THE EFFECTS OF CLIMATE CHANGE ON NORTH-TEMPERATE LAKE TROUT (*SALVELINUS NAMAYCUSH*)

POPULATIONS

By

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ABSTRACT

Aquatic ecosystems are expected to undergo major changes in response to climate change. Lake trout

(*Salvelinus namaycush*) is predatory fish found in oligotrophic lakes of Canada and is considered a

sentinel species for studying the impacts of warming on lakes due to its requirement for cold water. The

objective of this thesis was to determine the impacts of warming on north-temperate lake trout

populations. In Chapters 1-3, I used long-term datasets collected from small lakes near the southern

extent of lake trout's distribution to determine how warming impacts thermal habitat and how these

habitat changes cascade to alter the behaviour and growth of individuals and ultimately population-level

characteristics of this species. I found that over a period when annual air temperatures increased by ≈ 2

˚C there was a 14-day reduction, on average, in the ice-free season and an equal extension of summer

— a period when littoral zone temperatures exceed the metabolic optimal for lake trout. Years with

shorter springs and longer summers negatively impacts lake trout by limiting access to littoral prey,

resulting in slower growth and reduced condition. I also found that the growth and size structure of an

unexploited lake trout population shifted during this warming period; the population is now made up of

a larger number of small individuals with lower condition and reduced life span. Lake trout also began to

mature at younger ages and had reduced maximum size. Results suggest these changes in size-structure

were not due to changes in the amount or size of prey fish or density-dependence, as the biomass of

adult lake trout remained constant over time. In Chapter 4, I collected data from a northern lake to

describe the seasonal ecology of this northern lake trout population and predict how warming might

alter growth. I found that lake trout displayed similar seasonal cycles in habitat use and diet as in

southern lakes, but that the use of littoral habitat was far reduced, likely due to the presence of pelagic

prey fish and northern pike (*Esox lucius*) in this lake. Lastly, bioenergetic simulations indicated that the

under a 2 ˚C warming scenario, the growth and consumption of lake trout would increase in this

northern lake assuming prey was readily available.

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the Experimental Lakes Area, northwestern Ontario, Canada. For air temperature, a linear trend line and corresponding slope estimate are present in plots where a Mann-Kendall test indicated a significant monotonic trend at $P < 0.1$. Because precipitation follows a 31-year cycle in the region, a loess curve has been used to visualize cyclic patterns in precipitation.

isotherm and 4 mg L^{-1} oxycline) boundaries and corresponding habitat volumes (panel c). Horizontal dot-and-dash lines on panels a and b indicate the bottom of each lake and in panel c indicate zero lake volume meeting usable or optimal habitat criteria.

transformed; *n* = 11) to the number of (a) spring and (b) summer days.

program.

 "Warming of the climate system is unequivocal, and since the 1950s, many of the observed changes are unprecedented over decades to millennia. The atmosphere and ocean have warmed, the amounts of snow and ice have diminished, and sea level has risen".

- p. 2 *Intergovernmental Panel for Climate Change 2014, AR5, Synthesis Report*

Global surface temperatures warmed by an average of 0.85 °C between 1880 and 2012 (IPCC 2014). The timing of this rise in temperatures coincides with the start of industrialization, a period when anthropogenic greenhouse gasses (GHG) were first released into the atmosphere. Concomitant with trends in surface temperatures, levels of anthropogenic GHGs in the atmosphere have increased since the start of industrialization, with annual emissions growing by 81 % between 1970 and 2012 (IPCC 2014). This strong positive correlation between anthropogenic GHG emissions and global surface temperatures in addition to the fact that temperatures were relatively stable prior to this period provide evidence that the cause of warming is anthropogenic in nature (IPCC 2014). Although GHG emissions are expected to increase in the future, climate models predict that even under scenarios where GHG emissions are reduced, the upward trend in temperature will only be slowed and not reversed. Increases in mean global temperatures predicted by the end of the 21st century relative to 1986-2005 are expected to range 0.3-1.7 °C under the lowest GHG scenario (RCP2.6) and 2.6-4.8 °C under the highest GHG scenario (RCP8.5) (IPCC 2014). While these predicted changes in temperature may seem minor as a global average, the severity of warming is subject to high spatial heterogeneity. For example, north-temperate (23.5-66.5 °N latitude) and Arctic (> 66.5 °N latitude) regions of continental North America, Europe, and Asia have undergone increases in surface temperatures up to 2.5 times the global average (IPCC 2014). These spatial differences in temperature change are relevant in an ecological context, as organisms, populations and ecological communities do not respond to global averages, but rather to

local changes (Walther et al. 2002, Voss et al. 2012). Consequently, the prospect of a warmer world stresses the need to document the ecological impacts of past warming to allow more accurate predictions of impending impacts, particularly in regions where future warming will be greatest.

There exists ample evidence of the ecological responses to increasing temperatures from a broad range of organisms across a wide geographical distribution. The most documented ecological responses to warming have been changes in phenology, such as timing of bird migrations and plant flowering (Walther et al. 2002, Parmesan and Yohe 2003), as well as shifts species distributions toward the poles and higher elevations (Parmesan and Yohe 2003, Perry et al. 2005, Chen et al. 2011). More recently, studies have shown that warming temperatures can impact organisms through changes in behaviour, such as habitat use and feeding (Barton and Schmitz 2009, Tunney et al. 2014, Freitas et al. 2015), and through reductions in adult body size (Gardner et al. 2011, Sheridan and Bickford 2011). While studying each ecological response to warming in isolation is important, it is likely that several responses are in fact linked and should be studied through a holistic approach. The links among several ecological responses to warming is perhaps best depicted by the impacts of warming on some populations of polar bears (*Ursus maritimus*) in the Arctic. Polar bears have previously relied almost exclusively on marine-based energy (Ramsay and Hobson 1991); however, reductions in the extent and duration of Arctic sea ice have forced them to increase use of terrestrial habitats and food (McKinney et al. 2017). Unfortunately, these subsidies of land-based food are insufficient to offset reductions in energy-rich marine based prey like seals and have led to reduced condition and survival of polar bears (Rode et al. 2015). This polar bear example provides strong support that the impacts of warming on a given species are best understood through a sequential approach, where impacts of warming cascade from physical habitat (in this case, sea ice) to individual behaviour and growth, and finally manifest at the population level.

Although climate change is recognized as a major threat to all habitats types, lakes have been regarded as sentinels for studying the impacts of climate change on ecosystems because they integrate changes in their surrounding landscapes (Adrian et al. 2009, Williamson et al. 2009). The specific responses of lakes to climate related warming will depend on both geographical location and physical properties of lakes. Small dimictic north-temperate lakes are perhaps those most likely to be affected by climate change, as the physical characteristic of these systems have been found to rapidly respond to changes in temperature. Warming related to climate change has been found to result in increased surface water temperatures, earlier onset and extended duration of thermal-stratification, and reduced duration of ice-cover in small north-temperate lakes (DeStasio et al. 1996, Magnuson et al. 2000, Jansen and Hesslein 2004, Keller et al. 2007, Benson et al. 2012, O'Reilly et al. 2015). However, there are contrasting predictions of whether climate change will lead to increases or decreases in thermocline depth. Based on air temperature alone, where spring temperatures become elevated more rapidly, thermoclines may either become deeper (DeStasio et al. 1996, Plumb and Blanchfield 2009) or shallower and more intense (Keller et al. 2007). However, with increased precipitation and runoff of allochthonous dissolved organic matter, thermoclines in boreal lakes may become stronger and shallower, manifested by light attenuation (Fee et al. 1996, Schindler et al. 1996a, 1996b). As predictions of future precipitation in north-temperate regions of Canada vary regionally (Colombo et al. 2007, Keller 2007), warming is considered the most widespread impact of climate change on lakes in this climate zone.

Annual air temperatures in north-temperate regions of Canada are predicted to increase by 3-10 °C by the end of the 21st century, with the magnitude of warming expected to increase with latitude (CanRCM4; Scinocca et al. 2016). The predicted changes to the physical characteristic of north-temperate lakes imposed by climate change will also impact the organisms that inhabit these ecosystems, particularly fish. Fish are ectotherms whose body temperatures and in turn metabolic rates follow that of the habitat in which they reside. As a result, the aerobic performance of fish, including

growth of fish is heavily influenced by temperature, whereby performance at cold temperatures is low and increases with temperature up to an optimum and then rapidly declines as the thermal maximum for growth is exceeded due to increased metabolic demands (Fry 1947, Jobling 1997, Pörtner and Farrell 2008; Fig. 1). These thermal performance curves vary greatly among species, which has allowed fish species to be generally grouped into three thermal guilds corresponding to the temperatures at which their performance is optimized: warm-water eurotherms; cool-water mesotherms; and cold-water stenotherms (Magnuson et al. 1979). Therefore, it would be expected that increases in lake water temperatures should have impacts on the behaviour (Plumb and Blanchfield 2009, Freitas et al. 2015) and growth (Cheung et al. 2013, Baudron et al. 2014) of fish, especially stenothermic species due to their requirements for cold, well-oxygenated water.

A cold-water stenotherm commonly found in oligotrophic north-temperate lakes of Canada is the lake trout (*Salvelinus namaycush*). Lake trout is top predator in most lakes that preferably feeds on fish but can also be highly opportunistic in response to environmental variations such as temperature and food web structure (Tunney et al. 2014, McMeans et al. 2016). The effects of climate change on lake trout populations will vary depending on geographic location, size, and food web complexity of which they inhabit. In north-temperate lakes, lake trout preferentially feed on littoral prey during the periods when lakes are not stratified, of which the spring is thought to be most important (Martin 1954, King et al. 1999). However, during summer when lakes are thermally-stratified, warm surface water temperatures reduce access to littoral habitat (Plumb and Blanchfield 2009). This limited access to preferred prey would force lake trout to feed on pelagic prey. Further, lake trout are known to make forays into the littoral zone during summer to obtain prey fish, especially in small lakes without pelagic prey fish (Sellers et al. 1998, Morbey et al. 2006), highlighting the importance of this energy source. If the period of thermal stratification prolongs and surface water temperatures increase, it would be expected that this would reduce lake trout's access to littoral energy. However, if lake trout continue to

foray into this region during summer, this may subject them to warmer temperatures due to increases in surface temperatures or a greater exposure to water above optimal levels due to longer thermally-stratified periods. These two potential outcomes of warming on lake trout behaviour represent examples of both indirect (i.e. through reduced littoral energy use), and direct (i.e. impact of warmer or longer exposure to sub-optimal temperatures) impacts of warming on lake trout growth.

The overall goal of this thesis was to understand the sequential impacts of climate warming on north-temperate lake trout populations, where climate influences physical habitat which in turn directs annual behaviour and growth, and finally leads to changes in growth and size-structure of the population. The thesis is broken up into two sections. In the first section (Section A; Fig. 2), which is comprised of Chapters 1-3, I used long-term datasets from well-studied southern lake trout lakes within the IISD-Experimental Lakes Area (ELA) of northwestern Ontario to quantify how past warming has impacted various factors of lake trout habitat, ecology, and growth. I then used this knowledge and approach to direct analysis of Section B (Chapter 4; Fig. 2), which uses a comprehensive two-year dataset from a northern lake trout lake to understand how a more northern population may respond to future warming scenarios. In Chapter 1, I used long-term meteorological and limnological monitoring data collected over the past 44 years from ELA reference lakes containing lake trout to quantify how annual variations in air temperature and precipitation have altered lake trout habitat. In Chapter 2, I used 11 years of acoustic telemetry, stable isotope, and lake temperature monitoring data from one of the lakes studied in Chapter 1 (Lake 373) to understand how annual variations in lake water temperature during the open-water season alter the behaviour and diet of lake trout and what impacts this may have on annual changes in growth and condition. In Chapter 3, I used 26 years of mark-recapture data from Lake 373 to determine if changes in the body size, growth, and population characteristics of the lake trout population occurred in response to warming. I then used information on prey fish availability, as well as information gained on changes in habitat, behaviour, and diet from

Chapters 1 and 2 in a bioenergetics modelling approach to determine the mechanism behind observed changes in lake trout body size and growth. In Chapter 4, I use acoustic telemetry, air and lake temperature and diet data to describe how the habitat use, movement, and diet of lake trout in northern lakes varied with annual cycles in temperature. I then combine these data on lake trout behaviour and lake temperatures with lake trout size-at-age data in bioenergetics models to predict how its growth and consumption may change in a simulated year with 2 °C of warming, based on changes observed in ELA lakes. Lastly, in the Epilogue I provide a brief synthesis of Chapters 1-4 and comment on how my thesis advances our knowledge of how north-temperate lake trout populations are impacted by climate warming and suggest what the most imminent implications of future warming will be on these populations.

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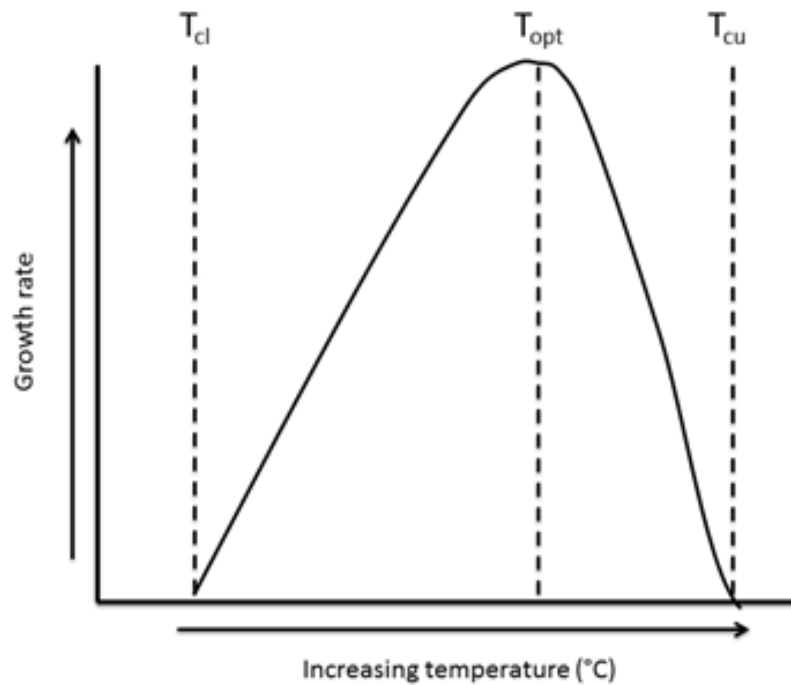
Figure 1 – Temperature-dependant growth capacity curve illustrating how changes in fish growth are follow a "tilted curve", where growth increases up to an optimal (T_{opt}) from the lower critical temperature (T_{cl}), after which it rapidly declines as temperatures approach the upper critical limit (T_{cu}). Growth is zero outside of the critical limits. Adapted from Portner and Peck (2010) and Neuheimer et al. (2011).
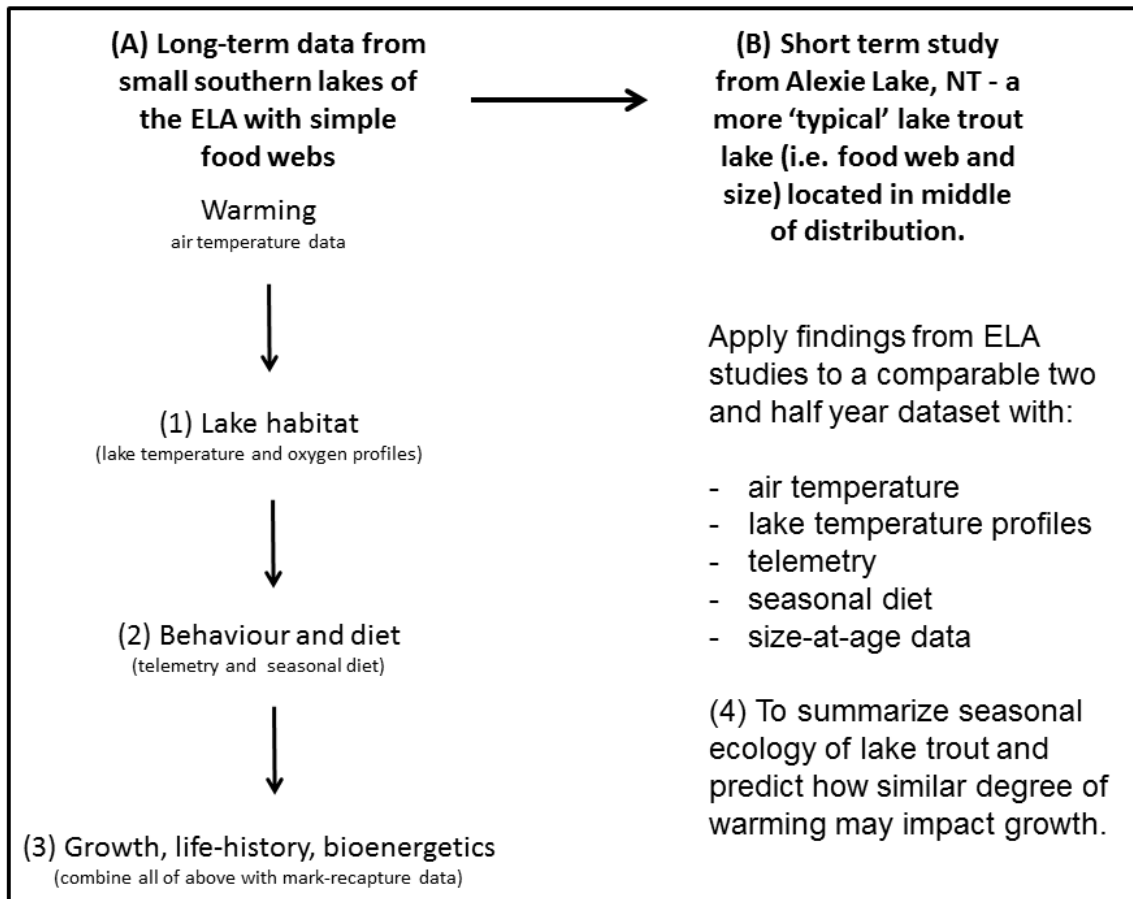
Figure 2 – Conceptual model of my thesis which consists of two sections (A and B) divided into four data chapters (1-4). Section A uses long-term data collected at the Experimental Lakes Area (ELA), located in northwestern Ontario near the southern extent of lake trout's distribution to quantify how changes in climate, specifically temperature impacts: (Chapter 1) the seasonal phenology and amount of summer habitat for lake trout; (Chapter 2) how observed changes in lake habitat impact lake trout behaviour, diet, and growth; and, (Chapter 3) how the growth, life-history, and population structure of lake trout have changed over a period of warming. Section B will take a similar approach as Section A, but uses data from a two-year study of more "typical" lake trout lake located in the Canadian north, where climate is forecast to have profound impacts. The northern lake is considered more typical in that it is located near the center of the lake trout distribution, has a more complex food web with other predators present and has pelagic prey fish, and is larger in size compared to ELA lakes. In Chapter 4, I quantify similar metrics as in Section A and then use this information to predict how lake trout growth would change in this lake based on changes observed in the long-term ELA dataset.

CHAPTER 1

Climate change alters the quantity and phenology of habitat for lake trout (*Salvelinus namaycush*) in small Boreal Shield lakes

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Contributions of Authors: All data in this chapter were collected as part of the long-term monitoring program at the Experimental Lakes Area. I analyzed all data and wrote and submitted initial and final drafts of the manuscript. P.J.B. assisted with revisions of drafts of the manuscript.

