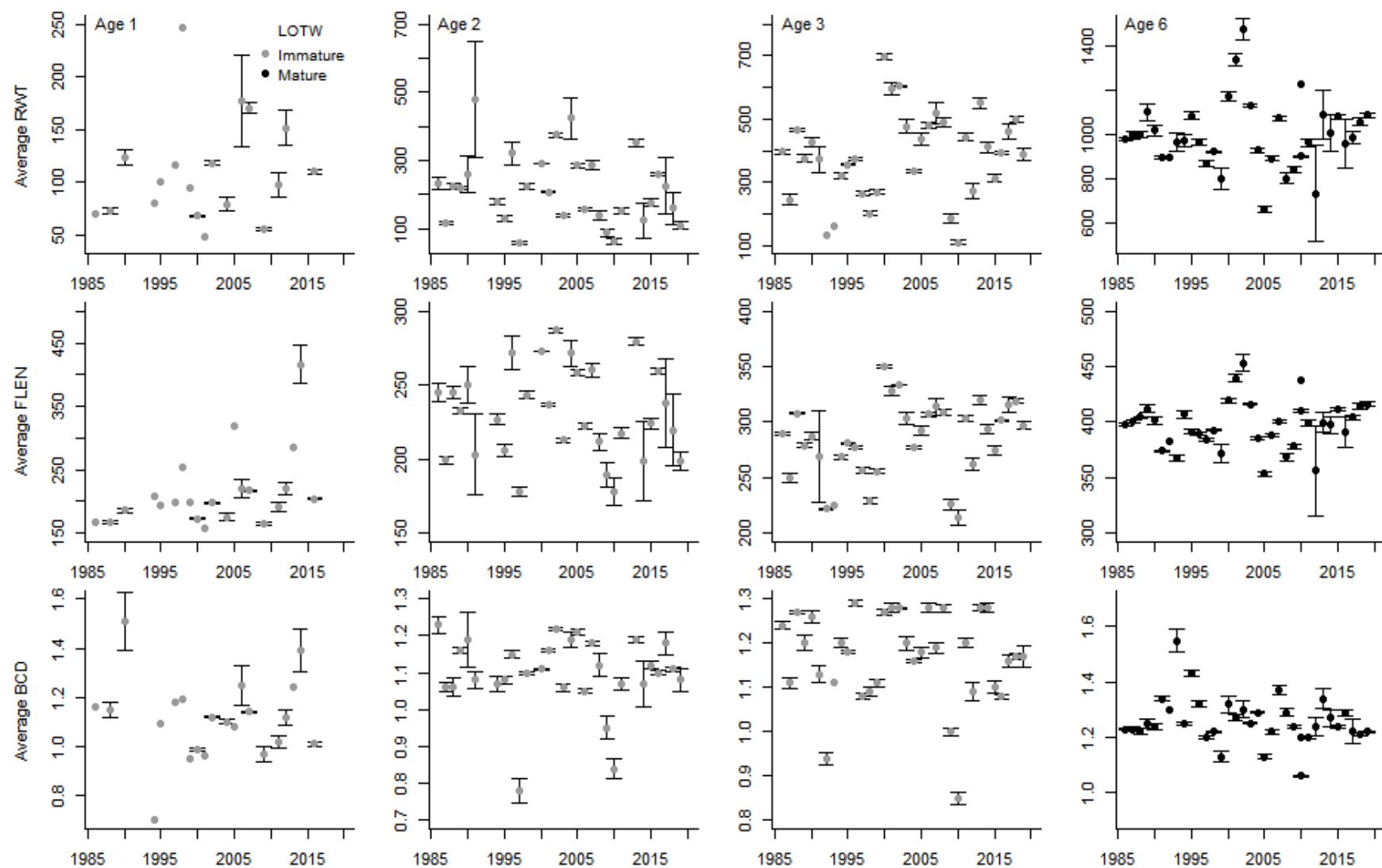


Figure 3.7. Representative age classes from Lake of The Woods depicting changes in size at age over time. Age classes are by column while size variables are by rows. Bars represent standard error of the mean. With the exception of immature and mature body conditions, R^2 values range from 0.62 (immature weight) to 0.7 (mature length) indicating overall moderate model fits

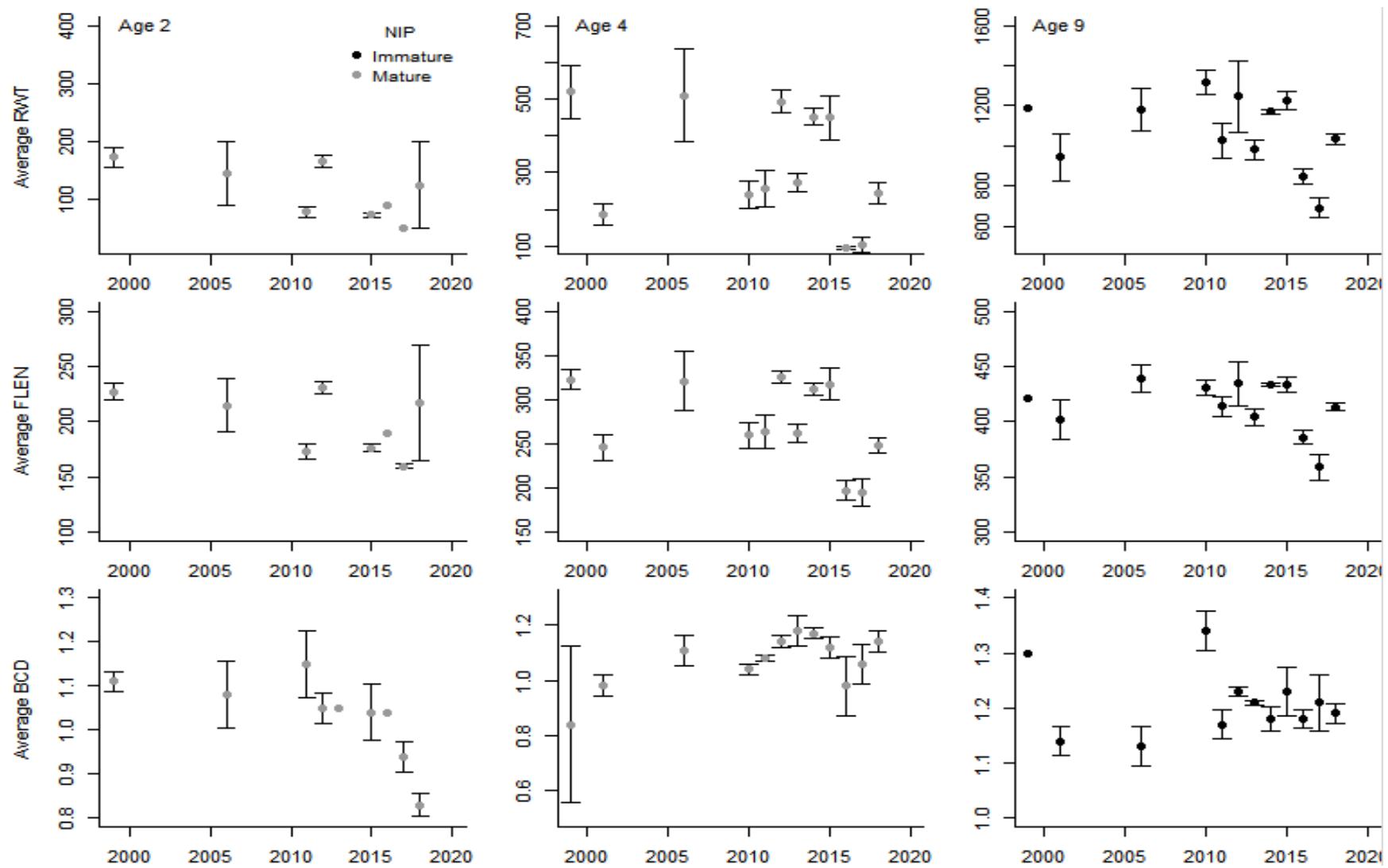


Figure 3.8. Representative age classes from Lake Nipigon depicting changes in size at age over time. Age classes are by column while size variables are by rows. Bars represent standard error of the mean. R^2 values range from 0.17 (mature body condition, year not significant) to 0.61 (mature weight) indicating generally fair model fits

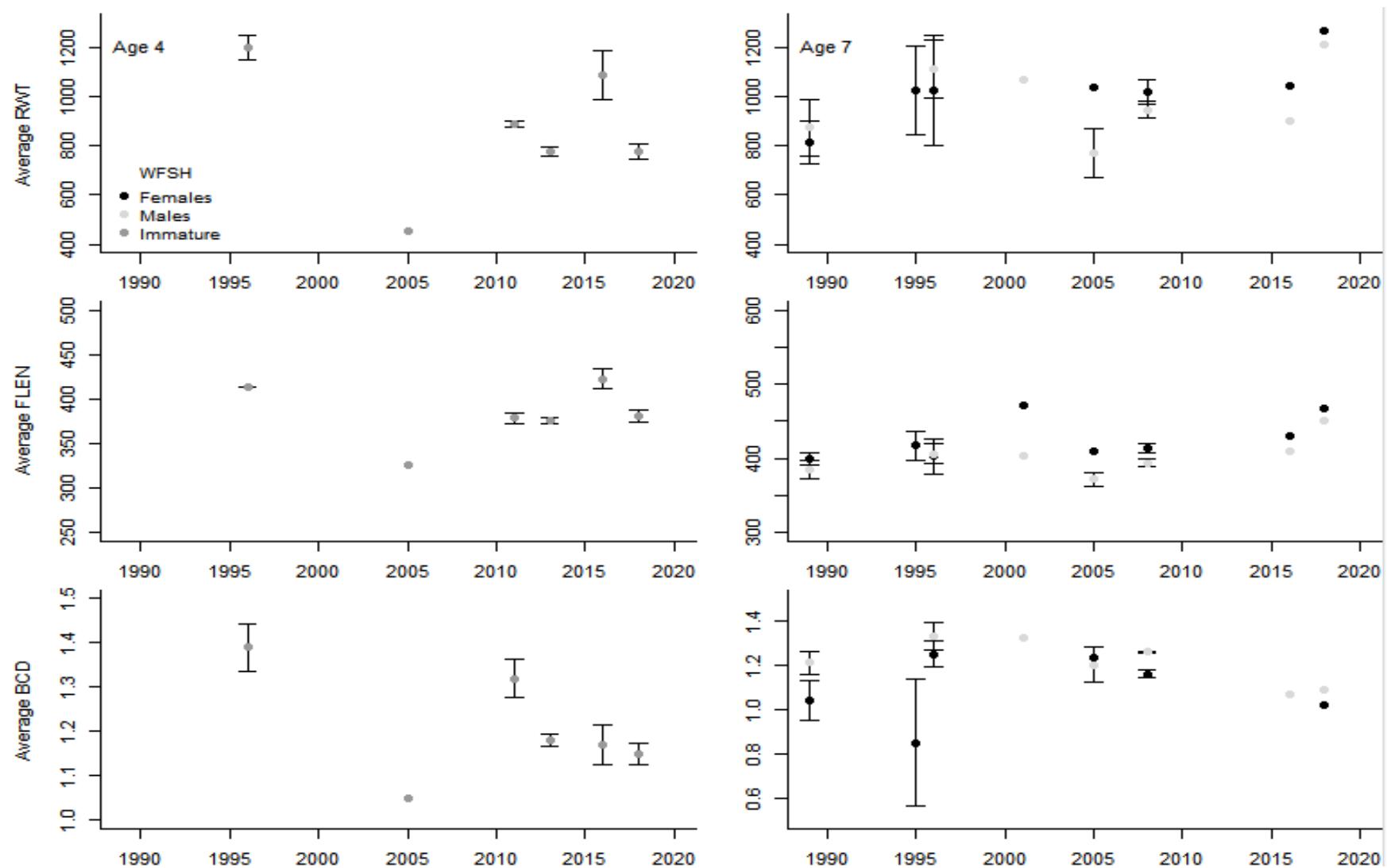


Figure 3.9. Representative age classes from Whitefish Lake depicting changes in size at age over time. Age classes are by column while size variables are by rows. Bars represent standard error of the mean. With the exception of mature body condition, R^2 values range from 0.5 (immature body condition, year not significant) to 0.91 (immature length) indicating overall stronger model fits.