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Abstract

We analyzed monitoring data (1970-2013) from small Boreal Shield lakes to understand how variations in air temperature and precipitation affect the phenology and amount of habitat for lake trout (*Salvelinus namaycush*). Annual air temperatures increased by ≈ 2 °C (significant in fall and winter). In response, ice cover was reduced by ≈ 19 days. Despite earlier ice-offs, springs became longer, allowing lake trout longer access to littoral regions when water temperatures were cool. Although summer surface water temperatures increased, the summer did not lengthen. Instead, later spring-warming and fall-cooling of lakes caused summer to shift later in the year, potentially delaying fall spawning. Complete loss of optimal oxythermal habitat volume occurred in all lakes and became more prevalent over time, more so in the darkest lakes. Although air temperatures did not become more variable, several habitat measures did, including mean summer surface water temperatures, duration of ice cover, timing of ice-off, and minimum volumes of optimal oxythermal habitat. Our results suggest that future warming will impose greater thermal stress on lake trout but may be tempered by longer springs.

Introduction

Cold water with high dissolved oxygen (DO) concentrations (i.e. oxythermal habitat) defines the habitat requirements of cold-water fish (Gibson and Fry 1954, Christie and Regier 1988). As such, the availability of suitable oxythermal habitat is accepted to be a critical factor determining the capacity of lakes to support cold-water fish (Evans et al. 1991, Ryan and Marshall 1994, Wilson and Mandrak 2004, Jacobson et al. 2010). In north-temperate regions, lakes containing cold-water fish typically undergo thermal stratification during summer — a period when suitable oxythermal habitat becomes limited to the hypolimnion (Wetzel 2001). Although thermal stratification represents a period of habitat limitation for cold-water fish, it is a critical feature of north-temperate lakes that preserves suitable oxythermal habitat during summer. Indeed, if lakes were to fully mix during summer they would be unable to support cold-water fish because water temperatures would exceed their thermal requirements (Gibson and Fry 1954, Christie and Regier 1988). Thus, the balance between duration and intensity of thermal stratification should be important for lakes to support cold-water fish. However, with recent evidence that lake surface temperatures have risen globally over the past 30 years (O'Reilly et al. 2015) and the expectation that strong warming and increased frequency of extreme temperatures will continue in north-temperate regions (IPCC 2014), the capacity for some lakes to support cold-water fish could diminish in the future.

Lake trout (*Salvelinus namaycush*) is a cold-water stenotherm that occupies oligotrophic lakes of northern North America (Martin and Olver 1980). To survive in cold, unproductive ecosystems, lake trout have evolved a life history characterized by slow growth, late maturation, and low reproductive output (Martin and Olver 1980). Taken together, narrow temperature and DO requirements combined with life history vulnerable to disturbances, make lake trout a sentinel species for studying the effects of

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climate change on north-temperate lakes (Schindler et al. 1996b, Jansen and Hesslein 2004, Plumb et al. 2014). Certainly, there is evidence that lake trout populations have gone extinct from central and eastern Ontario lakes where optimum summer habitat was absent or limited (MacLean et al. 1990). Lake trout populations are especially concentrated along the southern edge of the Boreal Shield ecozone near the southern extent of its geographic distribution, where they typically occur in small lakes (75 % of lakes < 500 ha, median size 169 ha) that undergo annual thermal stratification (Gunn and Pitblado 2004). Boreal Shield lakes are expected to experience changes in physical and biological properties because of climate change (Keller 2007), which heightens the need to understand how lake trout occupying lakes with marginal habitat near the southern extent of their distribution will be impacted by rising and potentially more variable air temperatures.

By the end of this century, annual air temperatures across the Boreal Shield are expected to increase by 4-7 °C, with greater frequency of extreme temperatures (Colombo et al. 2007, IPCC 2014). Air temperatures have direct and relatively rapid influences on the thermal structure of small Boreal Shield lakes. For example, seasonal air temperature strongly influences surface water temperatures (De Stasio et al. 1996, Stefan et al. 1998) and the phenology of the ice cover and stratification (Robertson and Ragotzkie 1990, De Stasio et al. 1996, Magnuson et al. 2000, Keller 2007, Shuter et al. 2013). Consequently, warmer air temperatures have been predicted to reduce the amount of time that lakes are cold in the spring and early summer (Jansen and Hesslein 2004) and extend the duration of the thermally stratified and open-water seasons (Keller 2007). As such, the predicted magnitude of warming, and potential impacts of this warming on the thermal structure and phenology of lakes implies that climate change could have serious implications to lake trout populations across the Boreal Shield.

Unlike air temperature, predictions of future precipitation for the Boreal Shield vary in direction regionally, with any increases potentially offset by greater evaporation (Colombo et al. 2007, Keller 2007). In small lakes (< 500 ha), the volume of oxythermal habitat during stratification is a function of the effect of water clarity on thermocline depth (i.e. clear lakes = deeper thermoclines), which is indirectly controlled by precipitation through its effects on terrestrial runoff of dissolved organic matter (DOM; Fee and Hecky 1996, Schindler et al. 1996a, Stasko et al. 2012). The shallower thermoclines found in darker lakes would be expected to result in larger volumes of cold-water habitat relative to clearer lakes of the same depth and size. However, because DO is consumed through bacterial respiration of DOM in the water column and sediments, darker lakes (i.e. due to increase terrestrial DOM) could be more susceptible to low hypolimnetic DO during summer stratification (Molot et al. 1992, Dillon et al. 2003, Couture et al. 2015). These counteractive effects of precipitation on oxythermal habitat highlight the importance of detailed long term empirical lake temperature and DO data collected during wet and dry periods for understanding how future climate scenarios may alter lake trout habitat in Boreal Shield lakes.

Most studies on lake trout habitat in Boreal Shield lakes have focused on volumes of late summer oxythermal habitat (Schindler et al. 1996a, Dillon et al. 2003, Jansen and Hesslein 2004, Herb et al. 2014). However, with increases in air temperature expected to occur across seasons, it is likely that changes in oxythermal habitat phenology may be profound, thereby modulating changes in lake thermal structure. Here, we use long-term meteorological and limnological monitoring data collected over the past 44 years to test the hypothesis that variations in air temperature and precipitation have altered the lake trout habitat in four small Boreal Shield lakes. Our specific objectives were to (i) quantify how variations in air temperature and precipitation relate to the temporal changes in thermal habitat for lake

trout and (ii) determine if long-term trends in oxythermal habitat have occurred and how they relate to both air temperature and precipitation.

Methods

Study site and data sets

This study used long-term monitoring data collected during 1970-2013 within the International Institute for Sustainable Development (IISD) – Experimental Lakes Area (ELA), located in the Boreal Shield of northwestern Ontario, Canada (49°40' N, 93°44' W). The IISD-ELA is a set of 58 lakes and their watersheds set aside since the late 1960s for conducting aquatic research (Blanchfield et al. 2009a). The forests of ELA are dominated by jack pine (*Pinus banksiana*) and black spruce (*Picea mariana*). Soils are mostly thin (≤ 1 m) and lay over Precambrian bedrock. Thin layers of *Spagnum* moss often cover soil and bedrock. In the small wetlands surrounding lakes, *Spagnum*-derived peat reaches depths more than 10 m (Schindler et al. 1996a).

As part of the long-term monitoring program at the ELA, daily air temperature and precipitation data have been collected at Environment and Climate Change Canada's Rawson Lake meteorological station since 1969. Annual dates of winter ice formation and break-up dates (hereinafter ice-on and ice-off dates, respectively) were also monitored at Lake 239 (54 ha). We assumed that ice-on and ice-off dates were the same for all study lakes because the lakes were relatively similar in size and located within ≈ 20 km from one another. The study lakes are all ELA long-term reference lakes that contain native, self-sustaining lake trout populations, but vary in several physical attributes relevant to their response to changes in air temperature and precipitation, including depth, surface area, watershed area, and water clarity (Table 1). Water temperature and DO of the study lakes were monitored every 2-4

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weeks during the open-water season for periods ranging from 26 to 45 years (Table 1). Water

temperatures were measured using a handheld probe (XRX-620 CTD, RBR, Ottawa, Ontario, Canada) at 1

m depth intervals, and DO was measured by Winkler titration at 5 m depth intervals (Stainton et al.

1977) from the lake surface to bottom. In 2013, DO data was collected using an optode probe (4330F

Aanderaa Data Instruments, Fall River, Massachusetts, USA). Sampling and laboratory methods were

consistent over the entire study period. When changes in equipment or methods took place, rigorous

calibrations were performed to ensure data were comparable (Stainton et al. 1977, Schindler et al.

1996a, Parker et al. 2009).

Air temperature and precipitation

Mean annual and seasonal air temperature and precipitation were estimated using mean daily air

temperature and precipitation values collected at the Lake 239 meteorological station. Annual means

were calculated as the grand mean of all mean daily air temperature or precipitation values in each

calendar year. Seasonal mean air temperature and precipitation for each year were calculated as the

grand mean of all mean daily air temperature or precipitation values for each of the following monthly

groupings, which roughly correspond to the four seasons at the ELA: March-May (Mar-May), June-

August (Jun-Aug), September-November (Sep-Nov), and December-February (Dec-Feb).

Oxythermal habitat and lake surface temperatures

Daily estimates of oxythermal habitat for each open-water season were obtained using water

temperature and DO profiles collected from each of the four study lakes (Fig. 1). Measured water

temperature and DO values were linearly interpolated between sampling dates to obtain daily profiles

at each measurement depth. Next, we linearly interpolated each of the daily water temperature and DO profiles to 0.1 m depth intervals to obtain daily profiles at 0.1 m resolution. For years where a lake was not sampled or had an insufficient number of summer sampling dates, data from that lake were excluded. The daily 0.1 m resolution water temperature and DO profiles were then used to calculate daily depths of ecologically relevant isotherms and oxyclines — the deepest depth at which a specific temperature or shallowest depth at which a specific DO concentration were found in the water column. Isotherms and oxyclines represented the theoretical upper thermal and lower oxygen habitat boundaries for lake trout, respectively. For all years of data available from each lake, we calculated the daily depths of each isotherm and oxycline representing optimal and usable lake trout habitat during each open-water season. Optimal oxythermal habitat for lake trout was considered to be the volume of water bound between temperatures < 10 °C and DO > 6 mg L^{-1}, while usable habitat was bound between temperatures < 15 °C and DO > 4 mg L^{-1} (Ferguson 1958, Coutant 1977, Evans et al. 1991, Ryan and Marshall 1994, Evans 2007). The daily depths of isotherms and oxyclines corresponding to optimal and usable habitat boundaries were converted to daily habitat volumes using lake-specific bathymetry and were presented as proportions of total lake volume that met the optimal or usable habitat criteria. Specifically, we presented the oxythermal habitat volumes and corresponding isotherm and oxycline depths when lake trout habitat was at its minimum each year, typically occurring in late summer or fall. When DO boundaries were shallower than temperature boundaries, optimal or usable habitat was considered to be absent (eliminated). Mean summer (Jun-Aug) surface water temperatures for each lake were calculated using daily water temperatures at 1 m depth from the interpolated water temperature profile data.

Thermal habitat phenology

The phenology of key events defining the transitions between thermal habitat periods for lake trout were defined using the existence of usable water temperatures (< 15 °C) for lake trout and the presence of ice cover (Fig. 1). For each year of data for each lake, four thermal habitat periods, each representing a distinct ecological period for lake trout, were defined (Fig. 1). We designated these four thermal periods for lake trout as follows: (1) Winter — a period of cold temperatures (1-4 °C), low light, and low lake production, defined as the days between fall ice on and the following spring ice-off; (2) Spring — a period of cool temperatures (4-15 °C) when lake trout feed heavily in the littoral zone of Boreal Lakes, defined as the period following spring ice-off and lasting until the lake surface water temperatures reached 15 °C; (3) Summer — a period of thermal stratification when water temperatures in the littoral zone exceed the usable limit for lake trout, defined as the period when lake surface water temperatures are ≥ 15 °C; and (4) Fall — the period occurring as lake temperatures cool to < 15 °C and lasting until fall ice-on. This is the period when lake trout spawn. We were unable to directly assess changes in seasonal lake trout habitat based on optimal water temperatures (< 10 °C) because lakes often had already reached 10 °C by the time spring sampling began. Furthermore, Plumb and Blanchfield (2009) have shown that the 15 °C better defines the depth use of lake trout in these small lakes. Nevertheless, we found moderate-strong correlations between the dates that surface water temperatures reached 10 °C and when they reached 15 °C for all lakes (Pearson correlation: r = 0.48-0.60, all P < 0.1), allowing findings from changes in seasonality based on usable thermal habitat to be generalized to optimal thermal habitat.

Statistical analyses

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We used Mann-Kendall tests to determine if long-term, monotonic trends occurred in time series of

annual and seasonal air temperatures and various lake trout habitat measures (Mann 1945, Kendall

1955). Mann–Kendall tests were not applied to precipitation data because we knew a priori that

precipitation at the ELA followed a 31-year cycle (Parker et al. 2009). Where Mann-Kendall tests

indicated significant time-series trends, corresponding slopes were estimated using Sen's slope (Sen

1968). We used a Levene's mean test of equal variance to determine if variability in annual and seasonal

estimates of air temperature and precipitation as well as lake trout habitat measures changed over the

course of the study, based on data from our longest studied lake, Lake 239. Levene's tests involved

comparing estimates of each measure taken during the first (1970-1991) and second (1992-2013) halves

of the 44-year study period. If a monotonic trend was found for a given measure, we used the residuals

in the Levene's test to ensure the trend did not impact the analysis. Where a Levene's test indicated a

significant difference, we presented the change in variation between the first and second half of the

study as the standard deviation (SD) in the results. We used analysis of covariance (ANCOVA) to test if

seasonal air temperatures or annual precipitation influenced the phenology of thermal habitat,

minimum volumes of oxythermal habitat, and lake surface water temperatures among study lakes.

Finally, we tested if the probability that the complete elimination of optimal lake trout habitat was

increasing over time in each lake using logistic regression.

      Assumptions of statistical models were tested as outlined in Zuur et al. (2010). Where necessary,

variables were transformed to meet assumptions of each statistical test. Due to the inherently high

variability of climate and limnological data and the interpolations necessary to produce our working

data set, we accepted a higher chance of type-1 error and considered $P < 0.1$ as statistically significant

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for all analyses. All data processing, analyses, and figures were completed in R (version 3.2.1, R Core Team 2015).

Results

Air temperature and precipitation

Annual air temperatures at the ELA increased at a rate of 0.043 °C year^{-1} from 1970 to 2013, representing a 1.84 °C increase in mean temperature, from 1.77 to 3.61 °C (Fig. 2a). Annual temperatures were quite variable over the study period, ranging by 4.37 °C, with a minimum of 0.86 °C and a maximum of 5.23 °C, but this variability did not increase over the study period ($F_{[1,42]} = 0.66$, $P = 0.42$). Changes in air temperature were most pronounced for Sep-Nov and Dec-Feb, where they increased significantly at rates of 0.039 and 0.078 °C year^{-1}, respectively. Air temperatures during Mar-May and Jun-Aug periods did not show evidence for monotonic trends over the study period (Fig. 2b). None of the seasonal air temperatures became more variable over the study period (Spring: $F_{[1,42]} = 0.58$, $P = 0.45$; Summer: $F_{[1,42]} = 0.17$, $P = 0.68$; Fall: $F_{[1,42]} = 0.73$, $P = 0.40$; Winter: $F_{[1,42]} = 0.58$, $P = 0.45$).

Unlike air temperature, annual precipitation did not exhibit a monotonic trend over time (Fig. 2c) and was consistent with previous studies (Parker et al. 2009), indicating that ELA precipitation is part of a 31-year cycle of wet and dry periods. During the study period, annual precipitation ranged by 1.45 mm day^{-1}, from a minimum of 1.33 mm day^{-1} to a maximum of 2.78 mm day^{-1} (Fig. 2c). Generally, the climate was drier at the ELA during late 1970s and 1980s and considered to be in a wet period during 1990s through the 2000s. Annual precipitation rates did not become more variable over the study period ($F_{[1,42]} = 0.25$, $P = 0.62$) and neither did spring, fall, or winter precipitation rates (Spring: $F_{[1,42]} = 0.50$, $P = 0.48$; Fall: $F_{[1,42]} = 2.53$, $P = 0.12$; Winter: $F_{[1,42]} = 1.41$, $P = 0.24$). We did, however, find evidence

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that summer precipitation rates were more variable in the latter half of the study ($F_{[1,42]}$ = 5.71, P = 0.02), where the SD of summer precipitation increased from 0.53 to 0.95 mm day^{-1}.

Thermal habitat phenology

The mean length of the winter ice-covered season decreased over time, becoming 19 days shorter in 2013 than it was in 1970 (Fig. 3). The length of winter also became more variable during the second half of the study ($F_{[1,42]}$ = 3.78, P = 0.06), where the SD of winter length was 4.35 days greater than in the first half of the study (Fig. 3). There was marginal, but nonsignificant evidence that spring ice-off dates became earlier over time (slope = -0.21 days year^{-1}, P = 0.11). Ice-off dates ranged by 42 days, with the earliest being on 5 April 2012 and the latest on 17 May 1996. Six of the seven earliest spring ice-off dates have occurred since 1999. Ice-off dates also become more variable over time ($F_{[1,42]}$ = 4.15, P = 0.04); the SD of ice off dates increased by 3.80 days in the second half of the study. In contrast, there was strong evidence that fall ice-on dates became later over time (slope = 0.21 days year^{-1}, P = 0.002), increasing since 1970. Seven of the eight latest ice-on dates have occurred since 1999. Fall ice on dates ranged by 31 days, with the earliest on 4 November 1991 and latest on 1 December 2009, but did not become more variable in the second half of the study ($F_{[1,42]}$ = 0.01, P = 0.93).

We did not find that summer for lake trout was starting (development of the 15 °C isotherm) earlier over time in any of the study lakes (Fig. 4a), which agrees with the fact that Mar-May air temperatures had not increased over time (Fig. 2b). We did find that the end of summer (breakdown of the 15 °C isotherm) was persisting later into the fall (Fig. 4b), corresponding to increases found in Sep-Nov air temperature (Fig. 2b). All study lakes showed evidence that the end of the summer period was becoming later, and for the longest studied lake, Lake 239, summers for lake trout were on average

ending 1 week later in 2013 than in 1970 (Fig. 4b). Despite the summer lasting later into the year, we did

not find that summers were getting longer over time (Figs. 3, 4c). This corresponded to our finding of

the spring period becoming longer over the study (Fig. 3) and indicates that the summer for lake trout

was shifting later into the year, but not getting longer (Fig. 4). Despite warming fall air temperatures, the

fall season for lake trout did not get longer over time (Fig. 3). We found no evidence that the length of

the spring ($F_{[1,42]}$ = 1.35, P = 0.25) or fall ($F_{[1,42]}$ = 0.02, P = 0.89) periods became more variable in the

latter half of the study and only marginal, but non-significant, evidence ($F_{[1,42]}$ = 2.65, P = 0.11) that

summer lengths became more variable during the second half of the study.

Spring ice-off ($F_{[1,42]}$ = 106.8, P < 0.001, r^2 = 0.71) and fall ice-on ($F_{[1,42]}$ = 66.40, P < 0.001, r^2 =

0.61) dates were strongly related to air temperatures experienced during their respective seasons (Figs.

5a, 5d). Ice-off was 4.38 days earlier for every 1 °C increase in mean Mar-May air temperature (Fig. 5a).

In contrast, warmer Sep-Nov air temperatures meant later ice-on dates, where ice formed 3.64 days

later for every 1 °C increase in mean Sep-Nov air temperature (Fig. 5d). The slopes (Lake × Spring: $F_{[3,126]}$

= 0.57, P = 0.63) and intercepts (Lake: $F_{[3,129]}$ = 0.39, P = 0.76) of the relationship between Mar-May air

temperature and the warming of lakes to ≥ 15 °C (i.e. the start of the summer) did not differ among

lakes. The start date of summer was significantly predicted by Mar-May air temperature ($F_{[1,132]}$ = 59.17,

P < 0.001, r^2 = 0.31; Fig. 5b) and began 2.51 days earlier for every 1 °C increase in Mar-May air

temperature. The number of days the lake was cool (< 15 °C) following ice-off (i.e. length of the spring)

was significantly predicted by Mar-May air temperature ($F_{[1,132]}$ = 20.39, P < 0.001, r^2 = 0.13), and the

slopes (Lake × Spring: $F_{[3,126]}$ = 0.62, P = 0.60) and intercepts (Lake: $F_{[3,129]}$ = 0.66, P = 0.58) did not differ

among lakes. The spring period for lake trout became longer by 1.82 days for every 1 °C increase in Mar-

May air temperature (Fig. 5c). Interestingly, the length of spring only decreased by 0.59 days for each

day that the ice retreated later into spring ($F_{[1,132]}$ = 73.56, P < 0.001, r^2 = 0.36), meaning in years when

ice-off occurred earlier, the lake took longer to reach 15 °C. The length of spring periods greatly varied in

the four study lakes, ranging from less than 1 week (5 days) to almost 2 months (59 days) (Fig. 5c). In the

fall season, the slopes (Lake × Fall: $F_{[3,126]}$ = 0.25, P = 0.86) and intercepts (Lake: $F_{[3,129]}$ = 0.60, P = 0.62) of

the relationship between the end of summer/start of fall and Sep-Nov air temperature did not differ

among lakes. The end of the summer (breakdown of the 15 °C isotherm) was significantly predicted by

Sep-Nov air temperatures ($F_{[1,132]}$ = 21.21, P < 0.001, r^2 = 0.14), where summer lasted 1.77 days longer

for every 1 °C increase in Sep-Nov air temperature (Fig. 5e). The length of fall was also significantly

predicted by Sep-Nov air temperature ($F_{[1,132]}$ = 25.05, P < 0.001, r^2 = 0.16); the slopes (Lake × Fall: $F_{[3,126]}$

= 0.27, P = 0.84) and intercepts (Lake: $F_{[3,129]}$ = 0.43, P = 0.73) of this relationship did not differ among

lakes (Fig. 4f). The fall period for lake trout lasted 38-74 days and increased in length by 2.15 days for

every 1 °C in Sep-Nov air temperature (Fig. 5f).

Summer surface water temperatures

We found an increase in mean summer surface water temperature of 0.03 °C year^{-1} in the longest

sampled lakes (39-43 years), while those sampled for shorter time periods (the last 26-27 years) showed

no trends (Fig. 6a). The surface water temperatures of all lakes were highly related to Jun-Aug air

temperatures ($F_{[1,134]}$ = 462.9, P < 0.001, r^2 = 0.78) (Fig. 6b). Because of the similarly strong relationships

between Jun-Aug air temperature and summer surface water temperature, we expect that Lakes 373

and 442 would have shown similar increases in surface water temperature had they been monitored for

longer periods. We also found that surface water temperatures in Lake 239 were more variable during

the latter half of the study period ($F_{[1,42]}$ = 3.48, P = 0.07), where the SD was 0.52 °C greater that

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observed during the first half of the study. Although the length of summer was not found to increase over time, this variable was only weakly correlated to Jun-Aug air temperature ($F_{[1,132]}$ = 13.13, $P < 0.001$, r^2 = 0.11; Fig. 6c). Instead we found that the length of summer was better predicted by Mar-May and Sep-Nov air temperatures, which promote the development and breakdown of the 15 °C isotherms that define the start and end of summer for lake trout (Figs. 4b, 4e).

Oxythermal habitat

We did not test for monotonic trends in the maximum extent of the isotherm, oxyclines, or minimum habitat volumes because these measures are highly dependent on precipitation and watershed processes that were cyclic over the study period (Figs. 2c, 2d, 7). Qualitative observation of Fig. 7, specifically the longest data sets from Lakes 239 and 224, suggest that the depth of thermal barriers for lake trout were deepest (most intense) when precipitation was low in the late 1980s and shallowest (i.e. least intense) in the 1990s and 2000s during wet cycles (Figs. 2c, 2d). This was corroborated by the fact that annual maximum depths of the 10 and 15 °C isotherms were significantly predicted by annual precipitation in three of four study lakes (Table 2). The maximum depths of the 10 °C isotherm were less variable (SD decrease of 0.31 m) in the latter half of the study ($F_{[1,38]}$ = 3.95, P = 0.05); however, this was not the case for the 15 °C isotherm ($F_{[1,38]}$ = 1.26, P = 0.26).

Generally, differences in isotherm depths among lakes were predicted by water transparency; the clearest (Lake 224) and darkest (Lake 442) lakes had the deepest and shallowest isotherms, respectively (Fig. 7a; Table 1). Because of the control of precipitation on runoff, annual precipitation predicted the depths of the annual maximum 10 and 15 °C isotherms in three study lakes, Lake 239 being the exception. For the 10 °C isotherm, the slopes of the relationships with annual precipitation did

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not differ (Lake × Precipitation: $F_{[3,102]}$ = 0.95, P = 0.42), while intercepts did (Lake: $F_{[3,105]}$ = 55.59, P < 0.001) among lakes. For the 15 °C isotherm, slopes of the relationships with annual precipitation differed among lakes (15 °C isotherm: Lake × Precipitation: $F_{[3,102]}$ = 3.00, P = 0.03). These differences in slopes and intercepts indicated that individual linear regressions should be run for each lake to individually assess the relationship between maximum isotherm depths and annual precipitation (see Table 2).

The annual maximum extent (i.e. minimum depths) of the 6 and 4 mg L^{-1} oxyclines were relatively constant over the study period, except for the 4 mg L^{-1} oxycline in Lake 239, which was highly variable throughout. Similar to trends observed in maximum isotherm depth, minimum oxyclines were shallowest (i.e. largest low oxygen zones) during wet periods and deepest (i.e. smallest low oxygen zones) during dry periods of the precipitation cycle (Figs. 2c, 2d, 7b). The maximum extent of the 6 mg L^{-1} oxycline became more variable over the study ($F_{[1,38]}$ = 2.93, P = 0.09), where its SD increased by 1.42 m. In contrast, the maximum extent of the 4 mg L^{-1} oxycline was not more variable during the second half of the study ($F_{[1,38]}$ = 0.08, P = 0.78).

Temporal changes in minimum annual oxythermal habitat volumes, reported as a proportion of total lake volume that met optimal or usable habitat requirements of lake trout, generally followed the cyclic pattern of precipitation (Fig. 7c). At their annual minimum, usable habitat for lake trout generally accounted for 20 % to 50 % of lake volume (Fig. 7c). All study lakes had complete loss of optimal habitat during the study period, but it occurred most frequently in the two darkest lakes (Lakes 442 and 239). In the longest studied lake (Lake 239), complete elimination of optimal habitat became more prevalent over time (logistic regression: Z = 2.22, df = 43, P = 0.02), but not in Lakes 442, 224, or 373 (Fig. 8). Optimal habitat for lake trout in Lakes 442 and 239 were eliminated for periods ranging from 1 week up

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to 75 and 100 days, and in Lake 442, optimal habitat has been eliminated each year since 1995 (Fig. 8).

The minimum amount of optimal oxythermal habitat available to lake trout each year was more variable

(SD increase of 6 % total lake volume) in the latter half of the study ($F_{[1,38]} = 4.38$, $P = 0.04$), but this was

not the case for usable habitat ($F_{[1,38]} = 2.11$, $P = 0.17$).

Discussion

We demonstrate that lake trout habitat in small Boreal Shield lakes undergoes distinct changes in

quantity and phenology as air temperature increases and precipitation rates vary. Most notably, we

show that despite summer surface water temperatures increasing, the length of summer (i.e. period

when lake surface temperatures exceed 15 °C) did not expand over time. Instead, evidence of earlier

ice-offs, longer springs, and the cooling of lakes to < 15 °C occurring later in the fall suggests that the

summer period has shifted later into the year. Due to the later onset of fall, ice-on became delayed, and

paired with earlier ice-offs, the winter ice-covered period became shorter over time. Moreover, we

show that the elimination of optimal habitat occurs in all study lakes to various degrees, but most

commonly in darker lakes. Elimination of optimal habitat also became more common over time in the

longest studied lake. Lastly, the minimum volume of optimal oxythermal habitat available for lake trout

during the late summer became more variable over time, while usable oxythermal habitat did not,

suggesting optimal habitat may be more sensitive to climate change. Together our results suggest that

the warmer and more extreme air temperatures forecasted should impact the ecology of lake trout in

Boreal Shield lakes, which is heavily tied to seasonal variations in water temperature (Martin 1952,

1970, Blanchfield et al. 2009b, Plumb and Blanchfield 2009). Moreover, for lakes with marginal suitable

habitat, especially those near the southern extent of lake trout's distribution, warmer conditions may

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result in more frequent elimination of optimal oxythermal habitat during late summer, potentially impacting the ability of these lakes to support lake trout.

Our findings of increasing annual air temperatures were expected, as these data were extensions of those previously published (Schindler et al. 1996a, Parker et al. 2009) and are in agreement with long-term data from the northeastern Boreal Shield (Keller 2007). Increases in annual air temperature were driven by warmer seasonal air temperatures during Dec-Feb and Sep-Nov, which provide a likely explanation for corresponding trends found in ice phenology. Higher air temperatures in late winter increase the rate of snow melt, which acts to insulate ice. Once snow is removed, light penetrates and warms water below the ice, rapidly degrading it (Gao and Stefan 1999, Wetzel 2001, Jansen and Hesslein 2004, Shuter et al. 2013). Although not significant, marginal evidence for a monotonic trend in Mar-May temperatures (Mann-Kendall P = 0.18) suggests that temperatures during this period could also be increasing at more variable rate than those observed in Sep-Nov and Dec-Feb, but still contributing to the increasing rate of ice melt and advance the timing of ice-off dates (Shuter et al. 2013). In contrast, warmer Sep-Nov air temperatures delay the cooling of lakes, resulting in later fall turnover and cooling of surface waters to 0 °C, slowing ice formation (Raymond Hesslein, *unpublished data*, Gao and Stefan 1999, Shuter et al. 2013). Mean depth has also been found to be a predictor of ice phenology (Shuter et al. 2013); although not relevant to our study of the same lakes over time, it suggests that deeper lakes may have more delayed ice formation due to the larger volume of water to be cooled. Indeed, the changes in ice phenology observed here agree with several studies that have found warming air temperatures to expedite spring ice-melt and delay fall ice formation, resulting in longer open-water seasons in north-temperate regions (Keller 2007, Benson et al. 2012, Sharma et al. 2016). Winter (i.e. period of ice cover) is often recognized to be a period when cold water temperatures

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slow metabolic processes and limit growth (Kerr 1971); however, indication that lake trout feed heavily

on fish during this period (Martin 1954), and evidence that lake trout may grow during this period (Eck

and Wells 1986), suggests that winter may be an underappreciated growth period in small lakes lacking

pelagic prey fish, such as our study lakes (Blanchfield et al. 2009b).

Spring periods for lake trout became longer over time. This unexpected extension of the spring

period during years with earlier ice-offs was likely caused by the differential impact of spring air

temperature on ice-off dates (start of spring) and heating of surface waters to 15 °C, signifying the start

of summer for lake trout (Plumb and Blanchfield 2009). Although the start dates of both spring and

summer were negatively correlated to spring air temperature (i.e. spring and summer both started

earlier during warmer springs), the slope of the relationship for the start date of summer was lower than

that for the start date of spring. Consequently, spring periods were longer in years with earlier ice-offs

and warmer air temperatures. We suspect this observation is because when the ice comes off the lake

earlier in spring, air temperatures are relatively cooler, with a greater chance for cold night

temperatures, than if ice were to come off later in spring, where air temperatures would be greater.

Furthermore, differences in sun angle and the longer day lengths that occur later in spring would also

promote more rapid heating of lakes in years with later spring ice-off (Shuter et al. 2013). These findings

of longer springs are contrary to the modelling study by Jansen and Hesslein (2004), which indicated

that increases in air temperature would reduce the number of days during spring and early summer

when lakes were cool. This extension of the spring period is particularly important for lake trout

occupying lakes without pelagic prey fish (Vander Zanden and Rasmussen 1996). In these lakes, lake

trout are highly dependent on their ability to access to littoral forage fish (i.e. minnows) and benthic

invertebrates when surface water temperatures are cool to achieve sufficient growth for reproduction

in fall (Martin 1952, 1970, Plumb et al. 2014). Moreover, King et al. (1999) found that in years when thermal stratification was earlier, lake trout had reduced growth, likely due to reduced access to littoral energy without thermal consequence. This is further supported by evidence that lake trout typically occupy the upper portions of the water column until surface waters reach 15 °C (Plumb and Blanchfield 2009) and achieve lower growth with reduced use of littoral habitat (Plumb et al. 2014). Therefore, an expansion of the spring period could be important for tempering the effects of future warming in lakes where littoral prey fish are the main source of energy for lake trout.

Our finding that the summer period has not lengthened over time is a result of changes occurring to its shoulder seasons. The observed delay in the onset of fall was only long enough to offset the lengthening of spring that came because of earlier ice-offs, in turn preventing a lengthening of the summer period. This finding is contrary to studies that have predicted longer stratified periods with warming (Robertson and Ragotzkie 1990, De Stasio et al. 1996); however, this disconnect could be because we looked at the existence of an ecologically relevant water temperature (15 °C) to define summer, not a planar thermocline. A recent study by Kraemer et al. (2015), which evaluated long-term stratification data from 26 lakes from various latitudes, suggested that deep lakes should be more susceptible to longer stratified periods. The lakes studied here were relatively shallow compared with most lake trout lakes, suggesting longer stratified period may be less of a concern to these lake types. Another potential explanation for the lack of trend in the length of the summer period could be that fall air temperatures were not always correlated to spring temperatures within a given year. However, as air temperatures continue to rise and spring ice-off continues to become earlier, the number of days where lake surface water temperatures exceed the useable limit for lake trout may inevitably increase,

especially if summer air temperatures in the Boreal Shield increase, as predicted by some recent climate models (Colombo et al. 2007, IPCC 2014).

Increases in Sep-Nov air temperatures corresponded to lakes cooling to < 15 °C later and delaying the onset of the fall season for lake trout. Therefore, the shift of the summer period, caused by longer springs and later arrival of fall conditions, could also have biological implications to lake trout. Lake trout is a fall spawner whose migration onto shoals is triggered when water temperatures reach 12 °C or lower (Redick 1967). Therefore, later fall cooling of lakes would delay spawning of lake trout. Indeed, there is evidence that the peak of lake trout spawning in several ELA lakes is now occurring 10 days later than it was in the late 1970s (Michael Rennie, *unpublished data*). This delay in the timing of spawning and evidence for shorter ice-covered periods could result in fry being less developed in spring. This reduction in development and the potential for earlier spring phytoplankton blooms (Peeters et al. 2007) may lead to mismatches between feeding ability of fry and peak food availability, potentially reducing recruitment (Cushing 1969, 1990).

Variations in minimum optimal and usable oxythermal habitat followed cyclic variations in precipitation, where deeper maximum thermal barriers (10 and 15 °C isotherms) occurred in years with reduced precipitation. The link between the depth of usable and optimal isotherms and annual rates of precipitation suggests that future changes (either increases or decreases) in precipitation for the Boreal Shield will alter the thermal barriers for lake trout (Fee and Hecky 1996, Schindler et al. 1996a). But these precipitation-induced changes will also depend on the magnitude of precipitation changes and potential increases in evaporation (Colombo et al. 2007, Keller 2007). The three study lakes that had the smallest watershed areas (Lakes 224, 442, 373) all responded relatively rapidly to annual changes in precipitation (i.e. on an annual basis); however, Lake 239, which has a watershed two to four times

larger than the other study lakes, did not show a similar response. Additionally, the Lake 239 watershed has three sub-basins each containing wetlands that increase the memory of the watershed and delay the response of the lake to precipitation (Schindler et al. 1996a). Potential decreases in late-summer isotherm depth that may occur if precipitation increases may also be offset by the shift of the stratified period later into fall, which will promote habitat-limiting isotherms to become deeper and potentially reach deeper maximum depths. Further, the delayed timing of fall turnover may result in a greater extent of low DO in the future, which will pose additional constraints on the volume of optimal habitat for lake trout (Fig. 6). Together, larger low DO zones and potentially deeper late-season maximum thermal barrier depths may increase the exposure of lake trout to non-optimal conditions.

All lakes experienced complete loss of optimal oxythermal habitat for lake trout at least once during the study. In most years, optimal habitat was nearly or completely eliminated from some of the study lakes, and this became more common over time in the longest study lake. Large reductions or elimination of habitat can force lake trout to occupy habitat outside of their thermal or DO optima, which can have metabolic implications (Gibson and Fry 1954, Evans 2007). The importance of optimal habitat is highlighted from the fact that several lake trout populations have become extinct from central and eastern Ontario lakes where optimum summer habitat volumes were absent or limited (MacLean et al. 1990) and that lake trout productivity declines as volume of suitable thermal habitat decreases (Christie and Regier 1988). We suspect that the presence of *Mysis* in our study lakes provides an important energy subsidy allowing lake trout to survive in lakes with marginal habitat. In other studies of lake trout occupying small lakes, lake trout have been found to use zooplankton as an alternative food source during thermal stratification (Martin 1952, Konkle and Sprules 1986, Vander Zanden and Rasmussen 1996).

Recent studies have suggested that greater temperature variation and shifts in skewness towards warmer temperatures may amplify or have greater impacts on the metabolic function of ectotherms than increases in mean temperature alone (Deutsch et al. 2008, Paaijmans et al. 2013, Vasseur et al. 2014). We did not find evidence that air temperatures, annually or seasonally, became more variable over time. The lack of evidence for increasing air temperature variation may be because we used grand means of daily mean air temperatures calculated over large scales (e.g., year or 4-month periods), which may have dampened any increases in variation occurring at shorter scales (e.g., days or weeks). Furthermore, our study did not evaluate if changes in maximum or minimum temperatures occurred, which would be a valuable avenue for future work. Interestingly, despite inconclusive findings for air temperature, we show that variability in some temperature-driven measures of lake trout habitat did increase over time. The length of winter (ice-cover), ice-off dates, and summer surface water temperatures were all more variable during the latter half of the study. Interestingly, minimum optimal oxythermal habitat became more variable over time, while usable oxythermal habitat did not, suggesting that optimal habitat may be more sensitive to climate change. With evidence that lake trout behaviour in these lake types follows usable habitat (Plumb and Blanchfield 2009), this suggest that lake trout growth, which is maximized at 10 °C (Christie and Regier 1988), may be more impacted by warming than metabolic function, which is maximized at 15 °C (Kelly et al. 2014). Moreover, this greater year-to-year variability in the amount and phenology of habitat suggests that lake trout will need to be highly adaptable in their use of littoral habitat and prey to minimize exposure to warm water (Plumb et al. 2014, Tunney et al. 2014). Indeed, temporal studies evaluating how individual populations adjust their resource use in response to changes in habitat availability will be important for understanding how the growth and abundance of lake trout and other cold-water fish respond to future warming.