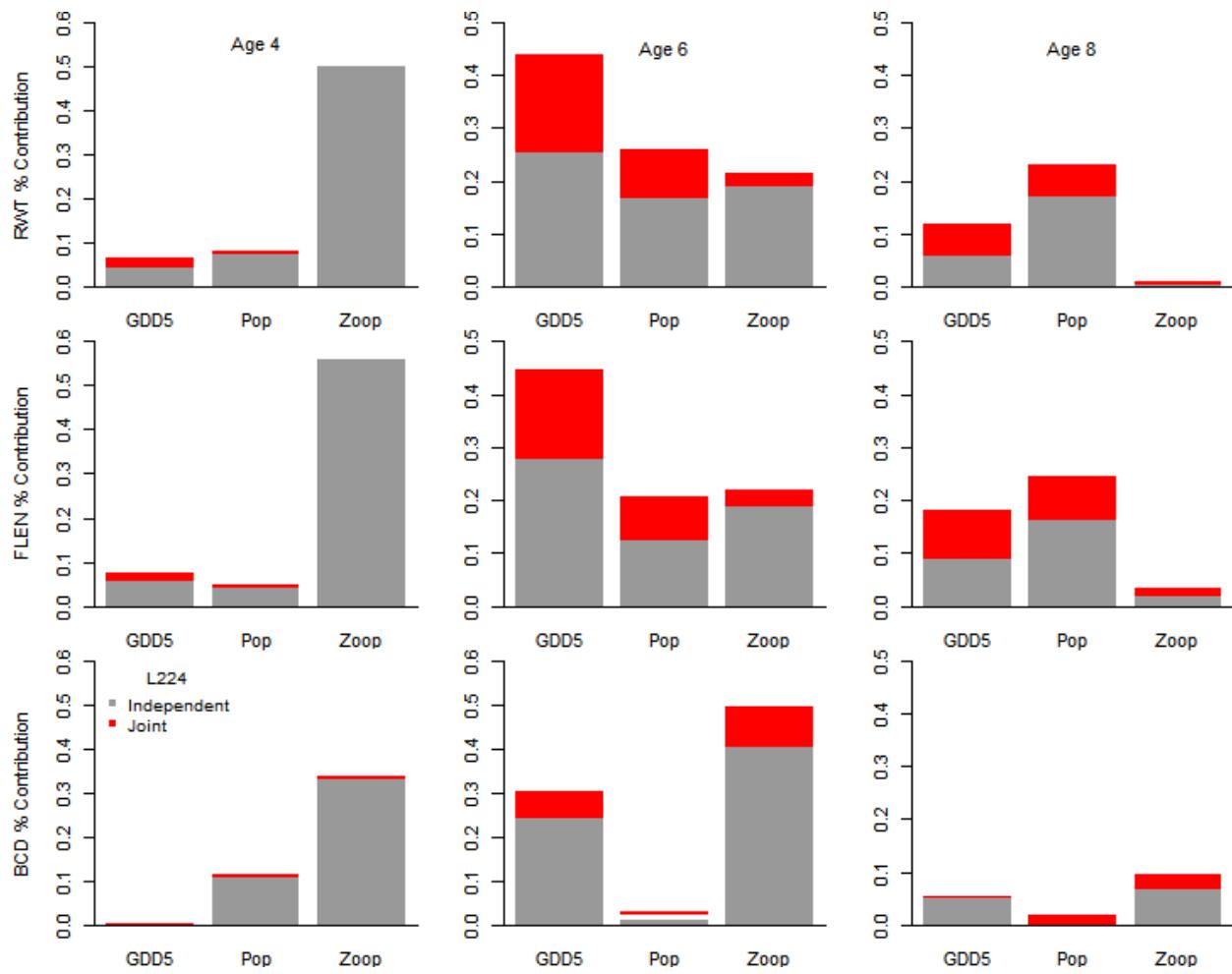


Figure 3.10. Hierarchical partitioning relating the percent independent and joint contribution each of the size predictor variables were responsible for in explaining size at age of White Sucker in Lake 224. Representative age classes were selected for brevity and are listed by column. Size variables are by row.

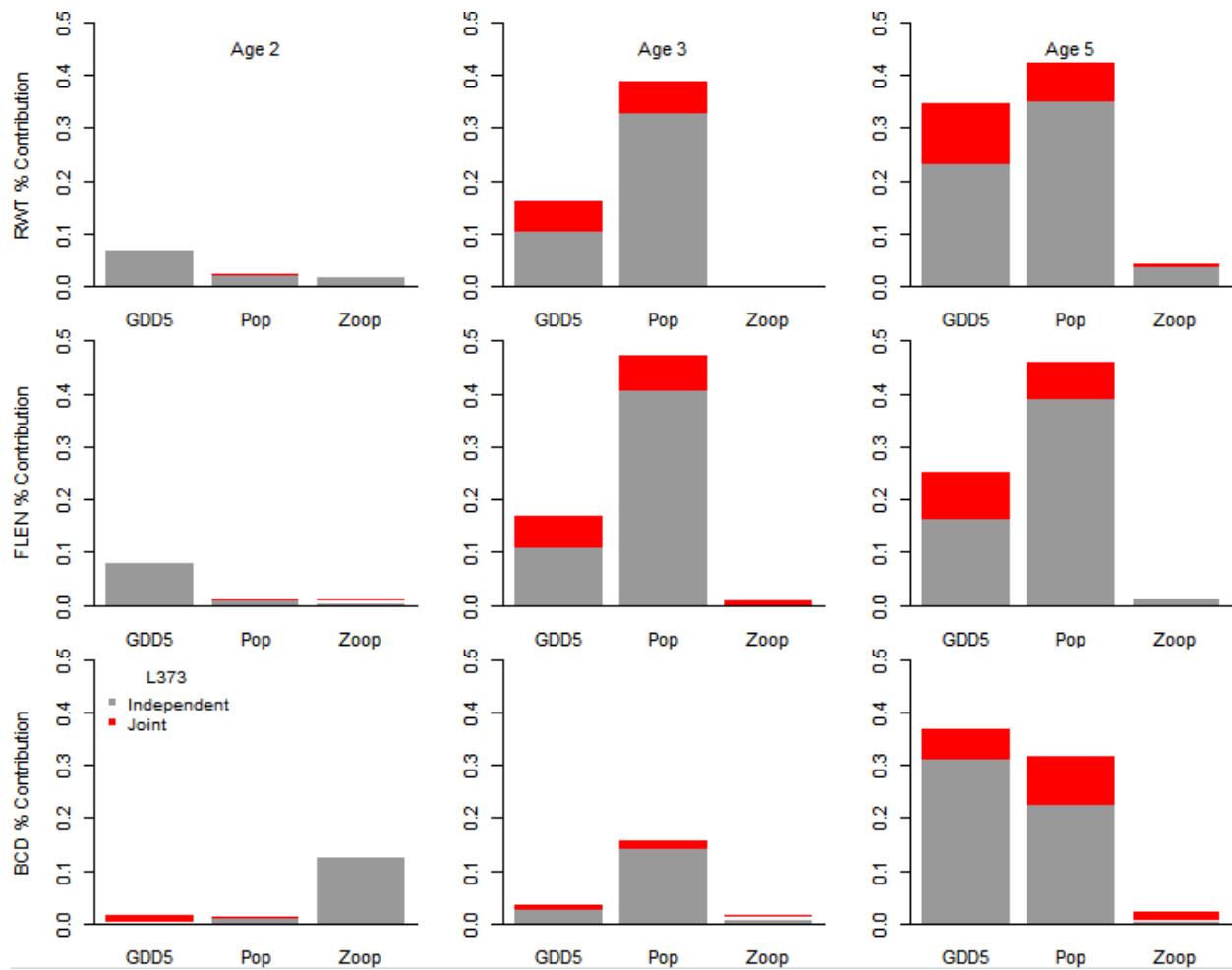


Figure 3.11. Hierarchical partitioning relating the percent independent and joint contribution each of the size predictor variables were responsible for in explaining size at age of White Sucker in Lake 373. Representative age classes were selected for brevity and are listed by column. Size variables are by row.

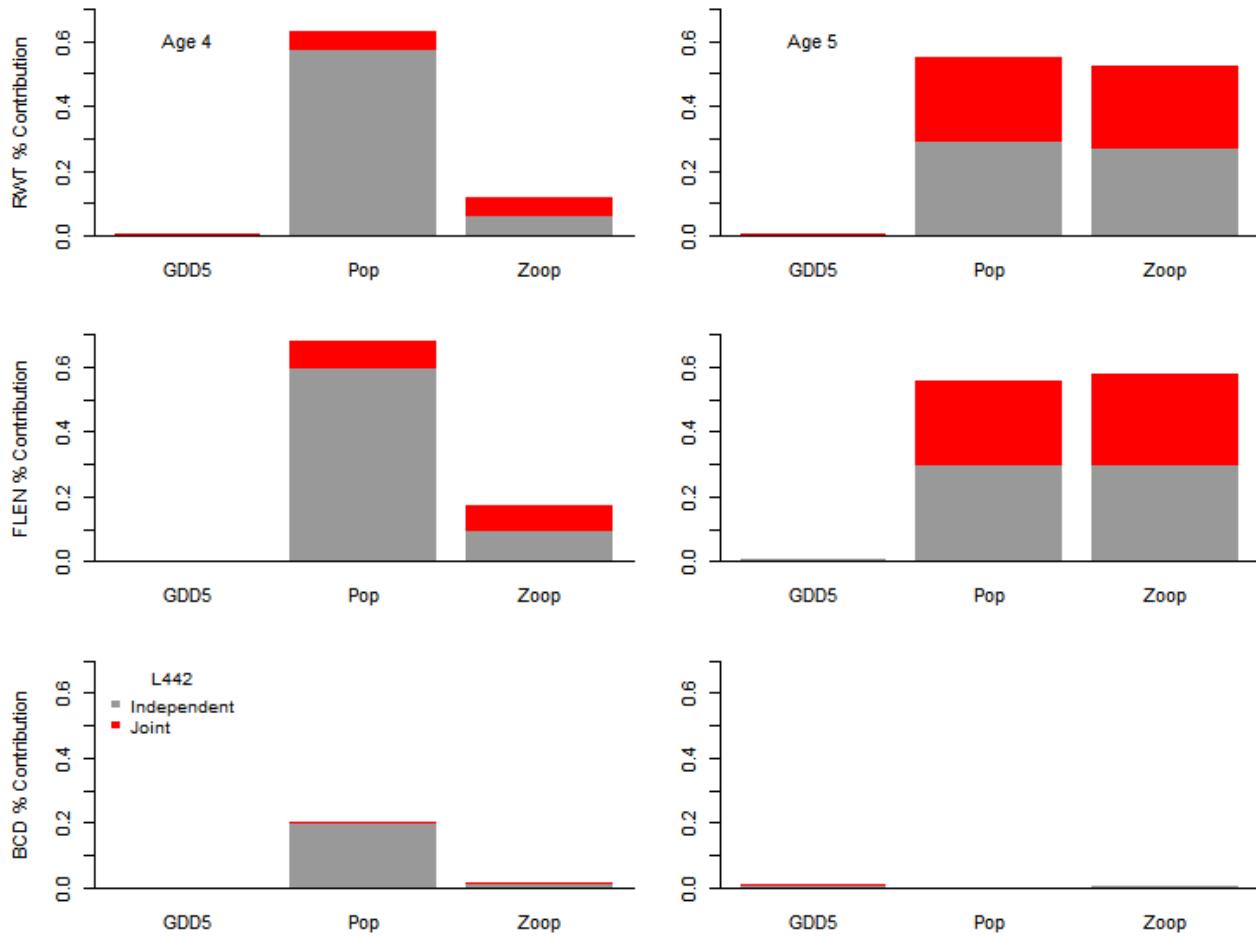


Figure 3.12. Hierarchical partitioning relating the percent independent and joint contribution each of the size predictor variables were responsible for in explaining size at age of White Sucker in Lake 442. Representative age classes were selected for brevity and are listed by column. Size variables are by row. A third, older age class was not included due lesser data in older age classes and misalignment of size values with predictor variables.

Chapter 4 General Conclusions

The broader objectives of this thesis were to evaluate changes to important life history characteristics in White Sucker and Lake Trout from observed patterns of climate change over the past 50 years. Two widely expected life history changes in response to climate change are shifting spawning phenology and shrinking of body sizes; both resulting from warmer temperatures. The findings of both data chapters corroborate these expected results as I displayed clear links between seasonal climate variation and longer-term climate trends with changes to the phenology of spawning in both White Sucker and Lake Trout. Additionally, my second data chapter supports the expectation that fish will shrink under increased warming, but interestingly this was for a species hypothesized to benefit from climate change. Ultimately, I have provided more observational evidence for the effects of climate change in two freshwater species and further support the growing body of evidence that climate change will negatively impact fish populations globally.

The main objective of the first chapter in this study was to assess whether climate change impacts experienced on a longer time scale have caused changes to the spawning phenology in resident populations of White Sucker and Lake Trout at the ELA. I discovered that the timing of peak spawning was heavily governed by thermal conditions of the spawning season and shifts in peak spawning were related to climatic patterns observed during the shoulder seasons. Average fall water temperatures in the 7 study lakes have increased by 1.4°C over 50 years and similarly, Lake Trout average peak spawning date has shifted by 5 days over 43 years in these lakes. No detectable change was observed in average spring water temperature in 8 lakes, and predictably, no detectable change was observed in the spawning phenology for White Sucker of those 8 lakes.

This chapter identified behavioural spawning responses to environmental conditions in the field, furthering our knowledge of the expected response to phenological events in species exposed to the effects of climate change.

Regarding my second chapter's objectives, I sought to describe and detail patterns in growth of White Sucker at the ELA potentially as a response to the effects of climate change. Additionally, I evaluated whether this species has merit as a sentinel for climate change by evaluating populations external to the ELA for similar changes. The White Sucker populations have experienced precipitous declines to growth and body size over the 43-years where spring captured morphometric data was available. This concerning trend appeared to be primarily governed by the density dependent effects of population size, likely as a result from increased juvenile survival and recruitment to adulthood. I did discover few changes to growth in all NDMNRF populations, where most of the growth impairments seem to be occurring in the immature age classes. The White Sucker is commonly used in environmental effects monitoring, and perhaps this finding proves that they have potential as a sentinel species useful in longer-term climate effects monitoring programs. Overall, this study provided some much-needed observational data on growth declines as a result from climate change, as much of today's focus is on projecting future changes to body sizes.

When considering the greater context that these studies contribute to the impacts of the success and fitness to fishes over periods of observed climate change, an interesting story emerges. First considering the White Sucker, a spring spawning species with a generally higher thermal tolerance among Ontario fishes, the phenology of spawning events and exposure to temperatures optimal for development have remained stable because spring-time thermal conditions have remained stable; my study shows White Suckers spawn between 14-17°C, and

other research suggests optimal incubation temperatures occur at ~15°C (McCormick et al. 1977). Further, no mismatch effect by advanced development and emergence should be expected for a significant portion of the hatching population because to this point, there has been no effect of climate change realized on the next generation.

Once emergent fry hatch and deplete their yolk sacs, they must switch to active feeding, of which zooplankton appears to be a primary diet component (Siefert 1972; Borgmann and Ralph 1985). Again, I show there has been no observed temperature increase during spring, thus resources cued by separate signals of stratification or water temperature are not likely to bloom out of synchrony, and peak abundances of phytoplankton and zooplankton should remain in-step with one another (Winder and Schindler 2004; Thackeray 2012). Alternatively, where overwintering dynamics of phytoplankton and zooplankton have occurred, lingering top-down effects (more consumer, less producer than expected) can persist into the first major bloom of the season, though the effect largely vanishes after 1 month of ice off (Hébert et al. 2021), suggesting summertime juvenile food sources should remain stable.

As the next generation of White Sucker approach the summer, this is a critical period of time where they must feed and grow somatically to achieve threshold sizes that reduce predation and allow their bodies to begin building lipid reserves for the winter (Biro et al. 2004, 2005; Mogensen and Post 2012). Research shows that juvenile White Suckers reared at 26.9°C achieve the most optimal rate of biomass gain; my study and Guzzo and Blanchfield (2017) show that summer maximum air and surface water temperatures are not increasing, but rather the length of the growing seasons above a biologically relevant thermal threshold of 5°C are. This indicates that the period in which juveniles have to attain critical somatic lengths and lipid reserves are increasing. Overwintering is a significant mortality source to juveniles (Biro et al. 2004), so the

longer growing period affords juveniles more time to attain their critical overwintering sizes. Further, (Guzzo and Blanchfield 2017) have found wintering seasons to be as much as 19 days shorter, which suggests that lipid reserves are likely robust to sustain more individuals through the winter season from a combination of a higher lipid reserve quantity and shorter duration than it needs to last for.

The expected result of increased juvenile overwintering survival would be a higher population density of White Suckers, and my data from Chapter 3 shows exactly that in all 3 ELA lakes. Populations have been steadily increasing during periods where growth and size at age has been declining. Further, population density was identified as a leading or secondary significant independent causal factor, for which the relationship between growth and abundance was negative in nearly all cases, and regardless of significance level identified in the HP analysis. In the absence of empirical work evaluating juvenile White Sucker survival at ELA, I can only hypothesize that higher juvenile recruitment is leading to higher population densities, though this is based on the peer-reviewed findings of others which I believe provides credibility to my hypothesis. Future research would be welcomed to better explain the mechanisms of juvenile survival and changes in population density of White Sucker in these lakes to confirm or refute this hypothesis.

The story for fall spawning Lake Trout is somewhat different, given the different life history strategies of the fish. Fortunately, the species appears to be adjusting its spawning phenology so that its eggs are not being exposed to warmer fall conditions that can advance development and cause overwinter mortality (Casselman 1995). As spring conditions are being held constant, the hatching time and initial forage base are likely not significantly impacted, suggesting zooplanktivorous juveniles (Ellen Marsden et al. 2022) of fall spawning fish are also

still experiencing the optimal rearing conditions. A longer growing season and shorter winter is likely to benefit Lake Trout fry as well, though their optimal rearing temperature is attained at 12.5°C (Edsall and Cleland 2000). This cooler optimal temperature suggests that somatic growth and fortification of lipid reserves may be paused with warm summer temperatures, a phenomenon observed in juveniles of other cold water species such as Rainbow Trout (*Oncorhynchus mykiss*; Mogensen and Post 2012). It is possible that the current effect of climate warming is providing juvenile Lake Trout a slight advantage, though warmer temperatures undoubtedly pose a greater threat to this species at all life stages compared to the White Sucker.

An interesting topic that emerged while researching spawning information on both of my study species was the potential for them to skip spawning (Trippel and Harvey 1990; Morbey and Shuter 2013), a phenomenon typically characterized by poor environmental conditions that leads to undeveloped gonads and the inability to participate in spawning (Rideout and Tomkiewicz 2011). It is plausible a direct effect of temperature on Lake Trout physiology during the summer is indirectly affecting spawning phenology at the ELA, considering that hypoxic conditions strain physiological and reproductive demands in Lake Trout (Evans 2007), and hypoxic conditions are becoming more common in ELA lakes due to climate change (Guzzo and Blanchfield 2017). This has already been shown to affect other species, as Trippel and Harvey (1989) have shown widespread hypolimnetic oxygen deficiencies are associated with poor reproductive condition in White Sucker. Future research evaluating the effect of hypoxia (presence/persistence) on peak spawning dates would be necessary to address whether this is affecting spawning activity of ELA fish.

This study addressed and provided evidence that White Sucker may be a valuable sentinel species for climate monitoring programs. That such significant declines were observed

in small shield lakes, and that those patterns were repeated in some of the largest lakes in Northwestern Ontario, I believe provides good evidence that this pattern is not restricted to one environment type and is likely representative of the general trends in a majority of White Sucker populations across the region that are being impacted by climate change. Fish growth at immature age classes best reflects environmental conditions as this is the period when excess energy is directed to somatic body growth. Some of our most significant size declines occurred in the immature age classes at ELA and most of the growth declines of external populations

To conclude, this thesis addressed several knowledge gaps identified in the literature. Regarding spawning, the first chapter identified in-field behavioural responses to varying effects of climate change during the appropriate spawning season. I addressed a knowledge gap identified by (Goetz et al. 2021), answering the effect temperature has on the timing of spawning in Lake Trout. My second chapter addressed several knowledge gaps identified in fisheries and climate literature by (Lynch et al. 2016); these knowledge gaps included the lack of observational evidence, lack of regional and species diversity, and lack of diversity in topics explored. Here, I presented observational discoveries of declines to growth and condition from datasets 20 – 41 years in length for 7 distinct populations of a non-game species spread across a geographic range of +300km in Northwestern Ontario. Fortunately, these data will continue to be collected through annual sampling at the ELA, ensuring that future climate effects monitoring can continue. Opportunities for more research into climate impacts may want to evaluate potential changes in fecundity, impacts to eggs and fry survival post-spawning and the effects hypoxia and increased metabolic burdens place on timing of spawning.

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APPENDIX

Appendix 1 – Map of study sites

Appendix 1 Figure A details a map of ELA lakes used in this study. For Chapter 1, all 8 lakes highlighted were studied for changes in White Sucker phenology, and only Lake 373 was not included for Lake Trout phenology analysis. Figure B details a map of the study sites across Northwestern Ontario used to evaluate changes in White Sucker growth.

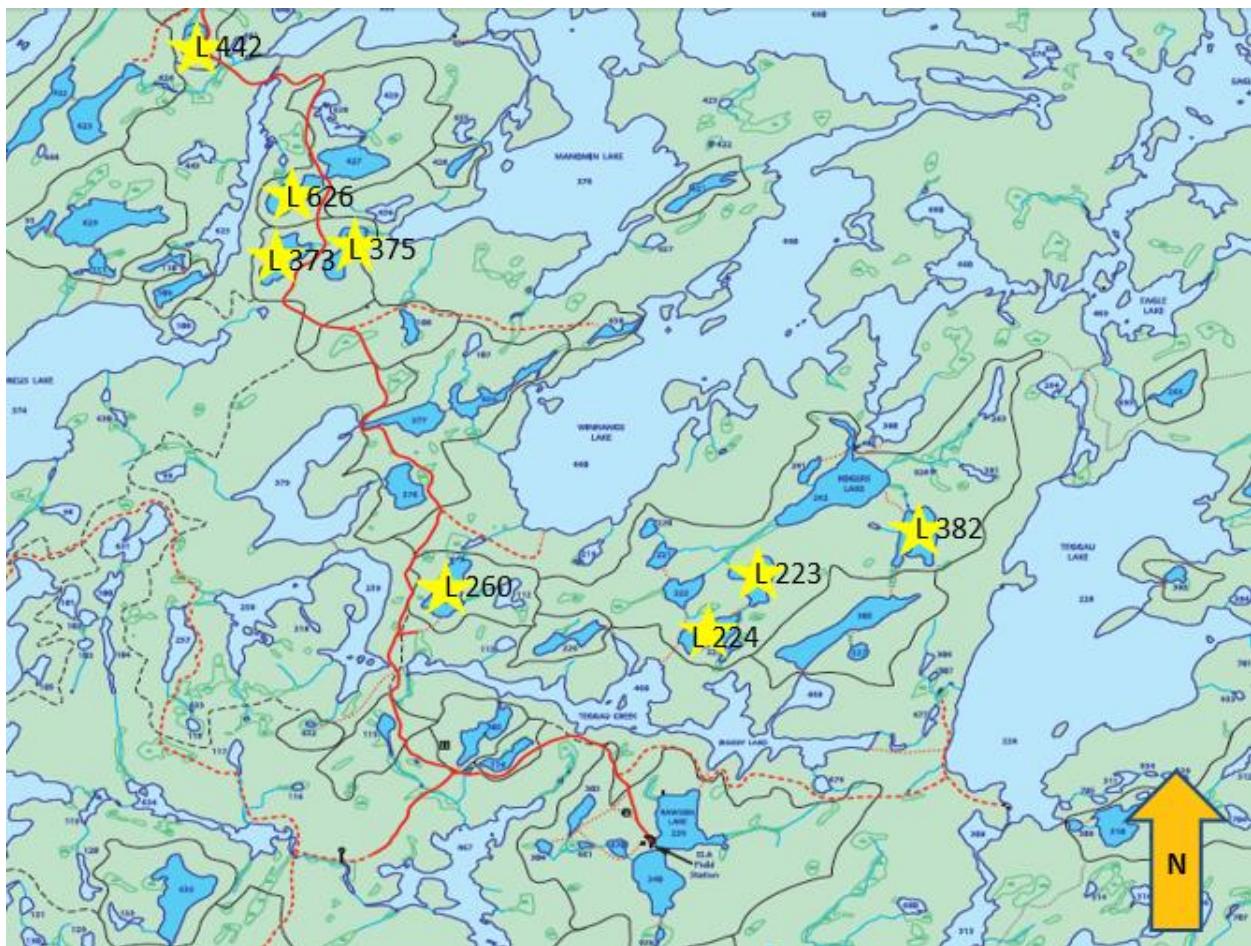


Figure A. Map of ELA study lakes used in Chapter 2



Figure B. Map of Northwestern Ontario study lakes used in Chapter 3

Appendix 2 – Chapter 2 Tables

Appendix 2 details Chapter 2 tables that display equations derived from predicting daily water temperatures over the past 50 years for all 8 study lakes (Table A). The following tables (Tables B – K) detail the results from the testing the heterogeneity of slopes in the ANCOVA analysis.

Table A. Unique water temperature equations produced from each lake from the "Enhanced Multi Year Model" from Matuzsek and Shuter (1996)

Lake	Model Equation Predicted	# Observations Used to Predict Model Fit
223	WTEMP = 13.81 + 0.483(ATEMP1) + .04526(YDAY) + - 0.0001915(YDAY)2 + -1478(INVADYD) + 0.2568(ATEMP2)	1263
224	WTEMP = 24.03 + 0.4.76(ATEMP1) + .04504(YDAY) + - 0.0002.527(YDAY)2 + -2705(INVADYD) + 0.233(ATEMP2)	3776
260	WTEMP = 70.5 + 0.4(ATEMP1) + -0.2.044(YDAY) + 0.000154(YDAY)2 + -5409(INVADYD)+ 0.3052(ATEMP2)	1527
373	WTEMP = 33.19 + 0.4352(ATEMP1) + -0.02088(YDAY) + - 0.0001252(YDAY)2 + -3095(INVADYD) + 0.2543(ATEMP2)	3672
375	WTEMP = 17.06 + 0.4122(ATEMP1) + 0.04154(YDAY) + - 0.00021(YDAY)2 + -1905(INVADYD) + 0.3345(ATEMP2)	394
382	WTEMP = 39.98 + 0.4507(ATEMP1) + -0.05505(YDAY) + - 0.00008785(YDAY)2 + -3654(INVADYD) + 0.3140(ATEMP2)	225
442	WTEMP = 62.88 + 0.3653(ATEMP1) + -0.1727(YDAY) + 0.0001128(YDAY)2 + -4882(INVADYD) + 0.3610(ATEMP2)	3367
626	WTEMP = 16.79 + 0.3824(ATEMP1) + 0.07378(YDAY) + - 0.0003008(YDAY)2 + -2107(INVADYD) + 0.3142(ATEMP2)	1726

Table B. Linear regressions testing the effect of Year on Lake Trout Estimated Spawning Date in each lake

Lake	F Value	p Value	Significant? Y/N
223	$F_{1,13} = 0.22$	0.65	N
224	$F_{1,20} = 5.09$	0.04	Y
260	$F_{1,18} = 3.04$	0.1	Y
375	$F_{1,16} = 9.05$	0.01	Y
382	$F_{1,11} = 0.47$	0.51	Y
442	$F_{1,11} = 8.95$	0.01	Y
626	$F_{1,7} = 1.36$	0.28	N

Table C. Linear regressions testing the effect of Year on White Sucker Estimated Spawning Date in each lake

Lake	F Value	p Value	Significant? Y/N
223	$F_{1,18} = 0.9$	0.36	N
224	$F_{1,14} = 2.38$	0.15	N
260	$F_{1,11} = 0.68$	0.43	N
373	$F_{1,20} = 0.24$	0.63	N
375	$F_{1,5} = 0.66$	0.45	N
382	$F_{1,12} = 0.94$	0.35	N
442	$F_{1,7} = 0.01$	0.92	N
626	$F_{1,6} = 0.37$	0.57	N

Table D. Linear regressions testing the effect of Year on the sum of Cooling Degree Days below 20°C in each lake

Lake	F Value	p Value	Significant? Y/N
223	$F_{1,48} = 15.83$	< 0.001	Y
224	$F_{1,48} = 15.72$	< 0.001	Y
260	$F_{1,48} = 15.66$	< 0.001	Y
375	$F_{1,48} = 15.79$	< 0.001	Y
382	$F_{1,48} = 15.70$	< 0.001	Y
442	$F_{1,48} = 15.66$	< 0.001	Y
626	$F_{1,48} = 15.60$	< 0.001	Y

Table E. Linear regressions testing the effect of Year on Average Fall Water Temperature in each lake

Lake	F Value	p Value	Significant? Y/N
223	$F_{1,48} = 11.84$	0.001	Y
224	$F_{1,48} = 11.78$	0.001	Y
260	$F_{1,48} = 11.60$	0.001	Y
375	$F_{1,48} = 11.56$	0.001	Y
382	$F_{1,48} = 11.66$	0.001	Y
442	$F_{1,48} = 11.43$	0.001	Y
626	$F_{1,48} = 11.53$	0.001	Y

Table F. Linear regressions testing the effect of Year on cumulative Growing Degree Days above 5°C in each lake

Lake	F Value	p Value	Significant? Y/N
223	$F_{1,48} = 0.0368$	0.85	N
224	$F_{1,48} = 0.0687$	0.79	N
260	$F_{1,48} = 0.0744$	0.79	N
373	$F_{1,48} = 0.0706$	0.79	N
375	$F_{1,48} = 0.0628$	0.8	N
382	$F_{1,48} = 0.0848$	0.77	N
442	$F_{1,48} = 0.0761$	0.78	N
626	$F_{1,48} = 0.0647$	0.8	N

Table G. Linear regressions testing the effect of Year on Average Spring Water Temperature in each lake