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Table 1 – Physical characteristics of study lakes, including surface area (A_s; ha), volume (V; m^3), maximum depth (Z_{max}; m), watershed area (A_w: ha), watershed to surface area ratio (A_w/A_s), light attenuation coefficient (mEinst m^{-1} sec^{-1}), and Secchi depth (m).

Lake	Period sampled	A_s	V	Z_{max}	A_w	A_w/A_s	Attenuation coefficient[1]	Secchi depth[1]
224	1974–2013	25.9	3.0 x 10^6	27.4	97.5	3.8	0.29	6.5
239	1970–2013	54.3	5.7 x 10^6	30.4	393.3	7.2	0.65	4.0
373	1986–2013	27.3	3.0 x 10^6	20.8	80.6	3.0	0.38	6.3
442	1987–2013[2]	16.0	1.4 x 10^6	17.8	161.0	10.1	0.56	4.5

[1] Average of all data available for each lake which includes data for all seasons, but only limited data from winter. [2] Dissolved oxygen data with sufficient resolution only collected 1995 onwards.

Table 2 – Results of linear regressions testing for relationships between the annual estimates of the maximum depth of the thermal barrier for lake trout and mean annual precipitation.

Lake	Measure	F-value	dfn, dfd	P-value	r^2	Equation
224	15 ˚C isotherm	26.62	1, 28	**<0.001**	0.49	y = -1.92x + 12.71
	10 ˚C isotherm	8.40	1, 28	**0.01**	0.23	y = -1.95x + 15.36
239	15 ˚C isotherm	2.26	1, 37	0.14	-	-
	10 ˚C isotherm	0.03	1, 37	0.32	-	-
373	15 ˚C isotherm	15.41	1, 21	**<0.001**	0.42	y = -1.35x + 10.81
	10 ˚C isotherm	2.67	1, 21	0.12	-	-
442	15 ˚C isotherm	23.48	1, 16	**<0.001**	0.60	y = -1.29x + 8.39
	10 ˚C isotherm	4.71	1, 16	**0.05**	0.23	y = -1.16x + 9.84

Bold values are significant at $P < 0.1$. Individual regressions were performed because significant differences in slopes or intercepts were found for both isotherm measures (see Results for ANCOVA statistics).
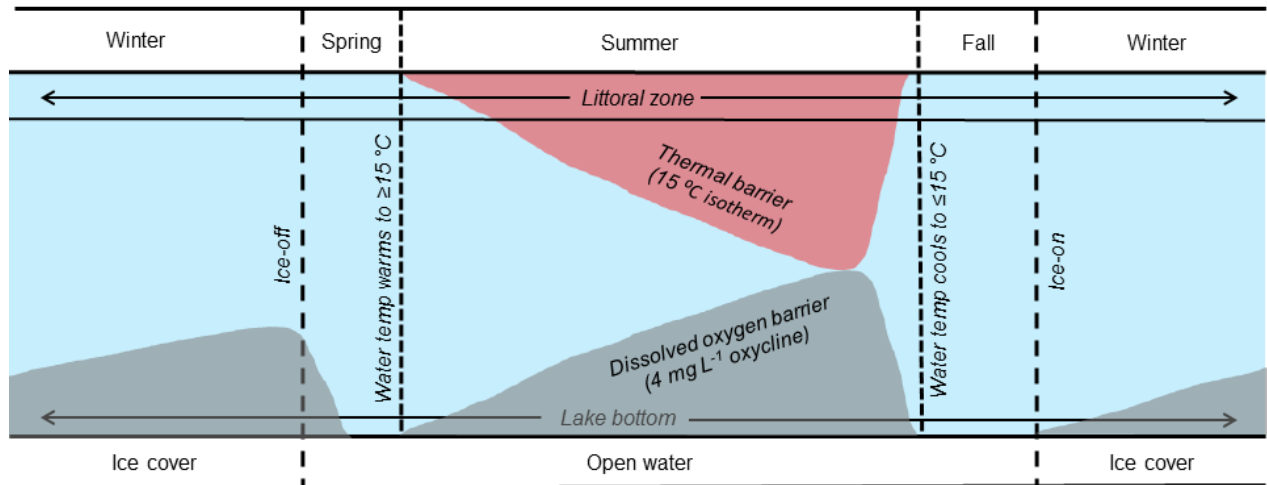
Figure 1 – Schematic illustrating the seasonal phenology of usable lake trout habitat in Boreal Shield lakes, as defined in the current study. Winter was the period of ice cover, when lake temperatures are between 1 and 4 °C. Fall and spring were the periods before and after ice cover when lake surface water temperatures are < 15 °C. Summer is the period between spring and fall, when lake surface water temperatures are ≥ 15 °C. During fall, winter, and spring, cool water temperatures allow lake trout to access littoral prey sources without thermal consequence. During summer, littoral zone temperatures are above the usable threshold for lake trout (≥ 15 °C), and deep water is low in dissolved oxygen (DO; < 4 mg L^{-1}), forcing lake trout to reduce use of the littoral zone and deep hypolimnetic regions to avoid unusable habitat. Low DO zones also occur during winter, but this is less constraining, as no upper thermal boundary exists. Low DO zones are replenished when lake waters mix during spring and fall turnovers.
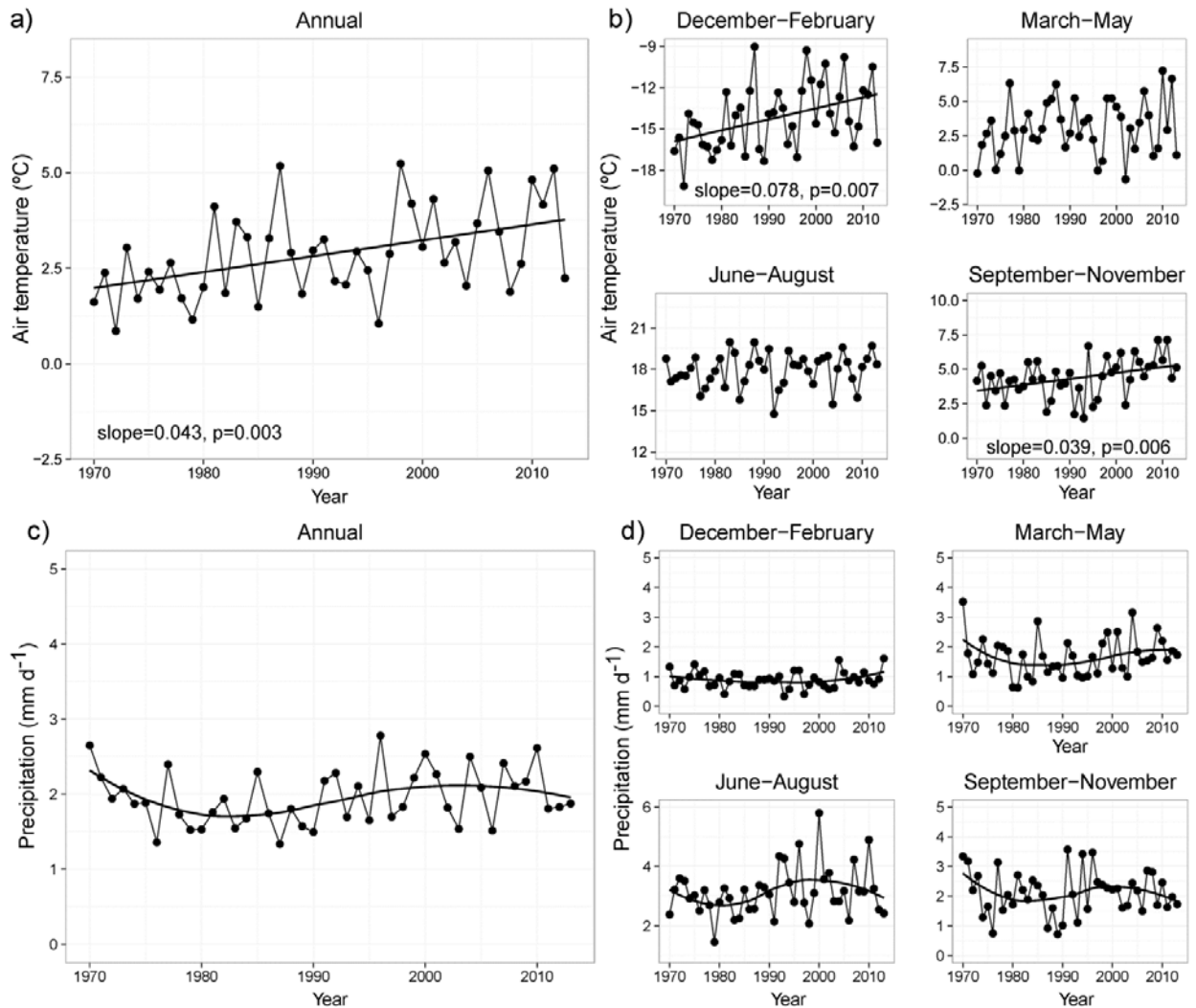
Figure 2 – Long-term variations in (a) mean annual air temperature, (b) seasonal air temperatures, (c) mean annual precipitation, and (d) seasonal precipitation since 1970 collected at the meteorological station within the Experimental Lakes Area, northwestern Ontario, Canada. For air temperature, a linear trend line and corresponding slope estimate are present in plots where a Mann-Kendall test indicated a significant monotonic trend at *P* < 0.1. Because precipitation follows a 31-year cycle in the region, a loess curve has been used to visualize cyclic patterns in precipitation.
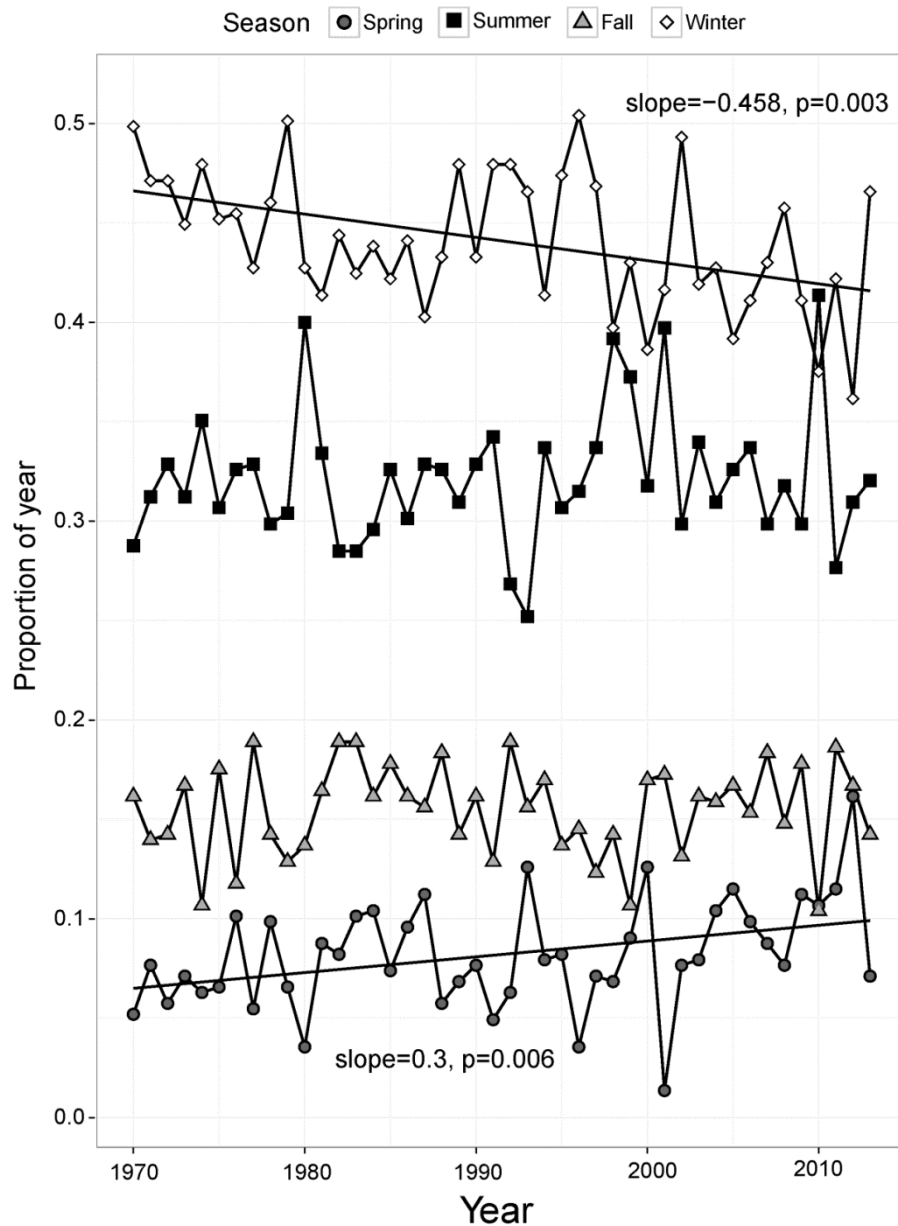
Figure 3 – Long-term variations in the proportion of each thermal season (as defined in Fig. 1) for lake trout based on our longest studied lake (Lake 239) located within the Experimental Lakes Area. Trend lines and corresponding Sen's slope estimate are present in plots where a Mann-Kendall test indicated a significant monotonic trend at *P* < 0.1.
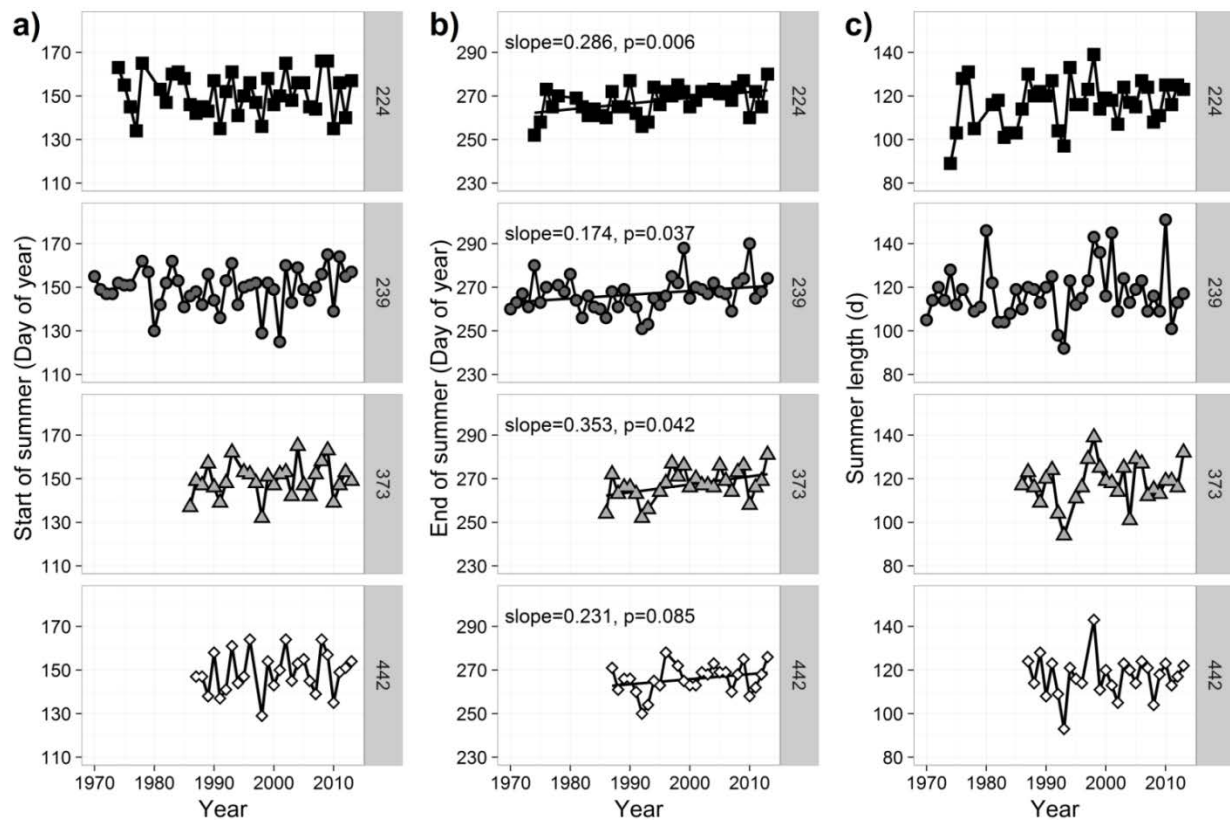
Figure 4 – Long-term variations in the phenology of lake trout thermal habitat constraint in four small Boreal Shield lakes within the Experimental Lakes Area, including (a) start date of summer (i.e. date that the 15 °C isotherm develops), (b) the end date of summer (i.e. date that the 15 °C isotherm breaks down), and (c) length of summer (i.e. number of days with a 15 °C isotherm). A trend line and corresponding Sen's slope estimate are present in plots where a Mann-Kendall test indicated a significant monotonic trend at *P* < 0.1. The label on the right of each plot indicates the individual study lake. The y axes among lakes are scaled the same so that differences in magnitude can be compared.
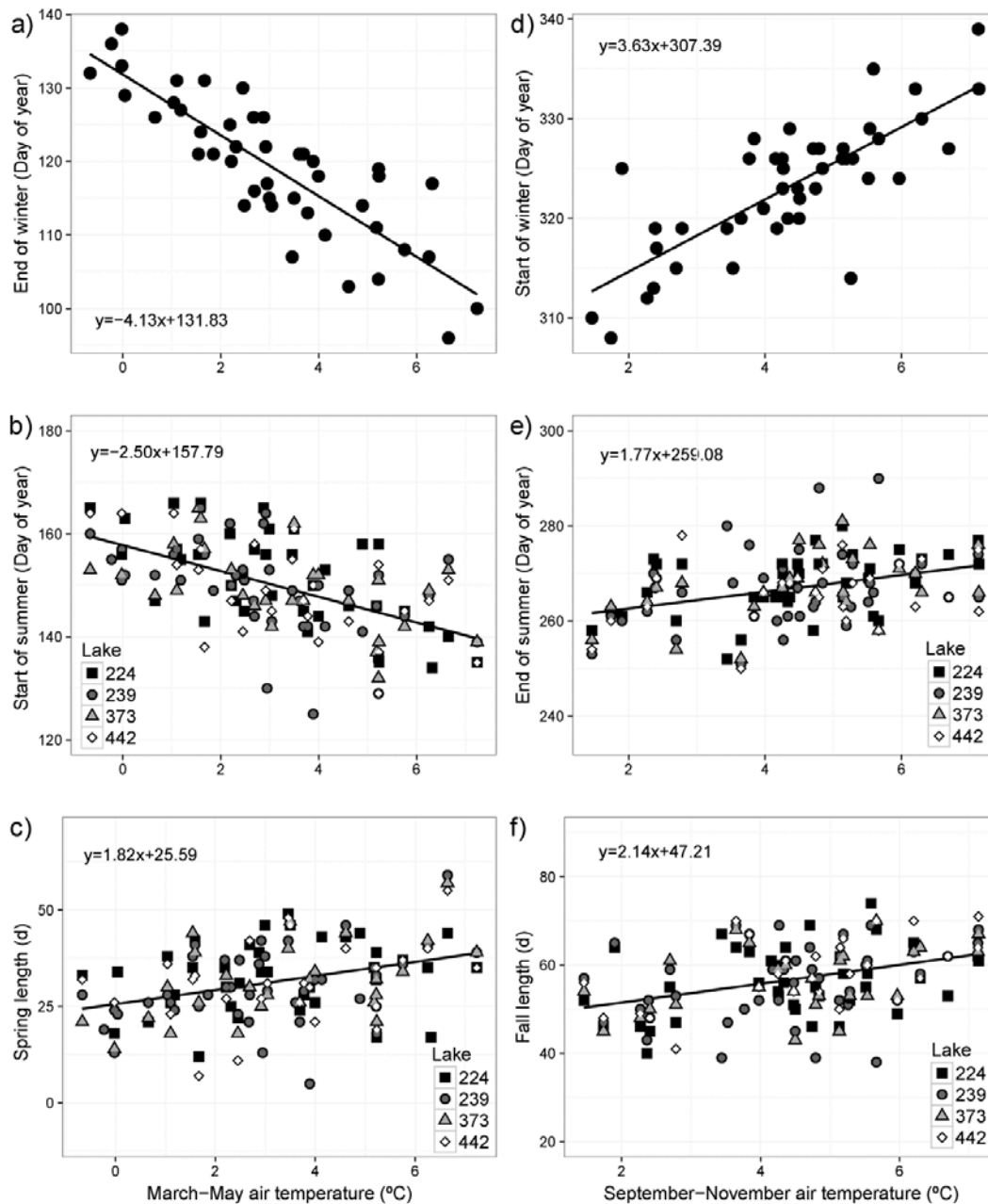
Figure 5 – Relationships between spring and fall air temperature and timing of important limnological events in four small Boreal Shield lakes located within the Experimental Lakes Area during 1970-2013. Panels a-c are relationships between spring air temperature and (a) end date of winter (i.e. spring ice-off date), (b) start date of summer (i.e. date that the 15 °C isotherm develops), (c) length of spring (i.e. number of days between end of winter and start of summer). Panels d-e are relationships between fall air temperature and (d) start date of winter (i.e. fall ice-on date), (e) end date of summer (i.e. date that the 15 °C isotherm breaks down), (f) length of fall (i.e. number of days between end of summer and start of winter).