Lake	F Value	p Value	Significant? Y/N
223	$F_{1,48} = 0.02$	0.88	N
224	$F_{1,48} = 0.02$	0.88	N
260	$F_{1,48} = 0.02$	0.9	N
373	$F_{1,48} = 0.02$	0.88	N
375	$F_{1,48} = 0.01$	0.92	N
382	$F_{1,48} = 0.02$	0.9	N
442	$F_{1,48} = 0.01$	0.92	N
626	$F_{1,48} = 0.01$	0.91	N

Table H. Linear regressions testing the effect of cumulative Cooling Degree Days below 20°C on Lake Trout Estimated Peak Spawn Date in each lake

Lake	F Value	p Value	Significant? Y/N
223	$F_{1,13} = 0.33$	0.58	N
224	$F_{1,20} = 4.67$	0.04	Y
260	$F_{1,18} = 2.94$	0.1	N
375	$F_{1,16} = 2.10$	0.17	N
382	$F_{1,11} = 0.29$	0.6	N
442	$F_{1,11} = 18.1$	0.001	Y
626	$F_{1,7} = 0.17$	0.74	N

Table I. Linear regressions testing the effect of the Average Fall Water Temperature on Lake Trout Estimated Peak Spawn Date in each lake

Lake	F Value	p Value	Significant? Y/N
223	$F_{1,13} = 0.93$	0.35	N
224	$F_{1,20} = 2.98$	0.1	N
260	$F_{1,18} = 3.44$	0.08	N
375	$F_{1,16} = 0.76$	0.4	N
382	$F_{1,11} = 0.02$	0.89	N
442	$F_{1,11} = 9.92$	0.01	N
626	$F_{1,7} = 0.004$	0.95	N

Table J. Linear regressions testing the effect of cumulative Growing Degree Days above 5°C on White Sucker Estimated Peak Spawn Date in each lake

Lake	F Value	p Value	Significant? Y/N
223	$F_{1,18} = 4.07$	0.06	Y
224	$F_{1,14} = 4.61$	0.05	Y
260	$F_{1,11} = 15.19$	0.002	Y
373	$F_{1,20} = 18.77$	< 0.001	Y
375	$F_{1,5} = 5.61$	0.06	Y
382	$F_{1,12} = 24.07$	< 0.001	Y
442	$F_{1,7} = 3.81$	0.09	Y
626	$F_{1,6} = 24.73$	0.003	Y

Table K. Linear regressions testing the effect of Average Spring Water Temperature on White Sucker Estimated Peak Spawn Date in each lake

Lake	F Value	p Value	Significant? Y/N
223	$F_{1,18} = 0.84$	0.37	N
224	$F_{1,14} = 6.00$	0.03	N
260	$F_{1,11} = 12.29$	0.005	N
373	$F_{1,20} = 9.9$	0.01	N
375	$F_{1,5} = 5.41$	0.07	N
382	$F_{1,12} = 51.12$	< 0.001	N
442	$F_{1,7} = 3.57$	0.1	N
626	$F_{1,6} = 33.12$	0.001	N

Appendix 3 – Chapter 2 Assessment of temporal changes to critical spawning temperatures, histograms of ANCOVA model residuals, and plots from nonsignificant correlations between spawning dates and physical lake characteristics

Appendix 3 displays figures from Chapter 2 of the histograms from ANCOVA residuals where data failed normality tests (Figure A), and plots from evaluating whether physical lake characteristics were correlated with determining when the study species within those lakes would achieve peak spawning activity (Figure B -E). Additionally, a statistical test from Chapter 2 where temperatures deemed critical to spawning were evaluated for temporal changes (e.g., has the date when temperature X was achieved significantly shifted through time; Methods, Results, Figure F).

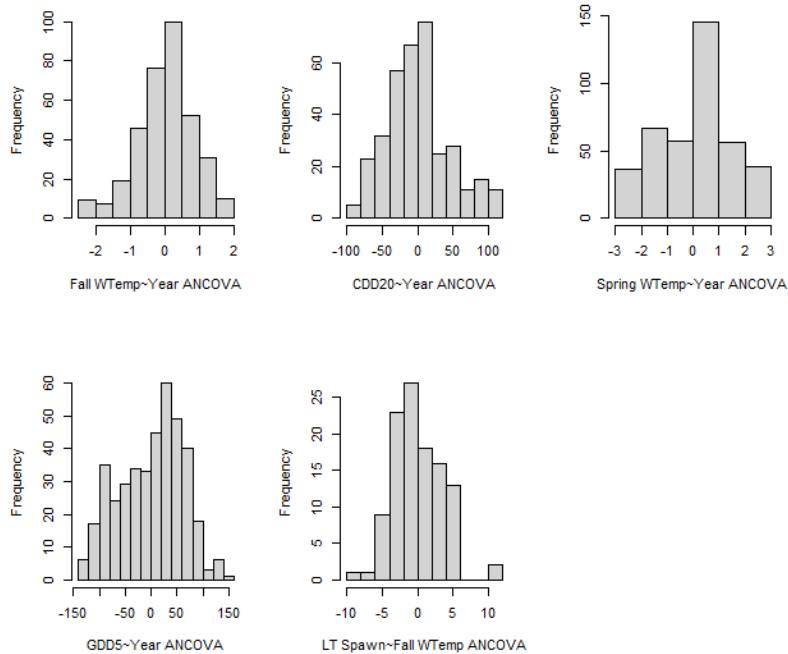


Figure A. Histogram plots of ANCOVA model residuals where the residuals failed Anderson-Darling's Test for Normality. Observed skewness appears minor and all distributions seem generally normal.

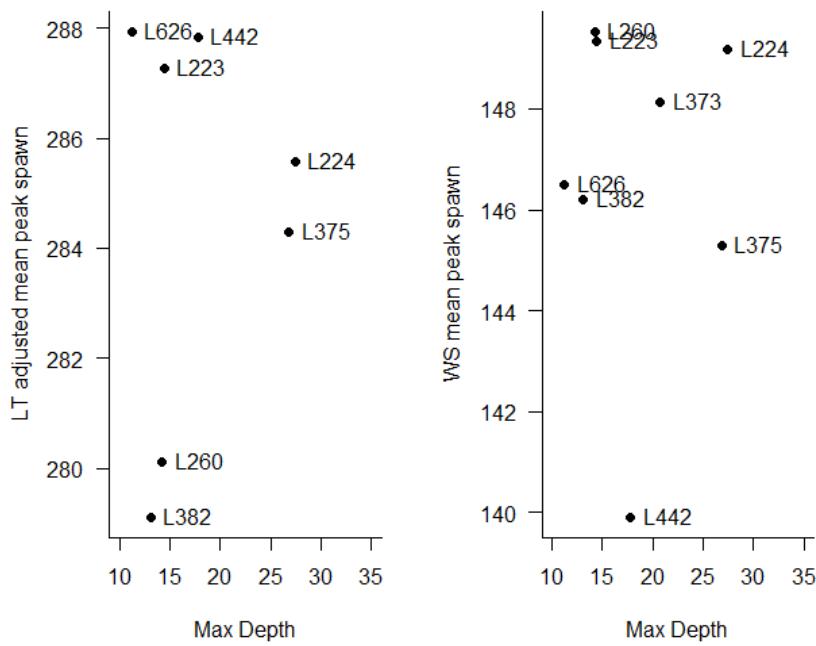


Figure B. Correlation plot between estimated peak spawning date of Lake Trout (left) and White Sucker versus the physical lake characteristic maximum depth. Neither relationship was found to be significantly correlated.

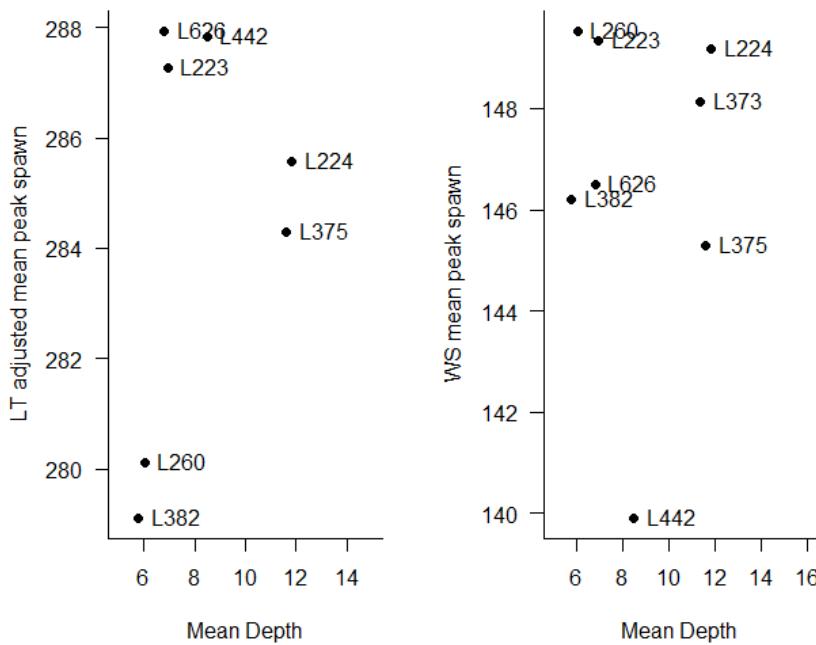


Figure C. Correlation plot between estimated peak spawning date of Lake Trout (left) and White Sucker versus the physical lake characteristic mean depth. Neither relationship was found to be significantly correlated.

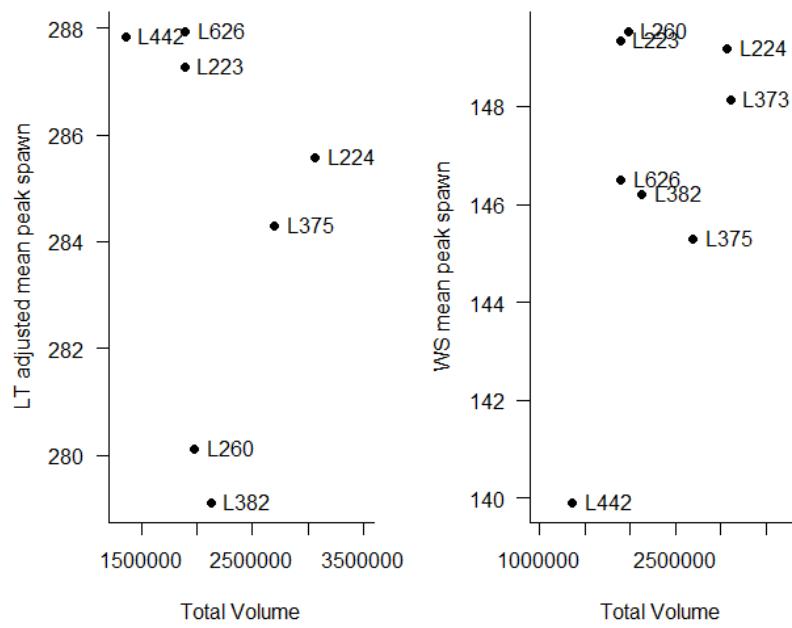


Figure D. Correlation plot between estimated peak spawning date of Lake Trout (left) and White Sucker versus the physical lake characteristic maximum depth. Neither relationship was found to be significantly correlated.

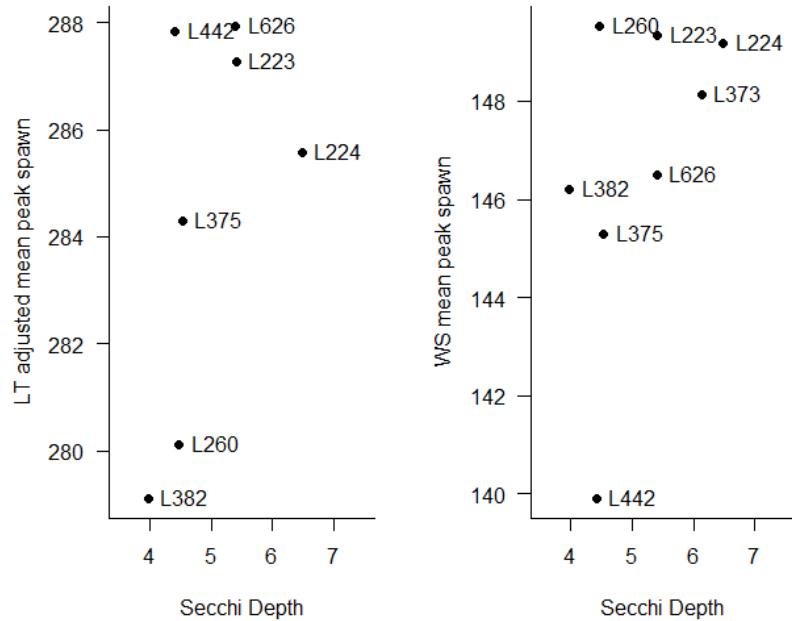


Figure E. Correlation plot between estimated peak spawning date of Lake Trout (left) and White Sucker versus the physical lake characteristic maximum depth. Neither relationship was found to be significantly correlated.

Evaluating temporal changes in the timing of critical spawning temperatures - Methods

Based on my findings indicating the consistency of Lake Trout spawning with water temperatures, and delays in Lake Trout spawning over time (see results), I sought to evaluate whether a temporal shift in the water temperature associated with Lake Trout peak spawning was sufficient to explain observed delays in Lake Trout spawning among ELA lakes. For each year where an estimated peak spawn date was present, the Julian date on where the water temperature was closest to the Lake Trout spawning temperature was determined and defined as the critical spawning temperature date. Important to the selection of this date was the trend in temperature; to be selected, the date was required to be in a temperature trend where daily water temperature values passed through the mean spawning water temperature for the first time. Occasionally, water temperatures would get close to that mean prior to or beyond the first cooling event, but because these temperature values were not associated with a trend of cooling that passed through the mean, they were not considered. This new estimated critical spawning temperature date was compared to the original estimated spawn date using correlation. Further, a mean difference and 95% confidence intervals (CI) were estimated.

Evaluating temporal changes in the timing of critical spawning temperatures - Results

There was no difference between the critical spawning temperature date and estimated peak spawning date for Lake Trout (95% CI -1.1 to +1.25 days) and the two dates were significantly, but weakly correlated ($r = 0.32$, $t_{108} = 3.46$, $p < 0.001$, Figure F). Though Lake Trout temperature at spawning was estimated to occur at 11°C over all lakes, there was significant variation (Figure B), and this alone could not explain temporal changes in spawning timing.