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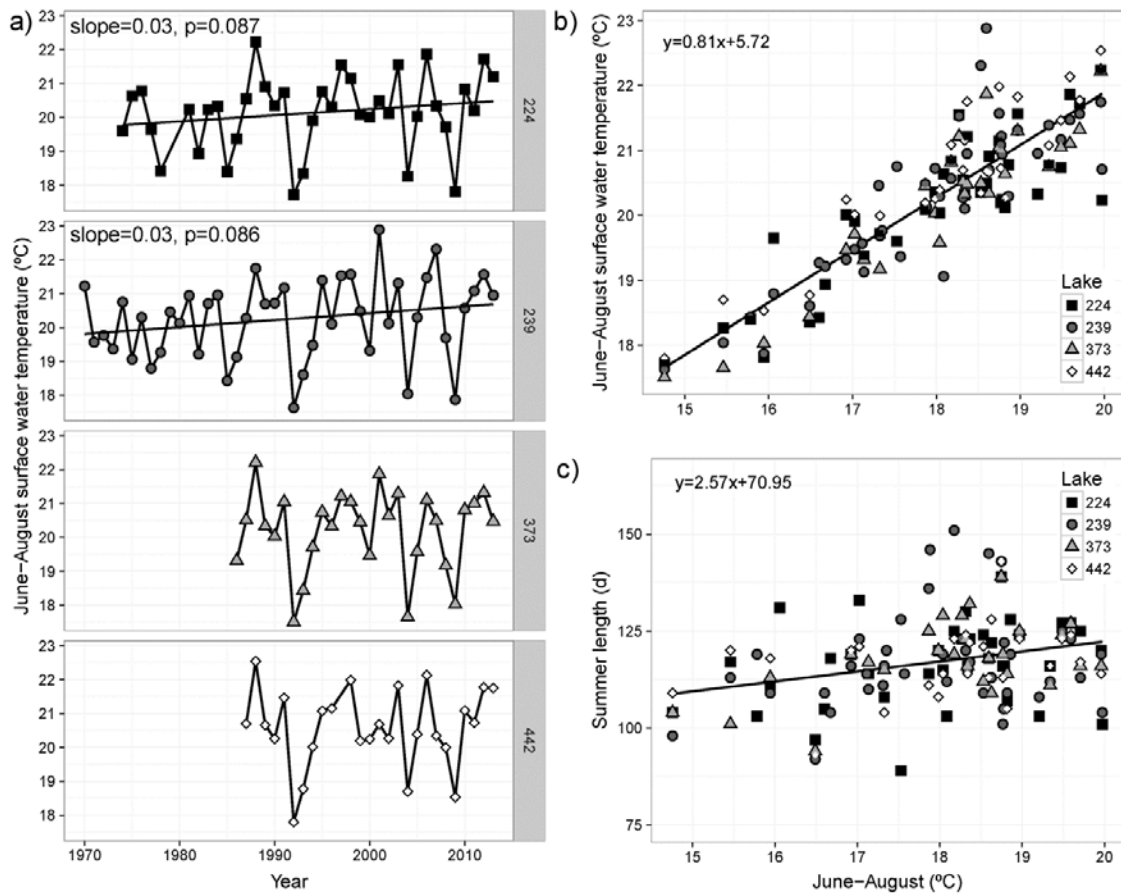
Figure 6 – Long-term variations in (a) surface (1 m depth) water temperature and relationships between summer air temperature and (b) surface water temperature and (c) summer length, in four small Boreal Shield lakes within the Experimental Lakes Area. A trend line and corresponding statistics are present in plots where a Mann-Kendall test or regression indicated a significant relationship at *P* < 0.1.
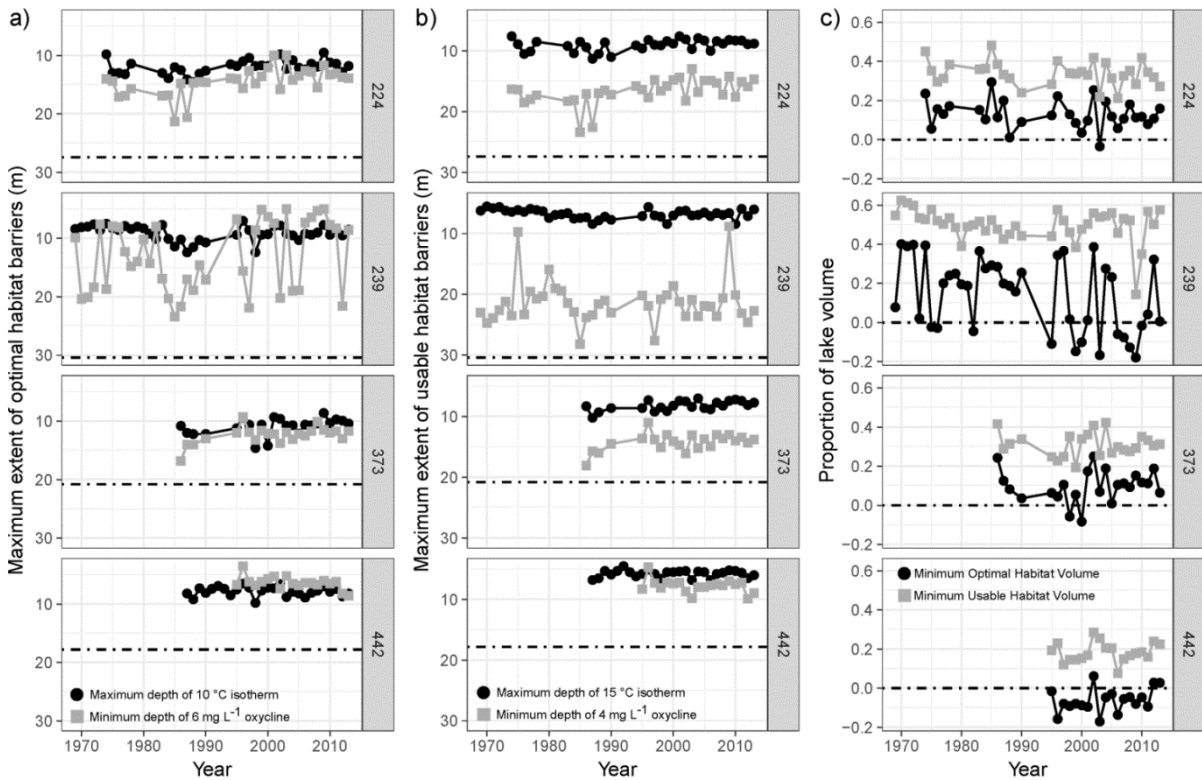
Figure 7 – Long-term variations in theoretical thermal and dissolved oxygen habitat boundaries that correspond to the maximum extent of habitat oxythermal constraint for lake trout in four small Boreal Shield lakes within the Experimental Lakes Area during 1970-2013. Solid lines and points refer to theoretical usable lake trout thermal habitat (panel a, 10 °C isotherm and 6 mg L^{-1} oxycline) and dissolved oxygen (panel b, 15 °C isotherm and 4 mg L^{-1} oxycline) boundaries and corresponding habitat volumes (panel c). Horizontal dot-and-dash lines on panels a and b indicate the bottom of each lake and in panel c indicate zero lake volume meeting usable or optimal habitat criteria.
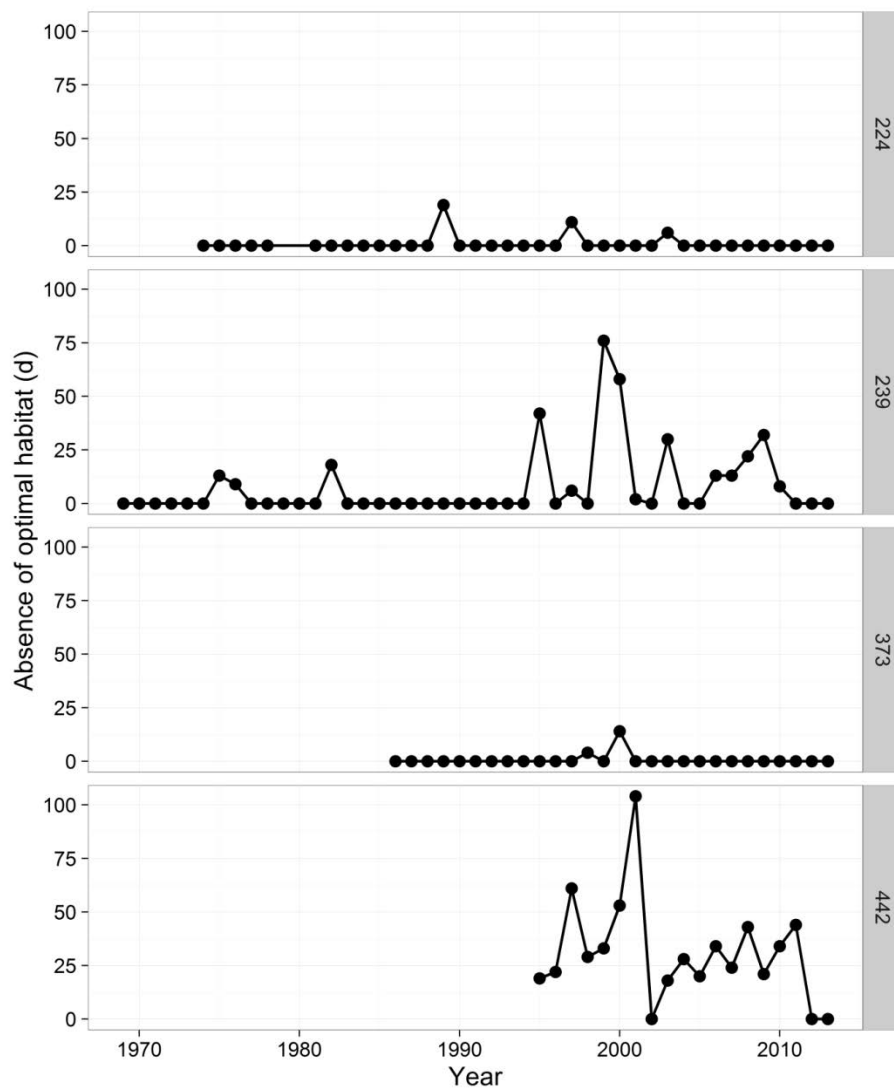
Figure 8 – Variations of the number of days each year where optimal summer oxythermal habitat (water temperatures < 10 °C and DO > 6 mg L^{-1}) for lake trout was eliminated in four small Boreal Shield lakes within the Experimental Lakes Area.

CHAPTER 2

Behavioral responses to annual temperature variation alter the dominant energy pathway, growth, and condition of a cold-water predator

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Abstract

There is a pressing need to understand how ecosystems will respond to climate change. To date, no long-term empirical studies have confirmed that fish populations exhibit adaptive foraging behavior in response to temperature variation or described the potential implications this may have on fitness. Here, we use an unparalleled 11-year acoustic telemetry, stable isotope, and mark-recapture dataset to test if a population of lake trout (*Salvelinus namaycush*), a cold-water stenotherm, adjusted its use of habitat and energy sources in response to annual variations in lake temperatures during the open-water season and how these changes translated to the growth and condition of individual fish. We found that climate influenced access to littoral regions in spring (data from telemetry), which in turn influenced energy acquisition (data from isotopes), and growth (mark-recapture data). In more stressful years — those with shorter springs and longer summers — lake trout had reduced access to littoral habitat and assimilated less littoral energy, resulting in reduced growth and condition. Annual variation in prey abundance influenced lake trout foraging tactics (i.e. the balance of the number and duration of forays) but not the overall time spent in littoral regions. Lake trout greatly reduced their use of littoral habitat and occupied deep pelagic waters during the summer. Together, our results provide clear evidence that climate-mediated behavior can influence the dominant energy pathways of top predators, with implications ranging from individual fitness to food web stability.

Introduction

There is growing urgency to understand how ecosystems are responding to climate change (Schmitz et al. 2003; IPCC 2014). Recent work, using latitudinal gradients as proxies to warming, has argued that the behavioral responses of mobile top predators to changing temperatures can drive fundamental shifts in aquatic food webs by altering the coupling of major energy pathways (Tunney et al. 2014, McMeans et al. 2016). Although this work is intriguing, no one has yet examined long-term empirical data that have explicitly tested if populations of top predators can shift their foraging behavior in response to annual changes in temperature or has evaluated what implications this might have for individual fitness. Temporal studies are critically important in this context because they control for the ecosystem specific adaptations that can confound latitudinal studies and instead focus on the active responses to changing conditions that are highly relevant to understanding the impacts of climate change.

Mobile top predators display adaptive foraging behavior by moving across spatially disparate habitats in response to changing conditions, most notably prey densities. For example, birds feed on both terrestrial and aquatic prey, effectively coupling these ecosystems (Murakami and Nakano 2002). Habitat coupling can also occur within ecosystems and has been well described in freshwater lakes, where predatory fish feed upon prey supported by dissimilar energy sources, such as offshore pelagic phytoplankton and nearshore littoral benthic algae (Schindler and Scheuerell 2002). These adaptive foraging shifts between littoral and pelagic food chains (i.e. littoral-pelagic coupling) in response to changes in prey densities can be a stabilizing force in aquatic food webs (Post et al. 2000, Kondoh 2003, Rooney et al. 2006). As ectotherms, the body temperatures of fish closely follow that of their ambient environment, and they must occupy species-specific temperature ranges to optimize physiological performance (Fry 1947, Magnuson et al. 1979, Pörtner and Knust 2007). Adaptive foraging behavior therefore should be particularly important in north-temperate lakes, because these systems undergo annual cycles in water temperatures and stratify thermally in summer. During thermal stratification,

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surface waters often exceed the temperature preferences of cold-water fish, substantially increasing the

metabolic costs associated with occupying littoral habitats (Fry 1947, Magnuson et al. 1979, Pörtner and

Knust 2007). In response, cold-water predators exhibit seasonality in their foraging, feeding in the

littoral zone in the spring and fall when surface waters are cool and relying on pelagic energy when

surface waters are warm in summer (Fry 1939, Martin 1952). Therefore, variations in both prey density

and seasonality should be important factors in directing the foraging behavior of fish in north-temperate

lakes.

Recent studies have shown that lake-surface temperatures have risen globally over the past 30

years (O'Reilly et al. 2015), with north-temperate lakes also having longer open-water seasons and

undergoing shifts in the phenology of seasonal water temperatures (Guzzo and Blanchfield 2017). These

observed changes in lake temperatures suggest that future warming may alter littoral-pelagic coupling

by mobile predatory fish. In fact, multi-lake studies of temperate food webs have shown that cold-water

predatory fish alter their littoral-pelagic coupling across gradients of abiotic factors that regulate the

physiological costs of foraging in the littoral zone. For example, littoral energy use by lake trout

(*Salvelinus namaycush*), a cold-water stenotherm, has been shown to increase with latitude, because

lakes at higher latitudes have littoral zones that are either thermally favorable for longer periods or

cooler in summer (Tunney et al. 2014). Lake trout acquisition of littoral energy also has been shown to

decrease with increasing littoral zone size due to the greater expanse of warm water to be traversed to

access nearshore prey during summer (Dolson et al. 2009). In both cases, the physiological constraint

imposed by temperature was suggested as the key factor in controlling littoral energy use by lake trout,

and together these studies suggest that the expected warmer conditions also could alter littoral-pelagic

coupling by cold-water fish populations within single lakes.

Here, we sought to understand if and how annual variations in water temperatures altered

littoral-pelagic coupling by a cold-water predatory fish population and what implications these dietary

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shifts had on individual fitness as inferred from growth and condition. Our study system was a small,

oligotrophic north-temperate lake that did not contain pelagic prey fish. In such lakes, lake trout obtain

the majority of their energy from prey fish and benthic invertebrates located in the littoral zone (Vander

Zanden and Rasmussen 1996), presumably during the spring and fall, when water temperatures are

cool. As the lake warms, water temperatures within the littoral zone exceed the thermal preference of

lake trout (> 15 °C), and they move offshore to deeper water within the pelagic zone and begin to rely

increasingly on smaller pelagic prey, including *Mysis diluviana* (i.e. freshwater shrimp) and zooplankton

(Fig. 1; Fry 1939, Martin 1952, Vander Zanden and Rasmussen 1996, Plumb and Blanchfield 2009). We

hypothesized that because of the direct influence of temperature on fish physiology, annual changes in

the phenology of littoral zone water temperatures, which are closely linked to air temperature

variations (Guzzo and Blanchfield 2017), would influence littoral-pelagic coupling by lake trout (Fig. 1).

We also expected that climate-driven year-to-year differences in access to prey-rich littoral regions

would be manifested in the growth and condition of lake trout. To test these hypotheses, we used 11

consecutive years of acoustic telemetry and stable isotope data to quantify annual littoral habitat use

and energy sources of our study population and related these findings to annual variations in water

temperatures, prey fish abundance, and the growth and condition of individual lake trout from annual

mark-recapture sampling.

Methods

Study site

The study occurred over 11 years (2003-2013) within the International Institute for Sustainable

Development (IISD)-Experimental Lakes Area, Canada (49°40'N, 93°44'W) (Blanchfield et al. 2009a). Lake

373 (L373) is an un-manipulated long-term reference lake used to monitor natural variation. It is a small

(surface area 27.3 ha, maximum depth 20.5 m), single-basin lake that thermally stratifies during

summer, when mean littoral zone temperatures typically range from 17-21 °C. The lake supports a

native, naturally reproducing lake trout population that consisted of ≈ 285 adults during our study (Mills

et al. 2002). The lake does not contain pelagic prey fish, and the main prey items for adult lake trout are

littoral prey fish (*Phoxinus eos*, *Phoxinus neogaeus*, *Margariscus margarita*, and *Cottus cognatus*),

benthic invertebrates, insects, *Mysis*, and zooplankton. The lake also contains white sucker (*Catostomus*

commersonii). We considered the littoral zone to be water depths < 6 m (Sandstrom et al. 2013).

Because L373 is bowl-shaped, with no islands or shoals, littoral regions were located only along the

perimeter of the lake.

Lake temperatures

Annual ice-on and ice-off dates were monitored at nearby (≈ 12 km) Rawson Lake (54.3 ha) and were

assumed to be the same for L373 because the lakes are similar in size and depth. Water temperatures in

L373 were measured every 30 min using a string of data loggers (HOBO Temp Pro H20-001; Onset)

deployed over the deepest point of the lake at 1 m depth intervals from 1-8 m and at 10 m, 15 m, and

19 m depth (Plumb and Blanchfield 2009). Logger data from 29 April to 20 June 2003 were not available

and were supplemented with biweekly temperature profile data.

We estimated the mean daily temperature of the littoral zone during each open-water season

using data from temperature loggers at 1-6 m. The period between ice-off and the date that the mean

littoral zone temperature exceeded 15 °C was denoted "spring." The period when the mean littoral zone

temperature exceeded 15 °C was denoted "summer." "Fall" was the period between the date that the

lake cooled to ≤ 15 °C and ice-on. "Winter" was considered the ice-covered period. Because lake trout

spawn inshore in the fall (Muir et al. 2012), we were unable to distinguish between foraging and

spawning behavior. By using the date when littoral water temperatures exceeded 15 °C, we provide a

measure of how access to littoral energy is controlled by temperature (Evans 2007, Plumb and

Blanchfield 2009). We did not use the existence of a planar thermocline to define summer, because this can occur when littoral temperatures are ≤ 15 °C and would not represent a physiological barrier for lake trout (Evans 2007).

Habitat use

We monitored the depths of lake trout using acoustic telemetry. Telemetry data were collected from 41 individual fish (fork length 380-501mm) implanted with depth-sensing transmitters (V16P-4L or V13P-1L; VEMCO Ltd.) that randomly transmitted a coded signal every 16-64 s (V16) or every 120-300 s (V13) (see Tables S1 and S2 for transmitter and biological details). The depths of transmitter-implanted fish were monitored year-round using four or five omnidirectional hydrophone receivers (VR2; VEMCO Ltd.) with overlapping detection ranges distributed throughout the lake (Blanchfield et al. 2009b, Plumb and Blanchfield 2009). Raw telemetry data were filtered before analyses (details are given in Supporting Information and Figs. S2, S3). The final telemetry dataset for estimation of spring, summer, and fall habitat use consisted of 1,979,775 detections (range 63,016-368,755 per year) from 29 individual fish (range two to nine fish per year). No telemetry data from 2005 were available, because all new transmitters were implanted that spring, and we did not use data from the year in which transmitters were implanted to avoid potential effects of tagging on behavior. Using data for each fish, we calculated daily estimates of (i) the number of forays into the littoral zone; (ii) the average duration of each littoral foray; and (iii) the total time spent in the littoral zone during the spring, summer, and fall of each open-water season. A littoral foray was denoted by a fish's depth changing from ≥ 6 m to < 6 m between consecutive detections. The total number of forays performed by an individual fish on a given day was then summed. Daily estimates of the total time spent in the littoral zone by each fish were calculated as the ratio of littoral zone detections to total detections scaled to a 24-hour period. Daily estimates of average foray duration for each fish were then calculated as the total time spent in the littoral zone

divided by the number of littoral forays on that day. We note that our method would categorize a lake

trout moving into depths < 6 m in offshore regions as a littoral foray, but we assumed all forays occurred

in the nearshore region.

Energy sources

We used stable carbon (δ^{13}C) isotopes to estimate use of littoral- vs. pelagic-derived energy by lake trout

(France and Steedman 1996). Pectoral fin-ray tips (lake trout) and dorsal muscle (littoral prey fish) were

collected each fall. *Mysis* and bulk zooplankton were collected monthly during each open-water season.

Samples were dried, ground, loaded into tin capsules, and analyzed using standard methods at the

University New Brunswick or the University of Waterloo. Stable isotope values were conveyed in δ

notation (‰): δ^{13}C = [(^{13}C/^{12}C sample/^{13}C/^{12}C standard) − 1] × 1,000.

The δ^{13}C values of lake trout fins were first corrected to equivalent muscle values using the

equation δ^{13}C muscle = 0.73 × δ^{13}C fin - 8.11 (Wellman et al. 2017). We mathematically lipid-corrected

the δ^{13}C values of prey fish and *Mysis* using δ^{13}C muscle (normalized) = δ^{13}C muscle + [-3.32 + (0.99 ×

C:N)] (Post et al. 2007). The correction was not applied to lake trout because lipids should not be an

issue for fin tissue. From 2003-2005, stable isotope data for prey fish were not available; in these years

we estimated the δ^{13}C values of prey fish by adding the mean difference in δ^{13}C values of prey fish and

littoral mayflies during years when both these items were analyzed to the mean values of littoral

mayflies. We note that lake trout fin-ray tips have been found to turn over at similar rates to white

muscle (Wellman et al. 2017). We determined the proportion of littoral energy assimilated by each lake

trout using a two-source mixing model that treated *Mysis* and littoral prey fish as the pelagic and littoral

end members, respectively (Vander Zanden and Vadeboncoeur 2002): proportion littoral energy = (δ

δ^{13}C lake trout - δ^{13}C *Mysis*)/(δ^{13}C prey fish - δ^{13}C *Mysis*). The lake trout δ^{13}C dataset contained 194

samples (*n* = 15-20 per year) with fork lengths ranging from 199-502 mm.

A small number of lake trout stomach contents obtained from nonlethal gastric lavages were collected in the spring (23 and 28 May, $n = 14$) and summer (12 August, $n = 4$) of 2014 and from fall mark-recapture sampling mortalities (various dates between 1-21 October 1986-2012, $n = 24$) to support stable isotopes. Prey items from each stomach were identified and grouped into the following groups: benthic invertebrates and insects, prey fish, *Mysis*, and zooplankton. We then calculated the proportion of the total stomach content weight for each diet item.

Growth and condition

Lake trout growth was examined using data from annual mark-recapture sampling. Fish were captured each fall using trap nets and short (< 30 min) evening gill net sets on spawning shoals (Mills et al. 1987, 2002). Following capture, the weights (g), fork lengths (mm), and tag numbers from previously captured fish were recorded. Newly captured fish received a tag for future identification. Condition was estimated as a percentage of standard weight specific for lake trout (Piccolo et al. 1993). We identified 141 instances in which an individual fish was captured in consecutive years during the study period.

Prey fish abundance.

The relative abundance of littoral prey fish was calculated as CPUE based on annual collections (Mills et al. 1987, Guzzo et al. 2014). Each spring, two or three small-diameter mesh trap nets were set for 27-39 consecutive days to target the nearshore-littoral zone. Annual CPUE estimates were calculated by dividing the total number of prey fish by the number of net days (i.e. number of trap nets × number of fishing days). We included all cyprinid species and slimy sculpin in putative littoral prey fish CPUE values.

Statistical analysis

Analyses were carried out in R, v. 3.3.2 (R Core team 2015). Assumptions of linear mixed effect models (LMMs) and linear regression were evaluated (Zuur et al. 2009, 2010). Where necessary, data were transformed to meet assumptions as reported in Results. LMMs were fit using the *nlme* package (Pinheiro et al. 2016), and fits were evaluated (Zuur et al. 2009, 2010). We calculated least squares means for each factor level in LMMs using the *lsmeans* package (Lenth 2016). Because of the small sample size (11 years), we considered $P < 0.1$ as statistically significant.

We analyzed habitat use data from spring, summer, and fall seasons separately. LMMs were applied to each habitat measure (number of littoral forays, average foray duration, and total time in littoral zone) over all years for each season, for a total of nine LMMs, which treated year as a fixed factor and individual fish as random intercepts.

Mean estimates (± SD) of habitat use for each year/season were obtained using the least squares means from each LMM and were subsequently used as response variables in linear regression to test if each seasonal habitat use measure was predicted by the corresponding season length, prey fish CPUE, length of the preceding season (summer and fall only), and mean summer littoral zone temperatures (summer only). Mean estimates of the proportion of littoral energy assimilated for each study year were obtained by calculating means (± SD) over all individual lake trout analyzed for δ^{13}C within each year. The linear regression procedure described above for habitat use then was used to test if the mean proportion of littoral energy was predicted by season length (spring or summer), prey fish CPUE, and summer littoral zone water temperatures. Isotope data were not related to fall length, because samples were collected near the start of the fall in each year.

We determined how variations in littoral energy and habitat use translated to growth by treating annual changes in individual lake trout weight and condition as response variables in separate linear regressions with spring-summer littoral energy use, spring and summer littoral habitat use, and the length of the spring, summer, and winter periods used as predictor variables. Fall habitat use or fall

length was not used as a predictor for annual growth because fish collections occurred throughout this period.

Results

Lake temperatures

The length of spring, when lake trout can access the littoral zone without thermal consequence (≤ 15 °C), averaged 43 days and varied in duration by nearly a month (31-59 d) over the study. The summer period, when lake trout are putatively thermally restricted from accessing the littoral zone (> 15 °C), was on average 2.7 times longer than the spring and averaged 109 days with a difference of one-month (36 days) between the shortest (85 days) and longest (121 days) summers. Longer summers typically had warmer littoral zone temperatures (Pearson correlation: n = 11, r = 0.79, P < 0.01). The length of the fall season, when lake trout spawn but can also use the littoral zone for feeding without thermal consequence, averaged 61 days (range: 51-72 days) and was on average 1.5 times longer than the spring and 1.8 times shorter than the summer. In a given year, the length of the spring and summer seasons showed a negative correlation (n = 11, r = -0.59, P = 0.06), spring and fall lengths were not significantly correlated (n = 11, r = 0.42, P = 0.20), and neither were fall and summer lengths (n = 11, r = -0.32, P = 0.34).

Habitat use

Lake trout displayed clear seasonal shifts in habitat use and behavior that followed changes in mean littoral zone temperatures (Fig. 2). Immediately following ice-out, lake trout often spent several hours or entire days within the littoral zone (Fig. 2). As mean littoral zone water temperatures exceeded 15 °C (summer), lake trout greatly reduced their forays into the littoral zone until water temperatures cooled to 15 °C in the fall, when lake trout quickly reoccupied the littoral zone (Fig. 2). The total time spent by

lake trout in the littoral zone during the spring of each year averaged 550 h and increased with spring length (log$_{10}$; $F_{[1, 8]}$ = 6.75, P = 0.03, r^2 = 0.46) (Fig. 3a). In contrast, the number ($F_{[1, 8]}$ = 0.28, P = 0.61) or average duration ($F_{[1, 8]}$ = 1.13, P = 0.32) of littoral forays made in the spring was not predicted by spring length. Rather, lake trout made a greater number ($F_{[1, 8]}$ = 12.22, P < 0.01, r^2 = 0.60) of shorter ($F_{[1, 8]}$ = 5.24, P = 0.05, r^2 = 0.40) forays in springs with higher prey fish densities (Fig. 4a, b). The contrasting effect of number and duration of forays meant that prey fish abundance (measured as catch per unit effort, CPUE) did not alter the total time lake trout spent in the littoral zone during the spring but only how they used that time ($F_{[1, 8]}$ = 0.00, P = 0.98) (Fig. 4c).

The amount of time that lake trout spent in the littoral zone each summer averaged 43 h and was not predicted by summer length ($F_{[1, 8]}$ = 0.09, P = 0.77) (Fig. 3b) or prey fish CPUE ($F_{[1, 8]}$ = 0.01, P = 0.93). The number or average duration of littoral forays made by lake trout in the summer also was not predicted by summer length (log$_{10}$; number of forays: $F_{[1, 8]}$ = 0.55, P = 0.48; average foray duration: $F_{[1, 8]}$ = 2.31, P = 0.17) or prey fish CPUE (log$_{10}$; number of forays: $F_{[1, 8]}$ = 0.69, P = 0.43; average foray duration: $F_{[1, 8]}$ = 0.09, P = 0.78). The mean summer water temperature in the littoral zone also did not predict the time spent by lake trout within the littoral zone during the summer ($F_{[1, 8]}$ = 0.01, P = 0.92) (Fig. 4d) or the number of littoral forays (log$_{10}$; $F_{[1, 8]}$ = 1.76, P = 0.22). However, lake trout made shorter forays as mean summer littoral zone water temperatures increased ($F_{[1, 8]}$ = 3.79, P = 0.08, r^2 = 0.32) (Fig. 4e, f). The time spent within the littoral zone the during summer was not related to the length of the preceding spring ($F_{[1, 8]}$ = 0.01, P = 0.92).

The amount of time that lake trout spent in the littoral zone each fall averaged 301 hours but, unlike spring, was not predicted by fall length (square-root; $F_{[1, 8]}$ = 1.13, P = 0.32) (Fig. 3c) or prey fish CPUE (square-root; $F_{[1, 8]}$ = 0.04, P = 0.85). The number or average duration of littoral forays made by lake trout in fall also was not predicted by fall length (number of forays: $F_{[1, 8]}$ = 3.14, P = 0.12; average foray duration: $F_{[1, 8]}$ = 0.02, P = 0.90) or prey fish CPUE (number of forays: $F_{[1, 8]}$ = 0.58, P = 0.47; average

foray duration: $F_{[1, 8]} = 0.24$, $P = 0.64$). The time spent within the littoral zone during the fall also was not related to the length of the preceding spring (square-root; $F_{[1, 8]} = 0.20$, $P = 0.67$) or summer (square-root; $F_{[1, 8]} = 0.14$, $P = 0.72$).

Energy sources

The proportion of littoral energy assimilated by lake trout, estimated using $\delta^{13}C$ values (logit-transformed for analyses), averaged 0.66 (range 0.40-0.95) over the study and was positively related to spring length ($F_{[1, 9]} = 12.66$, $P < 0.01$, $r^2 = 0.59$) (Fig. 5a) and negatively related to summer length ($F_{[1, 9]} = 12.58$, $P < 0.01$, $r^2 = 0.58$) (Fig. 5b). The proportion of littoral energy assimilated by lake trout was not predicted by prey fish CPUE ($F_{[1, 9]} = 1.53$, $P = 0.25$) but was negatively related to mean summer littoral zone temperature ($F_{[1, 9]} = 7.49$, $P = 0.02$, $r^2 = 0.45$).

Lake trout stomachs contained more prey in spring (6.33 ± 6.15 g, mean ± SD) than in summer (1.73 ± 1.45 g) and fall (3.45 ± 2.75 g), and the composition of these prey items varied seasonally. Stomach contents collected in spring contained 60 % benthic invertebrates and insects, 37 % littoral prey fish, 3 % *Mysis*, and no zooplankton. Stomachs collected in summer contained 45 % littoral prey fish, 2 % benthic invertebrates and insects, 27 % *Mysis*, and 26 % zooplankton. Fall stomach contents contained 22 % littoral prey fish, no benthic invertebrates or insects, 72 % *Mysis*, and 6 % zooplankton.

Growth and condition

The growth (i.e. change in weight) and condition of individual lake trout were positively related to the time spent within the littoral zone during the spring (weight: $F_{[1, 127]} = 8.69$, $P < 0.01$, $r^2 = 0.07$; condition: $F_{[1, 127]} = 5.82$, $P = 0.02$, $r^2 = 0.04$) (Fig. 6a, b) and summer (weight: $F_{[1, 126]} = 30.39$, $P < 0.01$, $r^2 = 0.19$; condition: $F_{[1, 126]} = 11.95$, $P < 0.01$, $r^2 = 0.09$) (Fig. 6c, d). Growth and condition were also positively related to the proportion of littoral energy assimilated (weight: $F_{[1, 139]} = 13.96$, $P < 0.01$, $r^2 = 0.09$;

condition: $F_{[1, 138]}$ = 5.44, P < 0.01, r^2 = 0.04) (Fig. 6e, f). Consistent with behavioral data, growth and

condition of individual lake trout were also positively correlated to spring length (weight: $F_{[1, 139]}$ = 8.56, P

< 0.01, r^2 = 0.06; condition: $F_{[1, 138]}$ = 6.74, P = 0.01, r^2 = 0.05); however, neither was related to summer

length (weight: $F_{[1, 139]}$ = 0.17, P = 0.68; condition: $F_{[1, 138]}$ = 0.56, P = 0.46).

Discussion

We found that lake trout, a mobile cold-water predator, made consistent and predictable seasonal shifts

in habitat use that were triggered by changes in lake-water temperatures. As the phenology of littoral

zone temperatures shifted from year to year, so did lake trout use of nearshore habitat and acquisition

of energy from this prey-rich habitat. In warmer years, when littoral energy acquisition was lower,

individual lake trout had reduced growth and condition. This ability of a single population of aquatic top

predators to adjust its foraging behavior rapidly to inter-annual changes in climatic conditions and the

corresponding impacts on measures of fitness highlight the adaptability of this glacial relict species to

persist under adverse conditions. Indeed, recent evidence that many fish species from various thermal

guilds and trophic levels may be capable of flexible foraging behavior (Edmunds et al. 2016) suggest that

our results may be broadly applicable for understanding the impact of climate change on aquatic

ecosystems.

   Our results suggest that water temperature phenology (i.e. seasonality) supersedes prey density

as the main controller of littoral-pelagic coupling by lake trout. Although prey fish abundance and

summer littoral zone temperature influenced foraging strategy (i.e. the balance of the number and

duration of littoral forays), these factors did not affect the overall time spent within the littoral zone.

Rather, longer springs resulted in greater occupation of littoral habitat and acquisition of littoral energy.

Conversely, littoral energy use declined with increasing summer length, which was negatively correlated

to spring length in a given year. These results suggest that changes in temperature can fundamentally

rewire energy pathways, a result that has the potential to impact food web stability (Post et al. 2000, Kondoh 2003, Vadeboncoeur et al. 2005, Rooney et al. 2006), but of course the direction and magnitude of these impacts would vary depending on the how future warming alters the phenology of water temperatures.

Reductions in the growth and condition of individual lake trout observed in years with reduced littoral habitat use and littoral energy use could result from a combination of factors. First, increased reliance on *Mysis* and zooplankton would be less energetically efficient than foraging on larger prey fish or benthic invertebrates because predatory fish are more active when forced to feed on numerous, smaller prey (Pazzia et al. 2002). This increased energetic cost of feeding on small prey has been illustrated by studies that found predatory fish in lakes without pelagic prey fish had increased muscle activity and greater activity rates than those same species in lakes containing pelagic prey fish (Kaufman et al. 2006, Morbey et al. 2010, Cruz-font et al. 2016) and by studies showing that more active fish generally grow more slowly (Rennie et al. 2005). Additionally, in oligotrophic lakes, the littoral zone is often more productive and smaller in volume than the pelagic zone (Schindler and Scheuerell 2002, Dolson et al. 2009), and therefore the probability of a lake trout's encountering prey would be higher in the littoral zone than in the pelagic zone, increasing foraging success but also reducing the time required to find prey.