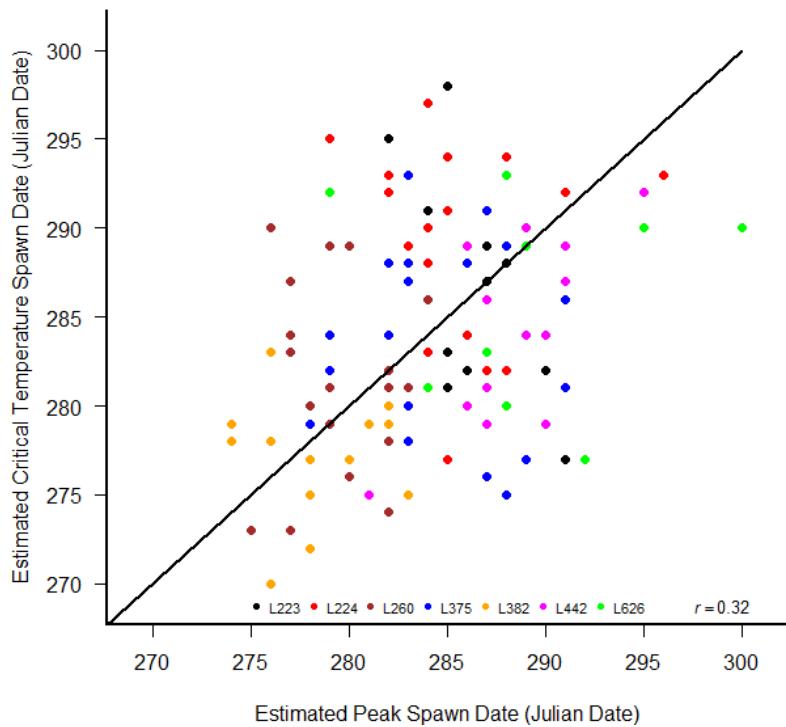


Figure F. Correlation plot between predicted spawning date from encountering critical water temperatures (date when water temperature of the lake is closest to 11°C) versus the estimated spawning dates derived from raw historical data. Black line indicates 1:1 agreement.

Appendix 4 – Chapter 3 Figures

Appendix 4 contains figures from Chapter 3 related to the maturity analysis (Figure A), Histograms where data failed normality tests (Figure B, C), plots of size predictor variables from the hierarchical partitioning analysis over time (Figure D, E, F), and correlation plot between Zooplankton Biomass and White Sucker Abundance (Figure D).

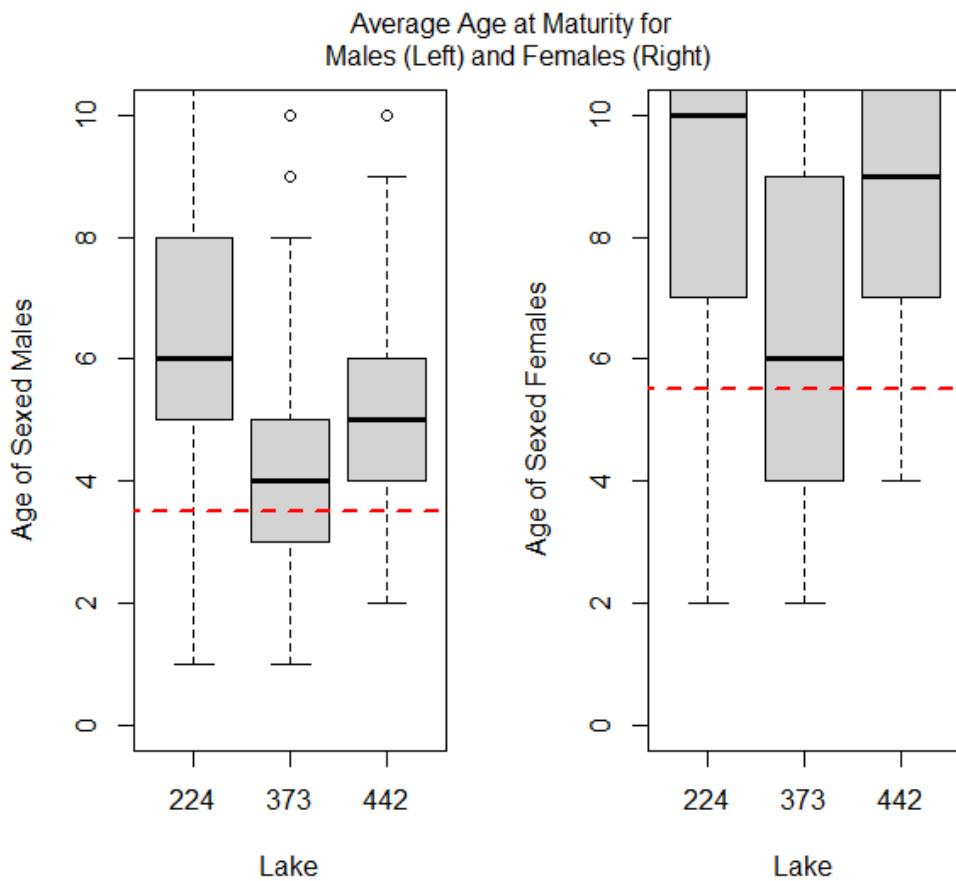


Figure A. Average age at maturity of males (left) and females (right) across Lakes 224, 373, and 442 based on a 20% quantile assessment of all ages where a sex has been identified (M. Rennie Pers. Comm.). Dashed line represents average age at maturity across lakes. Males mature around 3.5 years of age and females mature around 5.5 years of age.

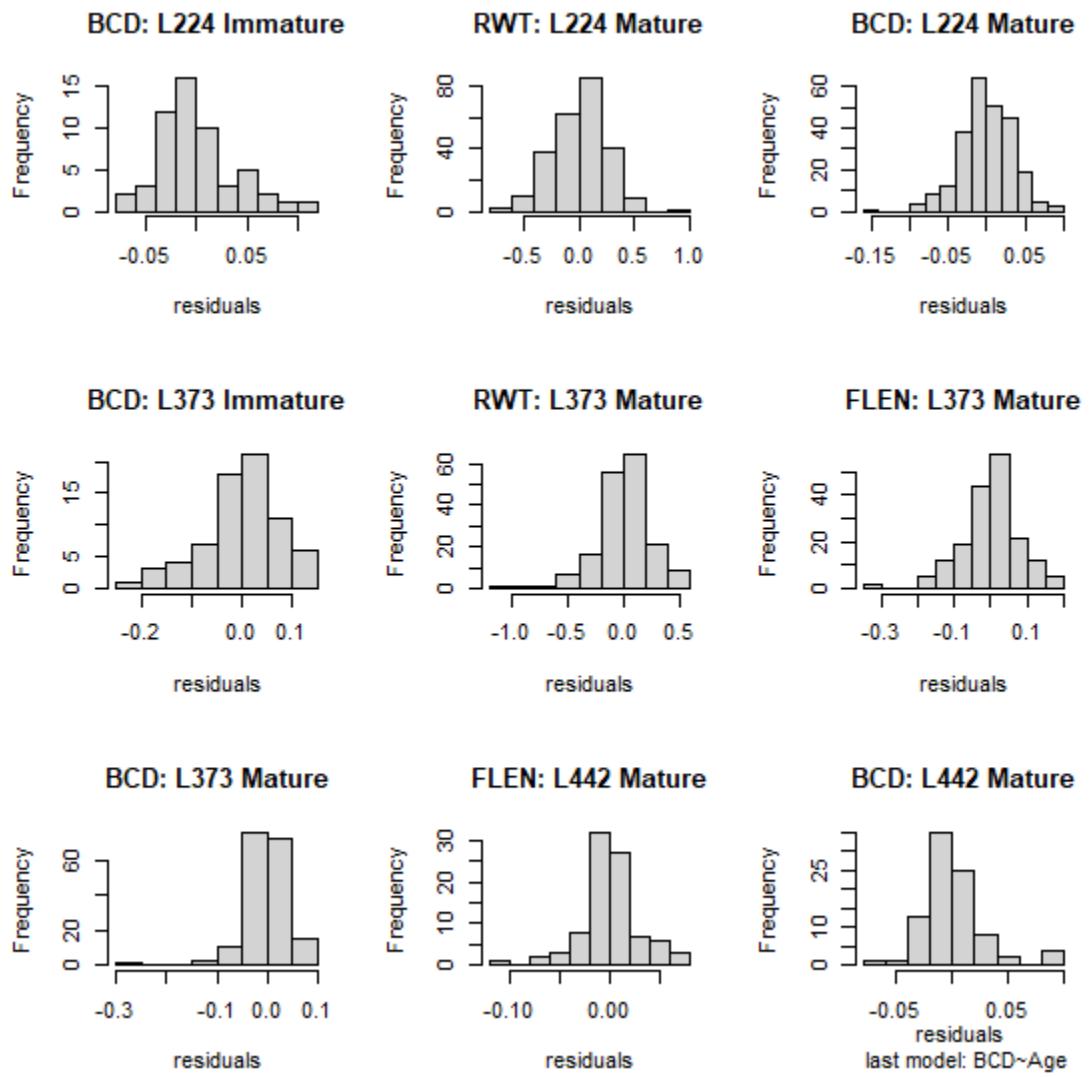


Figure B. Histograms of ELA White Sucker growth linear model residuals where residuals failed Anderson-Darling's Test for Normality. Observed skewness appears minor and all distributions seem generally normal

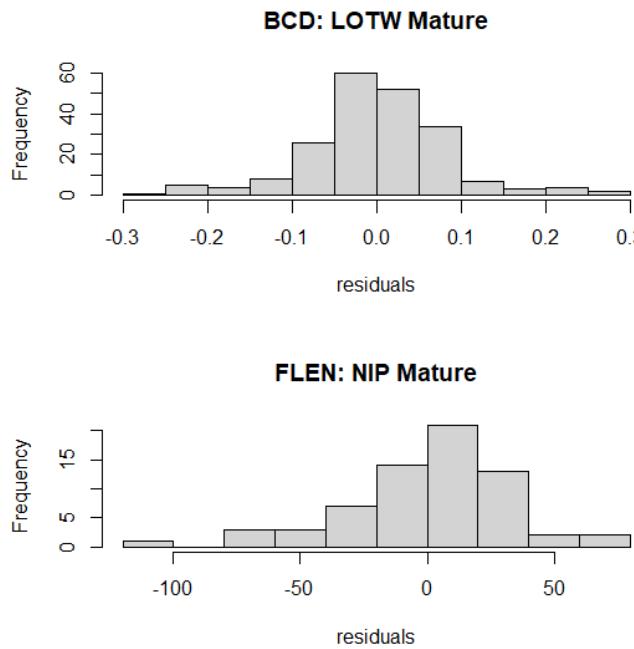


Figure C. Histograms of NDMNRF White Sucker growth linear model residuals where residuals failed Anderson-Darling's Test for Normality. Observed skewness appears minor and all distributions seem generally normal

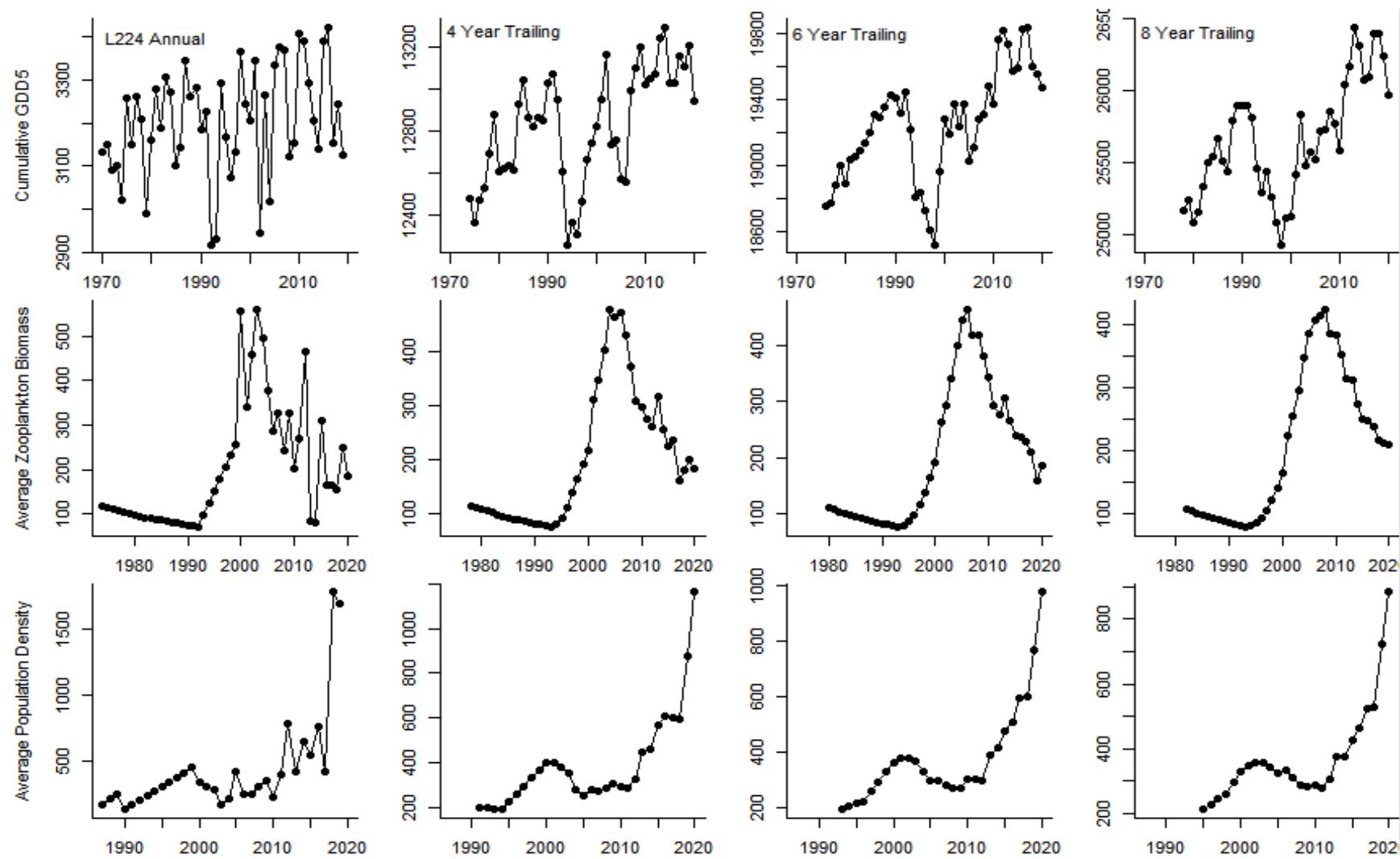


Figure D. Annual and trailing total/average of the size at age predictor variables in Lake 224. Each row represents one of GDD₅, zooplankton biomass (ug/L dry weight), and population density, and each column represents the averaging period. Annual estimates are not offset by 1 year, whereas trailing total are offset to better reflect the history of growing conditions for White Sucker of that year.