Despite thermally suboptimal temperatures in littoral regions during summer, lake trout used this habitat to access preferred prey in all years. Regular, although limited, foraging into waters with temperatures above their thermal preference indicates the energetic importance of acquiring large, energy-dense prey (Plumb et al. 2014). This suggests that capturing prey fish in warm water could be a more efficient strategy than foraging on small prey within the pelagic zone — at least for some parts of summer. These rapid forays into warm, shallow water have been documented previously for lake trout (Sellers et al. 1998, Morbey et al. 2006). However, during the peak of summer, when littoral

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temperatures were highest, lake trout seemed to reduce greatly and even stop use of the littoral zone.

This behavior also has been exhibited by other temperature sensitive fish, including brook trout

(*Salvelinus fontinalis*) and rainbow trout (*Oncorhynchus mykiss*), which have been documented to stop

foraging and seek cool-water refuge when temperatures exceed their thermal preferences (Biro 1998,

Breau et al. 2011). Therefore, continued warming of surface-water temperatures during the summer

(O'Reilly et al. 2015, Guzzo and Blanchfield 2017) could extend periods of limited littoral access in

salmonids, increasing their reliance on pelagic-derived energy.

The fall period also provides thermal conditions in which lake trout could exploit littoral prey

without consequence and presumably could offset the constraints imposed by the stressful conditions

during the preceding seasons. Although the fall periods generally were longer than the spring periods,

lake trout on average spent less time in the littoral zone during the fall than in the spring, even though

the littoral zone is also the region where spawning occurs. Moreover, lake trout did not increase their

use of this habitat in fall periods that were preceded by stressful conditions (i.e. shorter spring and/or

longer summers), and their fall diet reflected a reliance on pelagic prey, mainly *Mysis*, as earlier studies

have noted (Fry 1939, Martin 1952). At least in our study system, the fall does not seem to be a period

when lake trout make extensive use of littoral resources. Based on the apparent limited acquisition of

littoral energy in summer and fall periods, it appears that the spring period, which is strongly influenced

by climate (Guzzo and Blanchfield 2017), is critical for the annual growth and condition of lake trout.

Observed reductions in individual growth and condition associated with reduced access to

littoral energy also have important implications for population persistence through impacts on

reproduction and recruitment. Further reductions in access to littoral regions with future warming could

prevent lake trout from accumulating sufficient energy to spawn in the fall (Plumb et al. 2014),

potentially increasing the frequency of skip-spawning (Morbey and Shuter 2013, Sitar et al. 2014). The

prospective smaller post adult body size with warming could also lead to reductions in fecundity, which

is positively correlated with body size (Trippel 1993). Furthermore, increased reliance on pelagic energy by adult lake trout during longer and/or warmer summers would increase competition with juvenile lake trout that rely almost exclusively on *Mysis* and zooplankton (Trippel and Beamish 1993, France and Steedman 1996). Together, the potential for less frequent spawning, production of fewer eggs, and lower recruitment to adulthood posed by warming could have severe implications for the ability of lake trout populations within small lakes to persist through future climate change.

It is worth noting that our study lake did not contain pelagic prey fish (e.g., cisco, *Coregonus artedi*), and this type of food web represents only a subset of lake trout lakes (Vander Zanden and Rasmussen 1996). In lakes with cisco, lake trout would be able to access prey fish throughout periods of thermal limitation (Fry 1939), and so the impacts of seasonal phenology on foraging behavior and fitness in cisco-containing lakes may differ from our findings. However, a study by King, et al. (1999) found that lake trout inhabiting a cisco-containing lake had reduced growth in years with earlier onset of thermal stratification, likely because of reduced access to littoral prey in the spring. This suggests that the impacts of seasonal phenology on the foraging behavior and fitness of lake trout may be similar across lake types; however, the magnitude of these changes may vary. Finally, the adaptive behavior of lake trout illustrated here also has implications for predicting how future warming may alter the geographic distribution of cold-water fish species, particularly around southern range borders, where surface temperatures may exceed thermal limits. At these southern edges, adaptive foraging behavior and use of refuge may allow cold-water populations to persist for extended periods when simple surface models would predict range contractions (Schmitz et al. 2003).

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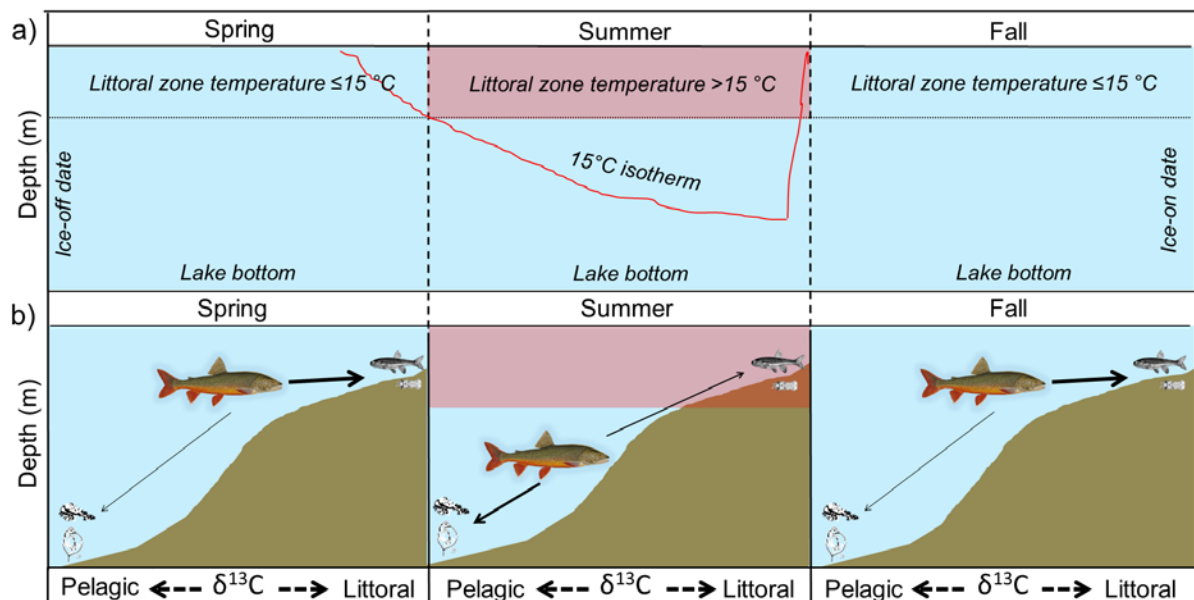
Figure 1 – Theoretical illustration of how seasonality in water temperatures during the open-water season impacts foraging behavior of lake trout in small Boreal Shield lakes. (a, b) Cold water temperatures immediately after ice-out in the spring and before ice-on in the fall allow lake trout to access the littoral zone (< 6 m depth) without thermal consequence. However, during summer warm littoral temperatures impose an energetic cost to lake trout accessing the littoral zone. Therefore, (b) lake trout should exhibit greater use of littoral habitat and prey (prey fish and benthic invertebrates/ aquatic insects) when springs and falls are longer, and conversely, should use more pelagic habitat and prey (*Mysis* and zooplankton) when summers are longer. In b, increasing arrow thickness denotes expected increased use of energy pathways based on littoral water temperatures.
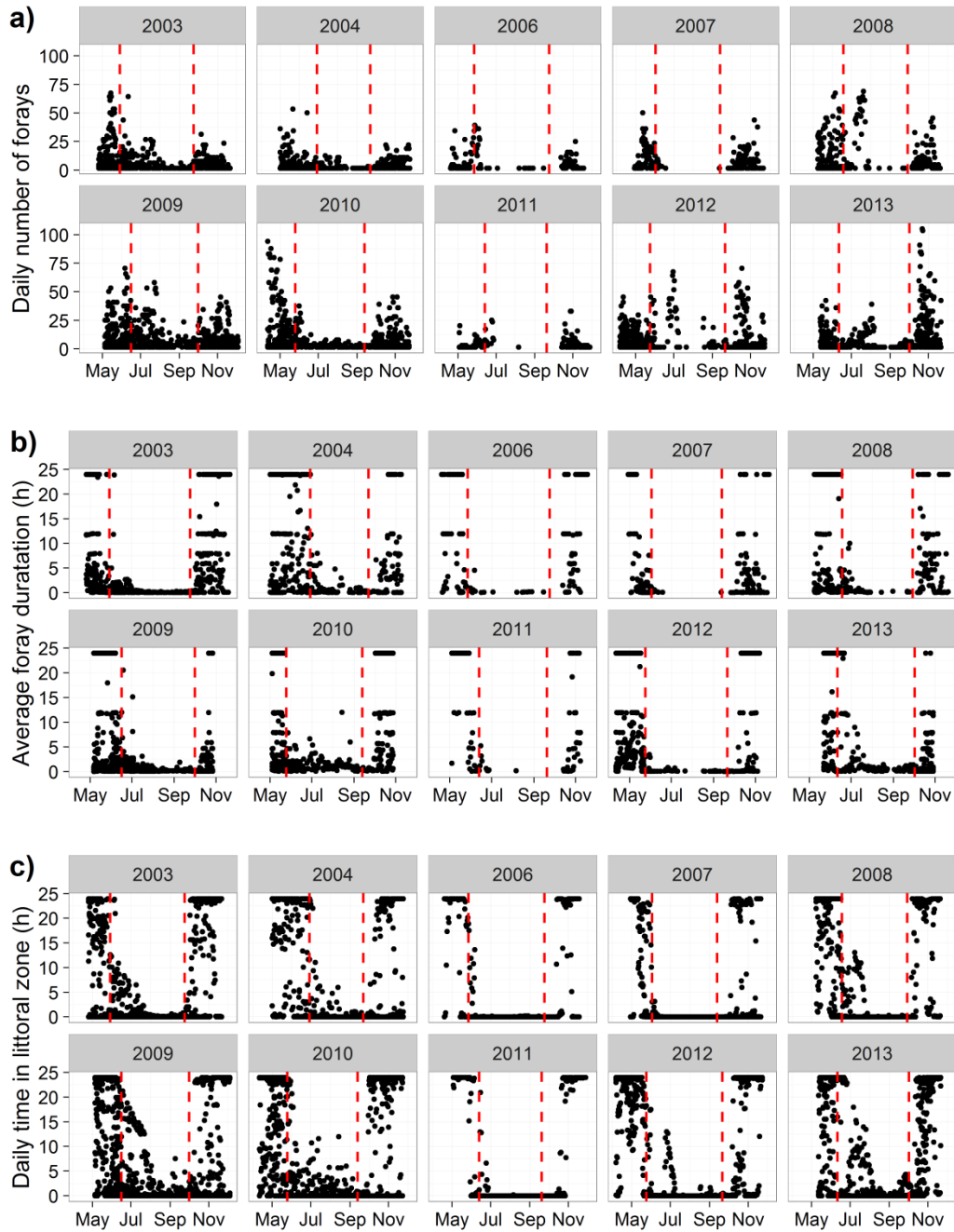
Figure 2 – Daily estimates of littoral zone use by individual lake trout implanted with acoustic transmitters during each annual open-water period (n = 420-1,906 per year), including (a) the number of littoral forays, (b) the average foray duration in hours, and (c) the total time in hours. Red vertical dashed lines indicated the start and end dates of the summer period (i.e. when the mean littoral zone temperature exceeds 15 °C) each year. Each data point is a daily estimate for an individual fish. Note there were no telemetry data for 2005 (see Methods).
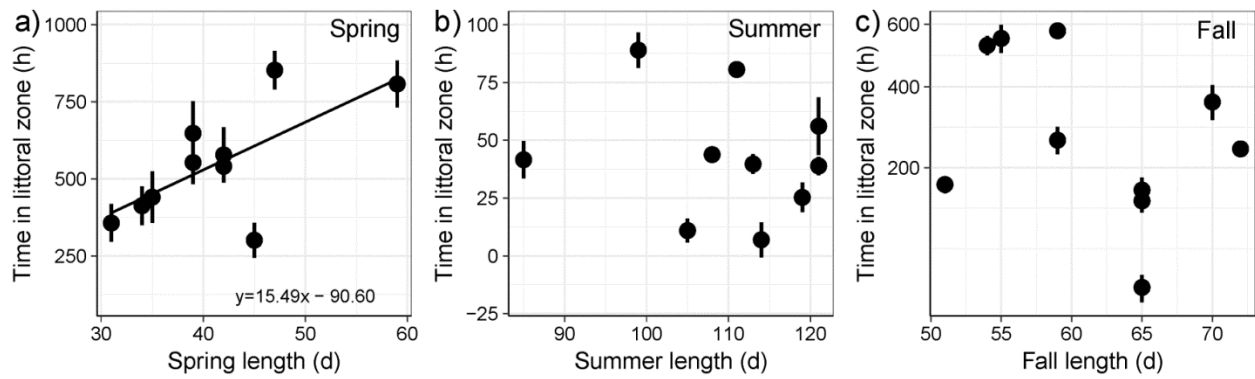
Figure 3 – Relationships between the length of (a) spring, (b) summer, and (c) fall and time spent in the littoral zone by acoustically tagged lake trout. Note differences in y-axis scales. Least squares mean (± SD) estimates of time in the littoral zone are shown. Spring data were $\log_{10}$ transformed for analysis.
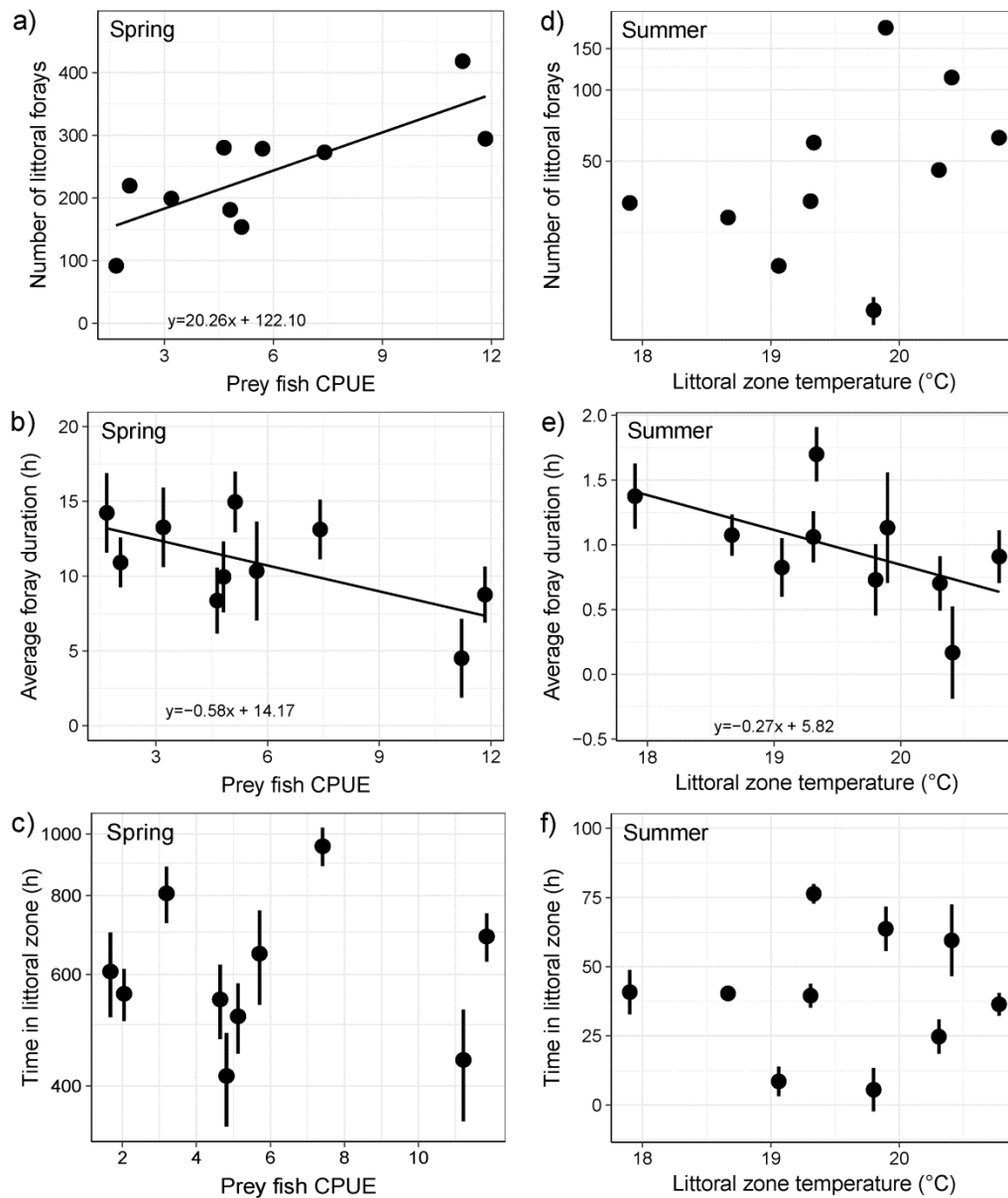
Figure 4 – Relationships between prey fish CPUE and least squares mean (± SD) spring littoral habitat use (a-c) and between mean summer littoral zone water temperatures and least square mean estimates (± SD) of summer littoral habitat use (d-f). Habitat use measures include the number of littoral forays (*n* = 10) (a, d), average littoral foray duration (*n* = 10) (b, e), and total time spent within the littoral zone (*n* = 10) (C and F). Note that error bars are very small in a, d.
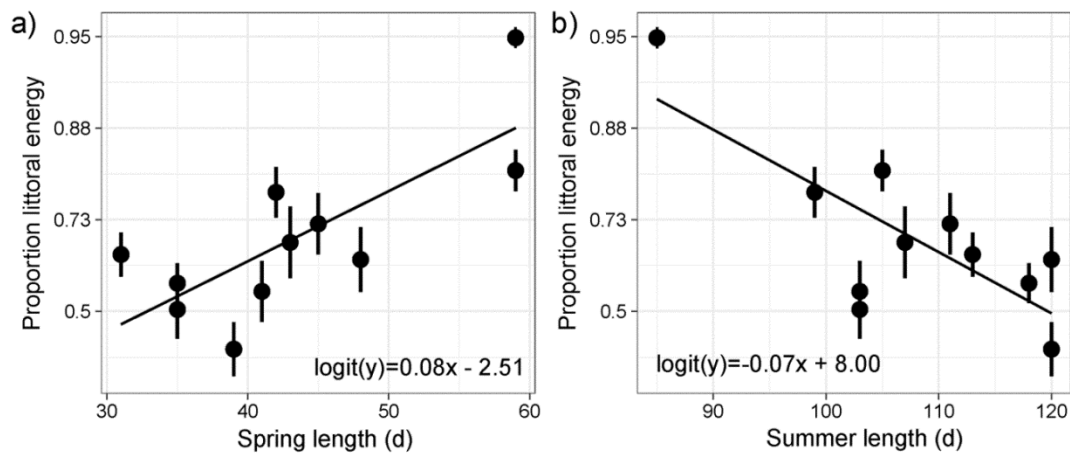
Figure 5 – Relationships of mean estimates (± SD) of littoral energy use (logit-transformed; *n* = 11) to the number of (a) spring and (b) summer days.
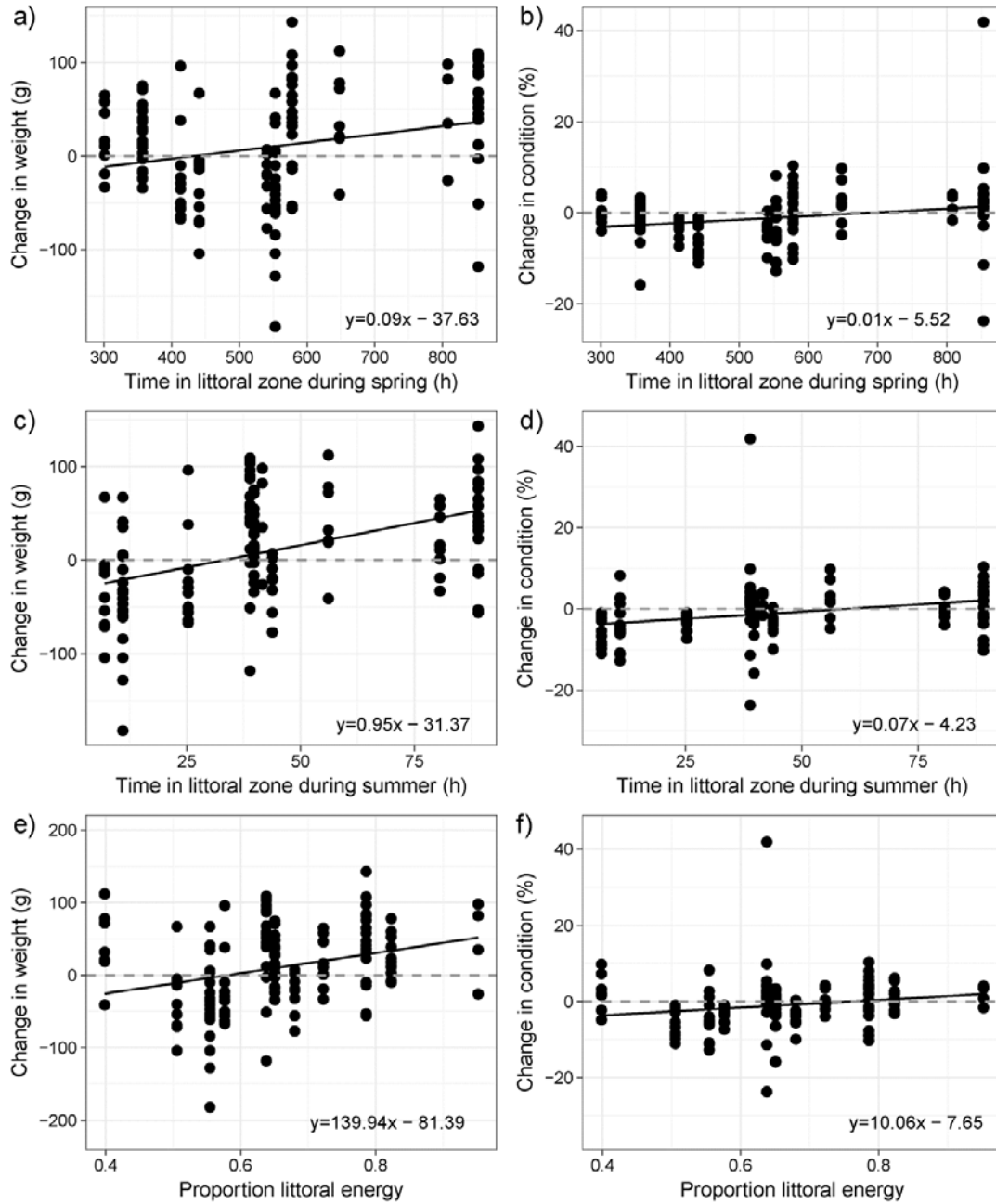
Figure 6 – Annual changes in the weight and condition of individual lake trout captured in consecutive years as a function of spring littoral habitat use (a, b) (*n* = 129), summer littoral habitat (c, d) (*n* = 129), and littoral energy use (e, f) (*n* = 141). The gray dashed lines indicate zero.