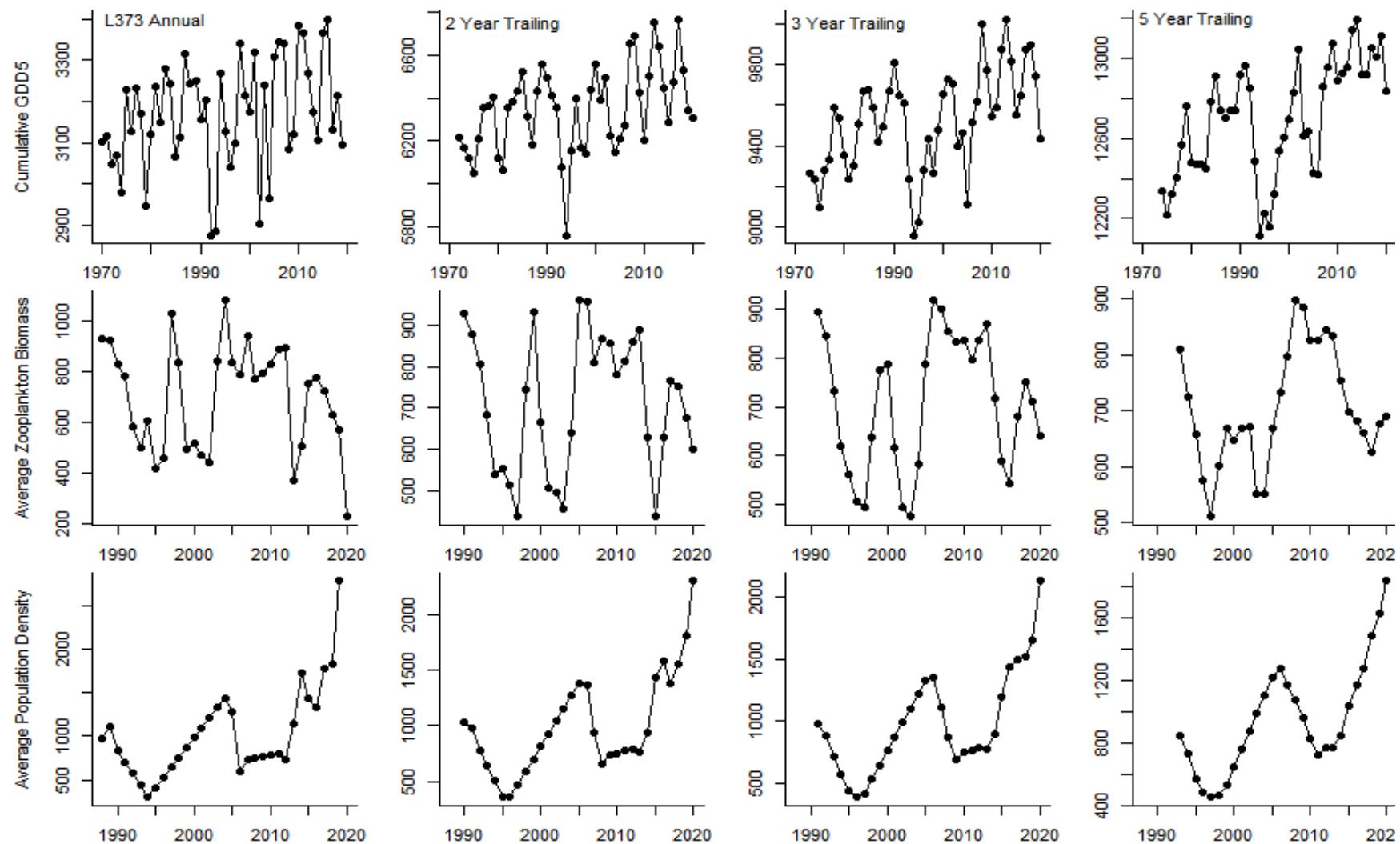


Figure E. Annual and trailing total/average of the size at age predictor variables in Lake 373. Each row represents one of GDD₅, zooplankton biomass (ug/L dry weight), and population density, and each column represents the averaging period. Annual estimates are not offset by 1 year, whereas trailing total are offset to better reflect the history of growing conditions for White Sucker of that year.

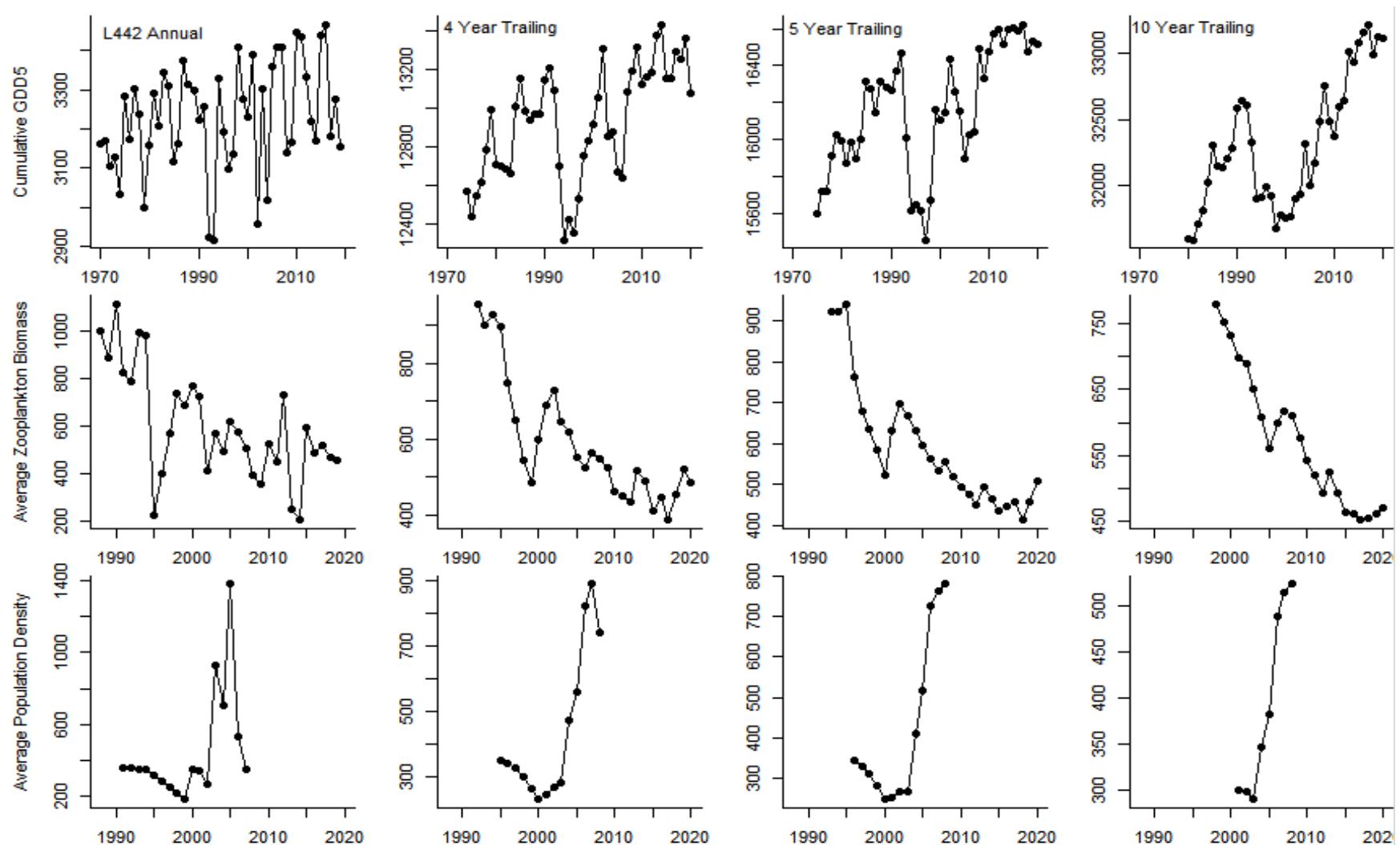


Figure F. Annual and trailing total/average of the size at age predictor variables in Lake 442. Each row represents one of GDD₅, zooplankton biomass (ug/L dry weight), and population density, and each column represents the averaging period. Annual estimates are not offset by 1 year, whereas trailing total are offset to better reflect the history of growing conditions for White Sucker of that year.

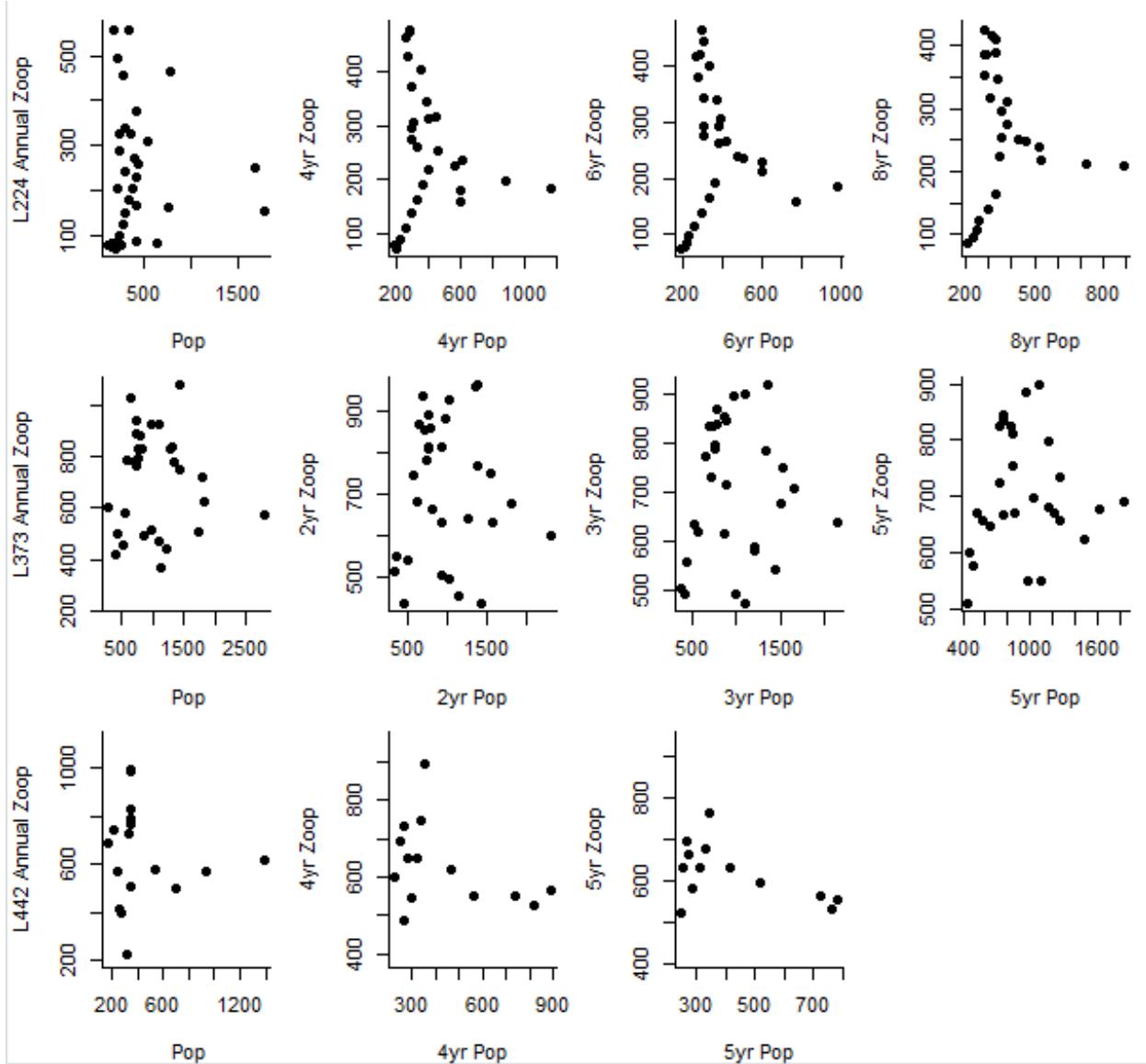


Figure G. Correlation plots of zooplankton biomass and White Sucker abundance for all 3 lakes annually, and at trailing averages of representative age classes considered. Note there is no positive or negative correlation between the two annually nor at a given age, suggesting observed changes in these variables (less zooplankton biomass, more White Sucker abundance) are occurring independently of each other. Zooplankton biomass has no effect on population size or vice versa.

Appendix 5 – Chapter 3 model summary outputs from ELA White Sucker populations

Appendix 4 details model summary outputs from the lake specific growth models for the ELA White Sucker populations. For each lake, there are 6 table summaries because the data was separated into an immature and mature dataset to run the models on. Recall RWT = round weight, FLEN = fork length, and BCD = body condition. Table A – F detail models for Lake 224, Table G – L detail Lake 373, and Table M – R detail Lake 442. Equations of the models are listed in the table captions, and coefficients of the terms are detailed within the tables under the “Estimate” column

Table A. Immature age classes Lake 224 RWT Equation: $\log_{10}\text{RWT} = \log_{10}\text{Yr} + \text{Age}$

	Estimate	Std.	Error	t	value	Pr(> t)
(Intercept)	531.2081	56.052		9.477	1.57E-13	***
logYr	-160.694	16.9832		-9.462	1.66E-13	***
Age2	0.5278	0.1177		4.483	3.38E-05	***
Age3	0.8954	0.114		7.856	8.61E-11	***
Age4	1.182	0.1142		10.35	5.73E-15	***
Multiple	R-squared:	0.7608	Adjusted	R-squared:	0.7448	

Table B. Mature age classes Lake 224 RWT Equation: $\log_{10}\text{RWT} = \log_{10}\text{Yr} * \text{Age} + \log_{10}\text{Yr} + \text{Age} + \text{Sex}$

	Estimate	Std.	Error	t	value	Pr(> t)
(Intercept)	613.3459	64.20534		9.553	<	2.00E-16 ***
logYr	-185.169	19.44442		-9.523	<	2.00E-16 ***
Age6	36.18544	86.79909		0.417		0.677143
Age7	-86.9724	85.15981		-1.021		0.308175
Age8	-297.038	87.91361		-3.379		0.000853 ***
Age9	-287.159	87.47266		-3.283		0.001185 **
Age10	-413.372	97.32609		-4.247		3.12E-05 ***
Sex2	0.16933	0.03172		5.338		2.22E-07 ***
logYr:Age6	-10.8813	26.28762		-0.414		0.679302
logYr:Age7	26.48297	25.79091		1.027		0.305559
logYr:Age8	90.15652	26.62486		3.386		0.000831 ***
logYr:Age9	87.18856	26.49116		3.291		0.001152 **
logYr:Age10	125.4409	29.4733		4.256		3.01E-05 ***
Multiple	R-squared:	0.7579	Adjusted	R-squared:	0.7455	

Table C. Immature age classes Lake 224 FLEN Equation: $\log_{10}\text{FLEN} = \log_{10}\text{Yr} + \text{Age}$

	Estimate	Std.	Error	t	value	Pr(> t)
(Intercept)	161.0715	17.67348		9.114	6.36E-13	***
logYr	-48.2188	5.3549		-9.005	9.70E-13	***
Age2	0.17285	0.03712		4.656	1.83E-05	***
Age3	0.29092	0.03593		8.096	3.36E-11	***
Age4	0.3798	0.03601		10.547	2.74E-15	***
Multiple	R-squared:	0.7576	Adjusted	R-squared:	0.7414	

Table D. Mature age classes Lake 224 FLEN Equation: $\text{FLENavg} = \text{Year} * \text{Age} + \text{Year} + \text{Age} + \text{Sex}$

(Intercept)	14642.58	1634.392		8.959	<	2.00E-16	***
Year	-7.2084	0.8154		-8.841		2.34E-16	***
Age6	2884.194	2214.985		1.302		0.19415	
Age7	1653.485	2183.317		0.757		0.44962	
Age8	-3785.92	2266.012		-1.671		0.09611	.
Age9	-2658.6	2262.496		-1.175		0.24116	
Age10	-6728.89	2520.076		-2.67		0.00811	**
Sex2	38.8582	6.1578		6.31		1.38E-09	***
Year:Age6	-1.4159	1.1052		-1.281		0.20142	
Year:Age7	-0.7822	1.0893		-0.718		0.47346	
Year:Age8	1.9477	1.1306		1.723		0.08627	.
Year:Age9	1.3951	1.1288		1.236		0.21773	
Year:Age10	3.4365	1.2566		2.735		0.00672	**
Multiple	R-squared:	0.7765	Adjusted	R-squared:	0.765		

Table E. Immature age classes Lake 224 BCD Equation: $\log_{10}\text{BCD} = \log_{10}\text{Yr} + \text{Age}$

	Estimate	Std.	Error	t	value	Pr(> t)
(Intercept)	62.34459	9.28037		6.718	1.52E-08	***
logYr	-18.9101	2.81171		-6.725	1.48E-08	***
Age3	0.03186	0.01382		2.306	0.02524	*
Age4	0.05438	0.01386		3.922	0.000263	***
Multiple	R-squared:	0.5113	Adjusted	R-squared:	0.4825	

Table F. Mature age classes Lake 224 BCD Equation: $\log_{10}BCD = \log_{10}Yr * Age + \log_{10}Yr + Age + Sex$

	Estimate	Std.	Error	t	value	Pr(> t)
(Intercept)	61.50729	9.330006		6.592	2.84E-10	***
logYr	-18.6357	2.825568		-6.595	2.80E-10	***
Age6	-7.2548	12.61322		-0.575	0.565726	
Age7	-27.0354	12.37501		-2.185	0.029906	*
Age8	-34.4691	12.77518		-2.698	0.007481	**
Age9	-33.2677	12.7111		-2.617	0.009443	**
Age10	-47.4218	14.14295		-3.353	0.000932	***
Sex2	0.020982	0.004609		4.552	8.54E-06	***
logYr:Age6	2.200835	3.819989		0.576	0.565077	
logYr:Age7	8.195175	3.747808		2.187	0.029758	*
logYr:Age8	10.45164	3.868995		2.701	0.00741	**
logYr:Age9	10.08996	3.849566		2.621	0.00934	**
logYr:Age10	14.3808	4.282915		3.358	0.000917	***
Multiple	R-squared:	0.5021	Adjusted	R-squared:	0.4766	

Table G. Immature age classes Lake 373 RWT Equation: $\log_{10}RWT = \log_{10}Yr * Age + \log_{10}Yr + Age$

	Estimate	Std.	Error	t	value	Pr(> t)
(Intercept)	5.297	91.921		0.058	0.954188	
logYr	-1.364	27.844		-0.049	0.96105	
Age2	202.292	122.475		1.652	0.102466	
Age3	425.913	121.804		3.497	0.000767	***
Age4	341.662	127.435		2.681	0.00889	**
logYr:Age2	-61.111	37.096		-1.647	0.103358	
logYr:Age3	-128.722	36.894		-3.489	0.000787	***
logYr:Age4	-103.076	38.6		-2.67	0.009154	**
Multiple	R-squared:	0.8249	Adjusted	R-squared:	0.8097	

Table H. Mature age classes Lake 373 RWT Equation: $\log_{10}RWT = \log_{10}Yr + Age + Sex$

	Estimate	Std.	Error	t	value	Pr(> t)
(Intercept)	258.8075	33.67302		7.686	1.21E-12	***
logYr	-77.7017	10.19821		-7.619	1.78E-12	***
Age6	0.26234	0.05862		4.475	1.40E-05	***
Age7	0.54567	0.06067		8.995	4.86E-16	***
Age8	0.65748	0.06081		10.813	< 2.00E-16	***
Age9	0.77284	0.0711		10.87	< 2.00E-16	***
Age10	0.79109	0.06839		11.567	< 2.00E-16	***
Sex2	0.19362	0.04008		4.831	3.05E-06	***
Multiple	R-squared:	0.6607	Adjusted	R-squared:	0.6466	

Table I. Immature age classes Lake 373 FLEN Equation: $\log_{10}RWT = \log_{10}Yr * Age + \log_{10}Yr + Age$

	Estimate	Std.	Error	t	value	Pr(> t)
(Intercept)	23.163	29.423		0.787		0.43341
logYr	-6.435	8.912		-0.722		0.47229
Age2	39.967	39.497		1.012		0.31456
Age3	110.34	39.277		2.809	0.00621	**
Age4	86.825	41.127		2.111	0.0378	*
logYr:Age2	-12.055	11.963		-1.008	0.31657	
logYr:Age3	-33.331	11.897		-2.802	0.00634	**
logYr:Age4	-26.172	12.457		-2.101	0.03872	*
Multiple	R-squared:	0.812	Adjusted	R-squared:	0.7959	

Table J. Mature age classes Lake 373 FLEN Equation: $\log_{10}FLEN = \log_{10}Yr + Age + Sex$

	Estimate	Std.	Error	t	value	Pr(> t)
(Intercept)	82.24631	10.8292		7.595		2.00E-12
logYr	-24.1915	3.27973		-7.376		6.99E-12
Age6	0.08081	0.01886		4.285		3.07E-05
Age7	0.17155	0.01952		8.789		1.66E-15
Age8	0.2157	0.0194		11.121	<	2.00E-16
Age9	0.25071	0.02287		10.961	<	2.00E-16
Age10	0.25504	0.022		11.591	<	2.00E-16
Sex2	0.05676	0.01288		4.407		1.86E-05
Multiple	R-squared:	0.6579	Adjusted	R-squared:	0.6438	

Table K. Immature age classes Lake 373 BCD Equation: $BCDavg = Year + Age$

	Estimate	Std.	Error	t	value	Pr(> t)
(Intercept)	11.29674	1.898805		5.949		1.09E-07
Year	-0.0052	0.000948		-5.491		6.65E-07
Age3	0.032776	0.02125		1.542		0.128
Age4	0.113959	0.021647		5.264		1.60E-06
Multiple	R-squared:	0.4825	Adjusted	R-squared:	0.4593	

Table L. Mature age classes Lake 373 BCD Equation: $\log_{10}BCD = \log_{10}Yr + Age + Sex$

	Estimate	Std.	Error	t	value	Pr(> t)
(Intercept)	32.32044	5.526361		5.848	2.53E-08	***
logYr	-9.78737	1.673714		-5.848	2.53E-08	***
Age6	0.031028	0.009621		3.225	0.001514	**
Age7	0.041979	0.009956		4.216	4.05E-05	***
Age8	0.054049	0.00998		5.416	2.08E-07	***
Age9	0.069999	0.011668		5.999	1.18E-08	***
Age10	0.076064	0.011224		6.777	1.99E-10	***
Sex2	0.025585	0.006578		3.889	0.000145	***
Multiple	R-squared:	0.4154	Adjusted	R-squared:	0.3911	

Table M. immature age classes Lake 442 RWT Equation: $\log_{10}RWT = \log_{10}Yr + Age$

	Estimate	Std.	Error	t	value	Pr(> t)
(Intercept)	619.0323	86.5879		7.149	6.13E-09	***
logYr	-187.261	26.2268		-7.14	6.32E-09	***
Age2	0.5128	0.1225		4.185	0.000131	***
Age3	1.0028	0.123		8.151	2.08E-10	***
Age4	1.3611	0.1208		11.268	1.08E-14	***
Multiple	R-squared:	0.8537	Adjusted	R-squared:	0.8407	

Table N. Mature age classes Lake 442 RWT Equation: $RWTavg = Year * Age + Year + Age + Sex$

	Estimate	Std.	Error	t	value	Pr(> t)
(Intercept)	16640.82	9275.295		1.794	0.076774	.
Year	-8.165	4.64		-1.76	0.082493	.
Age6	-8218.7	13630.9		-0.603	0.54834	
Age7	-11806.9	13199.69		-0.894	0.373886	
Age8	-28366	14405.24		-1.969	0.052582	.
Age9	-70706.8	30165.59		-2.344	0.021695	*
Age10	-90646.7	22536.78		-4.022	0.000135	***
Sex2	180.738	28.051		6.443	9.63E-09	***
Year:Age6	4.165	6.822		0.611	0.54334	
Year:Age7	6.024	6.604		0.912	0.364551	
Year:Age8	14.378	7.207		1.995	0.049636	*
Year:Age9	35.619	15.129		2.354	0.021141	*
Year:Age10	45.646	11.295		4.041	0.000126	***
Multiple	R-squared:	0.7628	Adjusted	R-squared:	0.7253	

Table O. Immature age classes Lake 442 FLEN Equation: $\log_{10}\text{FLEN} = \log_{10}\text{Yr} + \text{Age}$

	Estimate	Std.	Error	t	value	Pr(> t)
(Intercept)	200.1221	27.98942		7.15	6.11E-09	***
logYr	-60.0386	8.47778		-7.082	7.71E-09	***
Age2	0.16776	0.03961		4.235	0.000111	***
Age3	0.32259	0.03977		8.112	2.37E-10	***
Age4	0.44205	0.03905		11.321	9.26E-15	***
Multiple	R-squared:	0.8535	Adjusted	R-squared:	0.8405	

Table P. Mature age classes Lake 442 FLEN Equation: $\log_{10}\text{FLEN} = \log_{10}\text{Yr} * \text{Age} + \log_{10}\text{Yr} + \text{Age} + \text{Sex}$

	Estimate	Std.	Error	t	value	Pr(> t)
(Intercept)	72.35	1.61E+01		4.486	2.54E-05	***
logYr	-21.17	4.89E+00		-4.333	4.45E-05	***
Age6	-42.71	2.40E+01		-1.779	0.07928	.
Age7	-51.01	2.29E+01		-2.228	0.02884	*
Age8	-75.47	2.55E+01		-2.957	0.00414	**
Age9	-104.2	5.17E+01		-2.017	0.04725	*
Age10	-116.6	4.03E+01		-2.895	0.00495	**
Sex2	0.03573	6.84E-03		5.224	1.48E-06	***
logYr:Age6	12.95	7.28E+00		1.78	0.07902	.
logYr:Age7	15.47	6.94E+00		2.231	0.02864	*
logYr:Age8	22.89	7.73E+00		2.96	0.0041	**
logYr:Age9	31.61	1.57E+01		2.018	0.04711	*
logYr:Age10	35.36	1.22E+01		2.897	0.00492	**
Multiple	R-squared:	0.7465	Adjusted	R-squared:	0.7064	

Table Q. Immature age classes Lake 442 BCD Equation: $\log_{10}\text{BCD} = \log_{10}\text{Yr} + \text{Age}$

	Estimate	Std.	Error	t	value	Pr(> t)
(Intercept)	43.1688	8.934037		4.832	1.83E-05	***
logYr	-13.0878	2.706573		-4.836	1.81E-05	***
Age3	0.015807	0.008221		1.923	0.0613	.
Age4	0.033756	0.007832		4.31	9.64E-05	***
Multiple	R-squared:	0.4948	Adjusted	R-squared:	0.4587	

Table R. Mature age classes Lake 442 BCD Equation: $\log_{10}\text{BCD} = \text{Age} + \text{Sex}$ (year non-significant)

	Estimate	Std.	Error	t	value	Pr(> t)
(Intercept)	0.00759	0.006955		1.091	0.278312	
Age6	0.009296	0.00941		0.988	0.326133	
Age7	0.027541	0.009505		2.898	0.004822	**
Age8	0.029242	0.01021		2.864	0.005307	**
Age9	0.02866	0.011667		2.456	0.016144	*
Age10	0.025105	0.011378		2.207	0.030143	*
Sex2	0.023149	0.006337		3.653	0.000455	***
Multiple	R-squared:	0.3036	Adjusted	R-squared:	0.2526	

Appendix 6 – Chapter 3 model summary outputs from NDMNRF White Sucker populations

Appendix 6 details model summary outputs from the lake specific growth models for the NDMNRF White Sucker populations. For each lake, there are 6 table summaries because the data was separated into an immature and mature dataset to run the models on. Recall RWT = round weight, FLEN = fork length, and BCD = body condition. Table A – F detail models for Lac Des Mille Lacs (LDML), Table G – L detail Lake of the Woods (LOTW), Table M – R detail Lake Nipigon, (NIP), and Table S – X detail Whitefish Lake (WFSH). Equations of the models are listed in the table captions, and coefficients of the terms are detailed within the tables under the “Estimate” column.

Table A. Immature age classes LDML RWT Equation: RWT = Year + Age

	Estimate	Std.	Error	t	value	Pr(> t)	
(Intercept)	42621.65	13174.65		3.235		0.01435	*
Year	-21.172	6.553		-3.231		0.01443	*
Age2	43.135	152.695		0.282		0.78574	
Age3	246.545	112.95		2.183		0.06537	.
Age4	507.715	98.927		5.132		0.00135	**
Multiple	R-squared:	0.6705	Adjusted	R-squared:	0.5607		

Table B. Mature age classes LDML RWT Equation: RWT = Age + Sex

	Estimate	Std.	Error	t	value	Pr(> t)	
(Intercept)	660.15	65.43		10.089		8.61E-13	***
Age6	153.3	82.23		1.864		0.06929	.
Age7	169.74	96.96		1.751		0.087317	.
Age8	318.35	90.23		3.528		0.001028	**
Age9	388.01	92.25		4.206		0.000133	***
Age10	452.95	89.24		5.076		8.32E-06	***
Sex2	201.17	54.13		3.716		0.000591	***
Multiple	R-squared:	0.3445	Adjusted	R-squared:	0.2716		

Table C. Immature age classes LDML FLEN Equation: FLEN = Year + Age

	Estimate	Std.	Error	t	value	Pr(> t)
(Intercept)	7635.466	2609.689		2.926		0.01912 *
Year	-3.72	1.298		-2.866		0.020947 *
Age2	55.708	36.624		1.521		0.166732
Age3	75.32	25.402		2.965		0.018005 *
Age4	168.61	23.948		7.041		0.000108 ***
Multiple	R-squared:	0.8667	Adjusted	R-squared:	0.7905	

Table D. Mature age classes LDML FLEN Equation: FLEN = Age + Sex

	Estimate	Std.	Error	t	value	Pr(> t)
(Intercept)	351.304	9.451		37.17	<	2.00E-16 ***
Age6	19.42	11.696		1.66		0.103931
Age7	32.676	13.473		2.425		0.019465 *
Age8	39.013	13.049		2.99		0.004559 **
Age9	46.71	13.346		3.5		0.001079 **
Age10	50.553	12.909		3.916		0.00031 ***
Sex2	30.628	7.736		3.959		0.000271 ***
Multiple	R-squared:	0.5708	Adjusted	R-squared:	0.5095	

Table E. Immature age classes LDML BCD Equation: BCD = Year (nonsignificant model)

	Estimate	Std.	Error	t	value	Pr(> t)
(Intercept)	13.68658	76.11787		0.18		0.861
Year	-0.00612	0.037854		-0.162		0.875
Multiple	R-squared:	0.002611	Adjusted	R-squared:	-0.09713	

Table F. Mature age classes LDML BCD Equation: BCD = Year (nonsignificant model)

	Estimate	Std.	Error	t	value	Pr(> t)
(Intercept)	-3.91626	73.18377		-0.054		0.958
Year	0.002689	0.036417		0.074		0.941
Multiple	R-squared:	0.000116	Adjusted	R-squared:	-0.02116	

Table G. Immature age classes LOTW RWT Equation: $\text{sqrtRWT} = \text{Year} * \text{Age} + \text{Year} + \text{Age}$

	Estimate	Std.	Error	t	value	Pr(> t)
(Intercept)	-642.321	206.3302		-3.113		0.00236
Year	0.327	0.103		3.173		0.00195
Age2	794.4755	253.4805		3.134		0.00221
Age3	518.7642	249.3844		2.08		0.03983
Age4	619.6698	250.8078		2.471		0.01502
Year:Age2	-0.3959	0.1266		-3.127		0.00226
Year:Age3	-0.2557	0.1245		-2.053		0.04243
Year:Age4	-0.3033	0.1253		-2.422		0.01709
Multiple	R-squared:	0.6173	Adjusted	R-squared:	0.5929	

Table H. Mature age classes LOTW RWT Equation: $\text{RWT} = \text{Age}$

	Estimate	Std.	Error	t	value	Pr(> t)
(Intercept)	791.11	30.69		25.776	<	2.00E-16
Age6	206.4	43.71		4.722		4.39E-06
Age7	378.17	43.4		8.713		1.13E-15
Age8	474.42	44.38		10.69	<	2.00E-16
Age9	667.45	44.04		15.156	<	2.00E-16
Age10	708.92	44.74		15.845	<	2.00E-16
Multiple	R-squared:	0.6529	Adjusted	R-squared:	0.6442	

Table I. Immature age classes LOTW FLEN Equation: $\text{FLEN} = \text{Year} * \text{Age} + \text{Year} + \text{Age}$

	Estimate	Std.	Error	t	value	Pr(> t)
(Intercept)	-6277.52	1846.355		-3.4		0.00094
Year	3.2426	0.9221		3.516		0.000637
Age2	6974.52	2268.283		3.075		0.002657
Age3	4607.004	2231.628		2.064		0.04133
Age4	5772.701	2244.366		2.572		0.011442
Year:Age2	-3.475	1.1327		-3.068		0.002715
Year:Age3	-2.2668	1.1145		-2.034		0.044372
Year:Age4	-2.8222	1.1208		-2.518		0.013241
Multiple	R-squared:	0.6664	Adjusted	R-squared:	0.6451	

Table J. Mature age classes LOTW FLEN Equation: $\text{FLEN} = \text{Age}$

	Estimate	Std.	Error	t	value	Pr(> t)
(Intercept)	365.621	3.465		105.512	<	2.00E-16
Age6	32.139	4.935		6.512		5.87E-10
Age7	51.524	4.901		10.514	<	2.00E-16
Age8	64.102	5.011		12.793	<	2.00E-16
Age9	84.948	4.972		17.085	<	2.00E-16
Age10	91.153	5.051		18.045	<	2.00E-16
Multiple	R-squared:	0.7001	Adjusted	R-squared:	0.6926	

Table K. Immature age classes LOTW BCD Equation: BCD = Age

	Estimate	Std.	Error	t	value	Pr(> t)	
(Intercept)	1.11048	0.02449		45.338	<	2.00E-16	***
Age2	-0.01148	0.03194		-0.359		0.72	
Age3	0.05746	0.03115		1.845		0.0677	.
Age4	0.12922	0.03133		4.124		7.09E-05	***
Multiple	R-squared:	0.207	Adjusted	R-squared:	0.1861		

Table L. Mature age classes LOTW BCD Equation: BCD = Year

	Estimate	Std.	Error	t	value	Pr(> t)	
(Intercept)	3.697194	1.226029		3.016		0.00289	**
Year	-0.00121	0.000612		-1.976		0.0495	*
Multiple	R-squared:	0.01878	Adjusted	R-squared:	0.01397		

Table M. Immature age classes NIP RWT Equation: log10RWT = Year + Age

	Estimate	Std.	Error	t	value	Pr(> t)	
(Intercept)	35.73188	15.42165		2.317		0.02833	*
Year	-0.01672	0.007665		-2.181		0.0381	*
Age3	0.182087	0.116517		1.563		0.12976	
Age4	0.322646	0.111564		2.892		0.00747	**
Multiple	R-squared:	0.3408	Adjusted	R-squared:	0.2675		

Table N. Mature age classes NIP RWT Equation: RWT = Year + Age

	Estimate	Std.	Error	t	value	Pr(> t)	
(Intercept)	19583.39	8395.127		2.333		0.0231	*
Year	-9.477	4.173		-2.271		0.0268	*
Age6	116.288	80.207		1.45		0.1524	
Age7	410.648	82.041		5.005		5.34E-06	***
Age8	424.219	80.058		5.299		1.82E-06	***
Age9	545.123	78.461		6.948		3.32E-09	***
Age10	558.513	80.164		6.967		3.07E-09	***
Multiple	R-squared:	0.6051	Adjusted	R-squared:	0.5649		

Table O. Immature age classes NIP FLEN Equation: log10FLEN = Year + Age

	Estimate	Std.	Error	t	value	Pr(> t)	
(Intercept)	13.22412	4.965263		2.663		0.01288	*
Year	-0.00542	0.002468		-2.195		0.03692	*
Age3	0.051067	0.037515		1.361		0.18469	
Age4	0.100019	0.03592		2.785		0.00968	**
Multiple	R-squared:	0.3312	Adjusted	R-squared:	0.2569		

Table P. Mature age classes NIP FLEN Equation: FLEN = Year + Age

	Estimate	Std.	Error	t	value	Pr(> t)
(Intercept)	4410.834	1442.748		3.057		0.00335
Year	-2.0327	0.7171		-2.835		0.00627
Age6	24.9786	13.7839		1.812		0.07505
Age7	69.3091	14.0991		4.916		7.39E-06
Age8	78.5287	13.7585		5.708		3.93E-07
Age9	91.3256	13.4839		6.773		6.55E-09
Age10	92.7354	13.7765		6.731		7.69E-09
Multiple	R-squared:	0.5958	Adjusted	R-squared:	0.5547	

Table Q. Immature age classes NIP BCD Equation: BCD = Year * Age + Year + Age

	Estimate	Std.	Error	t	value	Pr(> t)
(Intercept)	21.7617	10.94763		1.988		0.05789
Year	-0.0103	0.005441		-1.894		0.06992
Age3	-23.0576	14.54292		-1.585		0.12543
Age4	-41.5865	14.3315		-2.902		0.00764
Year:Age3	0.011506	0.007231		1.591		0.12411
Year:Age4	0.020694	0.007125		2.905		0.00759
Multiple	R-squared:	0.3461	Adjusted	R-squared:	0.2153	

Table R. Mature age classes NIP BCD Equation: BCD = Age

	Estimate	Std.	Error	t	value	Pr(> t)
(Intercept)	1.12818	0.02313		48.775	<	2.00E-16
Age6	0.02636	0.03271		0.806		0.42345
Age7	0.08882	0.03352		2.65		0.01028
Age8	0.05727	0.03271		1.751		0.08508
Age9	0.08098	0.03202		2.529		0.01408
Age10	0.09091	0.03271		2.779		0.00727
Multiple	R-squared:	0.1766	Adjusted	R-squared:	0.108	

Table S. Immature age classes WFSH RWT Equation: log10RWT = Age

	Estimate	Std.	Error	t	value	Pr(> t)
(Intercept)	2.05765	0.07318		28.119		2.16E-14
Age2	0.51072	0.09256		5.518		5.91E-05
Age3	0.81441	0.09256		8.799		2.62E-07
Age4	0.85877	0.08962		9.582		8.73E-08
Multiple	R-squared:	0.8786	Adjusted	R-squared:	0.8543	

Table T. Mature age classes WFSH RWT Equation: RWT = Year + Age + Sex

	Estimate	Std.	Error	t	value	Pr(> t)
(Intercept)	-11336.2	3495.55		-3.243		0.001868 **
Year	6.069	1.746		3.476		0.000913 ***
Age6	-8.871	52.85		-0.168		0.867219
Age7	107.515	51.88		2.072		0.042201 *
Age8	146.098	52.762		2.769		0.00732 **
Age9	201.23	60.771		3.311		0.001519 **
Age10	216.008	55.274		3.908		0.000225 ***
Sex2	144.72	32.37		4.471		3.20E-05 ***
Multiple	R-squared:	0.5196	Adjusted	R-squared:	0.4679	

Table U. Immature age classes WFSH FLEN Equation: FLEN = Year + Age

	Estimate	Std.	Error	t	value	Pr(> t)
(Intercept)	1932.899	1355.939		1.426		0.174
Year	-0.864	0.6778		-1.275		0.222
Age2	102.3148	16.7498		6.108		2.00E-05 ***
Age3	169.7362	17.7003		9.589		8.65E-08 ***
Age4	186.4311	16.8815		11.044		1.33E-08 ***
Multiple	R-squared:	0.9106	Adjusted	R-squared:	0.8868	

Table V. Mature age classes WFSH FLEN Equation: FLEN = Year + Age + Sex

	Estimate	Std.	Error	t	value	Pr(> t)
(Intercept)	-1653.72	468.378		-3.531		0.000761 ***
Year	1.014	0.234		4.335		5.09E-05 ***
Age6	1.084	7.09		0.153		0.878984
Age7	21.294	6.835		3.116		0.002717 **
Age8	24.293	7.078		3.432		0.001038 **
Age9	33.086	8.152		4.058		0.000133 ***
Age10	35.516	7.415		4.79		9.83E-06 ***
Sex2	28.672	4.313		6.648		6.81E-09 ***
Multiple	R-squared:	0.6423	Adjusted	R-squared:	0.6044	

Table W. Immature age classes WFSH BCD Equation: BCD = Age

	Estimate	Std.	Error	t	value	Pr(> t)
(Intercept)	0.92333	0.07919		11.659		6.40E-09 ***
Age2	0.10467	0.10017		1.045		0.31264
Age3	0.31867	0.10017		3.181		0.0062 **
Age4	0.28667	0.09699		2.956		0.00982 **
Multiple	R-squared:	0.4988	Adjusted	R-squared:	0.3985	

Table X. Mature age classes WFSH BCD Equation: BCD = Sex (nonsignificant model)

	Estimate	Std.	Error	t	value	Pr(> t)	
(Intercept)	1.15242	2.10E-02		54.921		<2e-16	***
Sex2	-0.02967	2.84E-02		-1.047		0.299	
Multiple	R-squared:	0.0152	Adjusted	R-squared:	0.00133		