Preparation of telemetry data

Prior to analysis we filtered raw telemetry data to remove dead fish, malfunctioned tags, detections

outside the depth range of the lake, and multiple/ false detections. Because transmitters were

implanted during spring, data from the year a fish was tagged were excluded to avoid potential effects

of tagging on behaviour (Rogers and White 2007). Only fish that had data for an entire year from their

date of tagging were included in the final analyses. Because the two types of telemetry transmitters

used over the course of this 11-year study differed in how frequently they transmitted coded signals (i.e.

"pings") (V16: 15-64 s, V13: 120-300 s; Table S1). Both transmitter types recorded pressure, which was

converted to an instantaneous depth, and emitted this information, along with individual fish

identification, at random intervals within a prescribed period. When a transmission is detected by a

receiver it is given a time stamp. The V16 transmitters were implanted in spring 2002 and were active

between 1-4 years (Table S2). In spring 2005 we began using V13 transmitters and continued so for the

duration of the study (Table S2). Because V16 transmitters emitted pings about five times more

frequently than V13 transmitters, on average, the probability that a V16 transmitter would ping and be

detected during a quick foray by lake trout into the littoral zone was, by chance, greater than that of the

slower-pinging V13 transmitters. A difference in the probability of detecting a fish in the littoral zone

because of transmitter type would bias among-year comparisons of telemetry data in this 11-year

record. Therefore, to remove any potential bias we needed to "thin" detection data of fish implanted

with V16 transmitters so that their detection frequencies were comparable to those of the V13

transmitters. To achieve this, we removed detections from V16 data with intervals (i.e. time difference

between subsequent detections of that transmitter) that were less than the minimum ping frequency of

V13 transmitters (122.22 s; Table S1). To thin V16 data we used a function written in the R statistical

computing package that calculated the transmission intervals for all detections for each fish in a given

year, and then removed the first (chronologically) detection that had a transmission interval less than a

set time 122.22 s. This process was repeated until the new dataset contained only detections with

intervals less than 122.22 s.

To test if increasing minimum ping frequencies resulted in underestimates of littoral habitat use,

we used data collected in 2003 and 2004 from lake trout implanted with V16 transmitters, previously

reported as a "warm" and "cool" year (Plumb and Blanchfield 2009), for comparison of a range of littoral

usage. First, all dead fish/transmitters and multiple detections (where the same ping was detected by

multiple receivers, only the first detection was kept) were removed. Next, we created four separate V16

detection datasets with varying minimum ping frequencies for each fish/year of data (i.e. a fish with

data for both 2003 and 2004 would have eight separate detection datasets). The four datasets for each

fish/year included: (1) detection data that was not thinned (minimum ping frequency of the V16

transmitters - 17 s) and detection data that was thinned to minimum ping frequencies of (2) 52 s, (3) 87

s, and (4) 122.22 s, where 52 s and 87 s represent mid-points of the minimum ping frequencies of raw

V16 (17 s) and V13 (122.22 s) transmitters. Having multiple detection datasets with differing minimum

ping frequencies allowed us to determine if our estimates of the number of forays into, and total time

spent in the littoral zone by lake trout each year were altered by the minimum ping frequency of the

transmitters used and apply corrections as needed. Datasets were then divided into spring and summer,

based on the same criteria used in the paper. Hypotheses were tested separately for each season using

linear mixed effects models (LMM) with individual fish treated as random intercepts to account for

repeated measures, and minimum ping frequency treated as a continuous fixed factor (62). Assumptions

of LMM were tested using q-q plots, boxplots, and scatter plots of normalized residuals (62, 63). Where

necessary, data transformations were used to meet assumptions and are provided in the Results.

Results

Number of littoral forays

The numbers of littoral forays in both spring and summer were log_{10} transformed to meet assumptions of LMM. For spring data, we found that the estimated number of littoral forays decreased linearly as minimum ping frequencies increased (Minimum ping frequency: $F_{[1, 54]}$ = 5.34, P = 0.02). The slopes (Minimum ping frequency x Year: $F_{[1, 52]}$ = 0.28, P = 0.60) and intercepts (Year: $F_{[1, 53]}$ = 0.52, P = 0.47) of the relationship between the number of littoral forays and minimum ping frequency did not differ between years (Fig. 4a). Similarly, for summer data, we also found that the estimated number of forays decreased linearly as minimum ping frequencies lengthened (Minimum ping frequency: $F_{[1, 46]}$ = 4.48, P = 0.03). The slopes (Minimum ping frequency x Year: $F_{[1, 44]}$ = 1.89, P = 0.18) and intercepts (Year: $F_{[1, 45]}$ = 0.01, P = 0.96) of the relationship between the number of littoral forays and minimum ping frequency did not differ between years (Fig. 4b). The spring and summer analyses supported our hypothesis that when transmitters pinged more often they had a higher probability of being detected while a fish was in the littoral zone. However, for fall, we did not find any effect of minimum ping frequency (Minimum ping frequency: $F_{[1, 26]}$ = 1.53, P = 0.23), year (Year: $F_{[1,28]}$ = 0.02 P = 0.90), or their interaction (Minimum ping frequency x Year: $F_{[1,28]}$ = 0.01, P = 0.93) on the estimated number of littoral forays.

To determine the degree to which the number of forays was underestimated by increasing minimum ping frequencies during spring and summer we used the models described in the paragraph above to predict the average number of littoral forays that would be detected at minimum ping frequencies of 17, 52, 87, and 122.22 s. Assuming that a minimum ping frequency of 0 (model intercept) meant that a transmitter was continuously pinging, we calculated the percent difference between the modelled number of littoral forays of minimum ping frequencies of 17 s, 52 s, 87 s, and 122.22 s with that of the intercept (Table S3). Most important to our study, we found that a minimum ping frequency

of 122.22 s (that of V13 transmitters) underestimated the number of forays in spring by ≈ 63% and in

summer by 86 %. Therefore, we adjusted our estimates of the number of spring and summer littoral

forays based on tags with minimum ping frequencies of 122.22 s by 63 % and 86 %, respectively.

Time spent in the littoral zone

The total time spent within the littoral zone each spring and summer were square root transformed

prior to analysis to meet assumptions of LMM. For spring, we found that neither the interaction

between minimum ping frequency and year (Minimum ping frequency x Year: $F_{[1, 52]}$ = 0.10, P = 0.75), nor

minimum ping frequency alone (Minimum ping frequency: $F_{[1, 53]}$ = 0.06, P = 0.80), influenced our

estimates of time spent in the littoral zone. We did, however, find that estimates of littoral zone use

differed between years (Year: $F_{[1, 54]}$ = 58.84, P < 0.001; Fig. S2). Similarly, for summer, we found that

neither the interaction between minimum ping frequency and year (Minimum ping frequency x Year: $F_{[1, 44]}$ = 2.36, P = 0.13), nor minimum ping frequency alone (Minimum ping frequency: $F_{[1, 45]}$ = 1.02, P =

0.32), influenced our estimates of time spent in the littoral zone. We did, however, find that estimates

of littoral zone use differed between years (Year: $F_{[1, 46]}$ = 17.76, P < 0.001; Fig. S2). For fall, we found that

the interaction between minimum ping frequency and year (Minimum ping frequency x Year: $F_{[1, 27]}$ =

1.28, P = 0.27), year (Year: $F_{[1, 29]}$ = 0.01, P = 0.94), and minimum ping frequency (Minimum ping

frequency: $F_{[1, 29]}$ = 1.37, P = 0.25), all had no effect on our estimates of time spent in the littoral zone

(Fig. S2). The fact that estimates of time spent in the littoral zone with a minimum ping frequency of 17 s

(which is quite rapid) did not differ compared with those at 122.22 s provides confidence that our

estimates using minimum ping frequencies of 122.22 s.

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Table S1 – Comparison of transmitter type specifications used in the study. Ping frequency is how often a transmitter emits a signal with the transmitter identification number and associated depth of the fish encoded for receivers to detect. Burst duration is how long the encoded pings take to emit. Minimum ping frequency is therefore the shortest possible ping frequency plus the minimum burst frequency.

Type	Weight (g)	Length (mm)	Mean Ping Frequency (s)	Ping Frequency Range (s)	Mean Burst Duration (s)	Burst Duration Range (s)	Minimum Ping Frequency (s)
V16P	12.6	80.0	40.5	15-64	2.80	2.00-4.60	17.00
V13P	6.00	33.0	210.0	120-300	3.54	2.22-4.02	122.22

Table S2 – Biological characteristics and data collection details of the 41 lake trout implanted with acoustic transmitters and monitored during the study period (2003-2013). Date end is the date that the transmitter or fish was deemed dead, and data on or after this date was not used. Alive indicated the fish was alive at the end of the final study year (fall 2013).

Tag ID	Fork length (mm)	Weight (g)	Date implanted	Date end	Tag Type
11.0001	444	1000	2002-05-14	2005-04-29	V16P-4L
20.0001	439	916	2002-05-14	2004-08-23	V16P-4L
18.0001	427	825	2002-05-16	2005-07-07	V16P-4L
19.0001	480	1331	2002-05-16	2005-05-23	V16P-4L
12.0001	440	970	2002-05-21	2004-06-14	V16P-4L
13.0001	440	883	2002-05-21	2003-07-24	V16P-4L
14.0001	446	1056	2002-05-22	2005-07-02	V16P-4L
15.0001	443	894	2002-05-22	2003-07-18	V16P-4L
16.0001	462	1137	2002-05-22	2005-05-04	V16P-4L
129.001	394	700	2005-05-14	2005-09-27	V13P-1L
130.001	427	898	2005-05-14	2009-06-28	V13P-1L
131.001	427	759	2005-05-14	2010-05-31	V13P-1L
132.001	380	653	2005-05-14	2006-07-13	V13P-1L
133.001	417	822	2005-05-14	2009-11-14	V13P-1L
136.001	430	871	2005-05-14	2005-09-20	V13P-1L
157.001	418	816	2006-05-10	2008-06-25	V13P-1L
158.001	448	905	2006-05-10	2009-02-16	V13P-1L
159.001	408	858	2006-05-10	alive	V13P-1L
160.001	420	767	2006-05-10	2008-10-22	V13P-1L
161.001	399	789	2006-05-11	alive	V13P-1L
202.001	388	625	2007-05-10	2010-11-27	V13P-1L
203.001	448	998	2007-05-10	2010-11-28	V13P-1L
204.001	450	809	2007-05-10	2010-11-27	V13P-1L
219.001	419	746	2008-05-13	2012-01-13	V13P-1L
223.001	435	829	2008-05-13	2008-10-30	V13P-1L
224.001	429	829	2008-05-13	2012-01-12	V13P-1L
225.001	421	794	2008-05-13	2010-10-23	V13P-1L
226.001	465	1029	2008-05-13	2012-01-13	V13P-1L
227.001	459	952	2008-05-13	2011-05-11	V13P-1L
228.001	445	925	2008-05-13	2009-05-26	V13P-1L
244.001	400	701	2009-05-11	2013-01-10	V13P-1L
250.001	501	1018	2009-05-11	2009-08-17	V13P-1L
1.003	430	811	2011-05-20	alive	V13P-1L
2.003	412	773	2011-05-20	alive	V13P-1L
3.003	422	884	2011-05-20	2011-11-03	V13P-1L
4.003	401	733	2011-05-20	alive	V13P-1L

5.002	396	727	2011-05-20	alive	V13P-1L
227.002	426	879	2011-05-24	2012-01-26	V13P-1L
14.003	430	806	2012-05-15	alive	V13P-1L
15.003	444	959	2012-05-15	alive	V13P-1L
16.003	419	785	2012-05-15	2012-09-30	V13P-1L

Table S3 – The extent to which the number littoral forays by acoustically-tagged lake trout during spring and summer were underestimated as a result of transmitter minimum ping frequency. Differences were calculated using the slope estimate of the model in Fig. S1, and the percent underestimate were calculated using the estimated change in the number of forays at each minimum ping frequency relative to the intercept. For raw V16 data, only multiple detections were removed (i.e. successive detections with timestamp differences < 17 s). For thinned data, all detections with timestamps less than 52 s, 87 s, or 122.22 s were removed. Underestimates for fall are not provided as minimum ping frequency did not influence the number of forays estimated during this season.

Data type	Minimum ping frequency (s)	Underestimate of littoral forays (%)	
		Spring	Summer
Intercept	0.00	0	0
Raw V16	17.00	12	22
Thinned	52.00	33	54
Thinned	87.00	50	74
Thinned	122.22	63	86
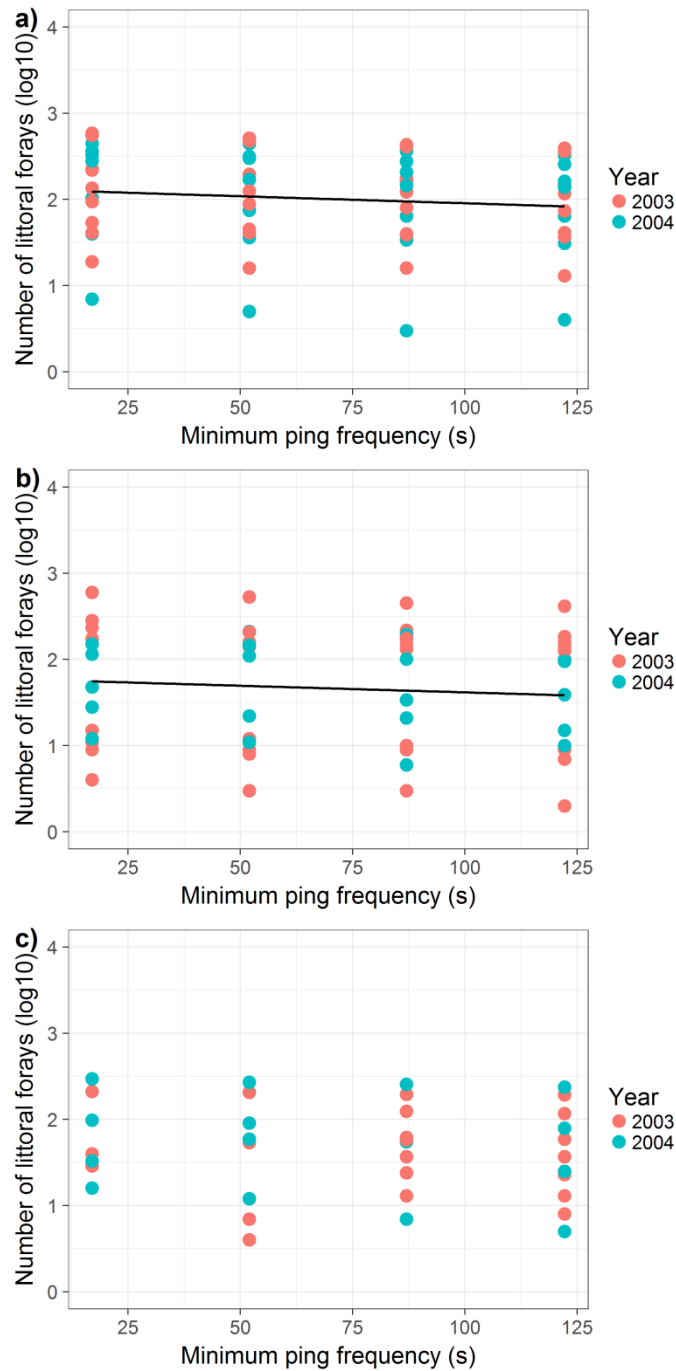
Figure S1 – Relationship between minimum ping frequency and estimates of the number of forays by individual lake trout into the littoral zone of L373 during the (a) spring (*n* = 54), (b) summer (*n* = 46), and (c) fall (*n* = 36) periods of 2003 and 2004. Points represent estimates for individual fish in each year at each minimum ping frequency. The slope of the relationship between minimum ping frequency and corresponding estimates of the number of littoral forays did not differ by year for either spring or summer and neither did estimates of the mean number of littoral forays also did not differ by year for either season. Best fit equation in (a): log(y) = -0.0016x + 2.13 and (b) log(y) = -0.0027x + 1.87, where x is minimum ping frequency, and y is estimate of the number of littoral forays. For fall, none of minimum ping frequency, year, or their interaction influenced the number of littoral forays estimated.
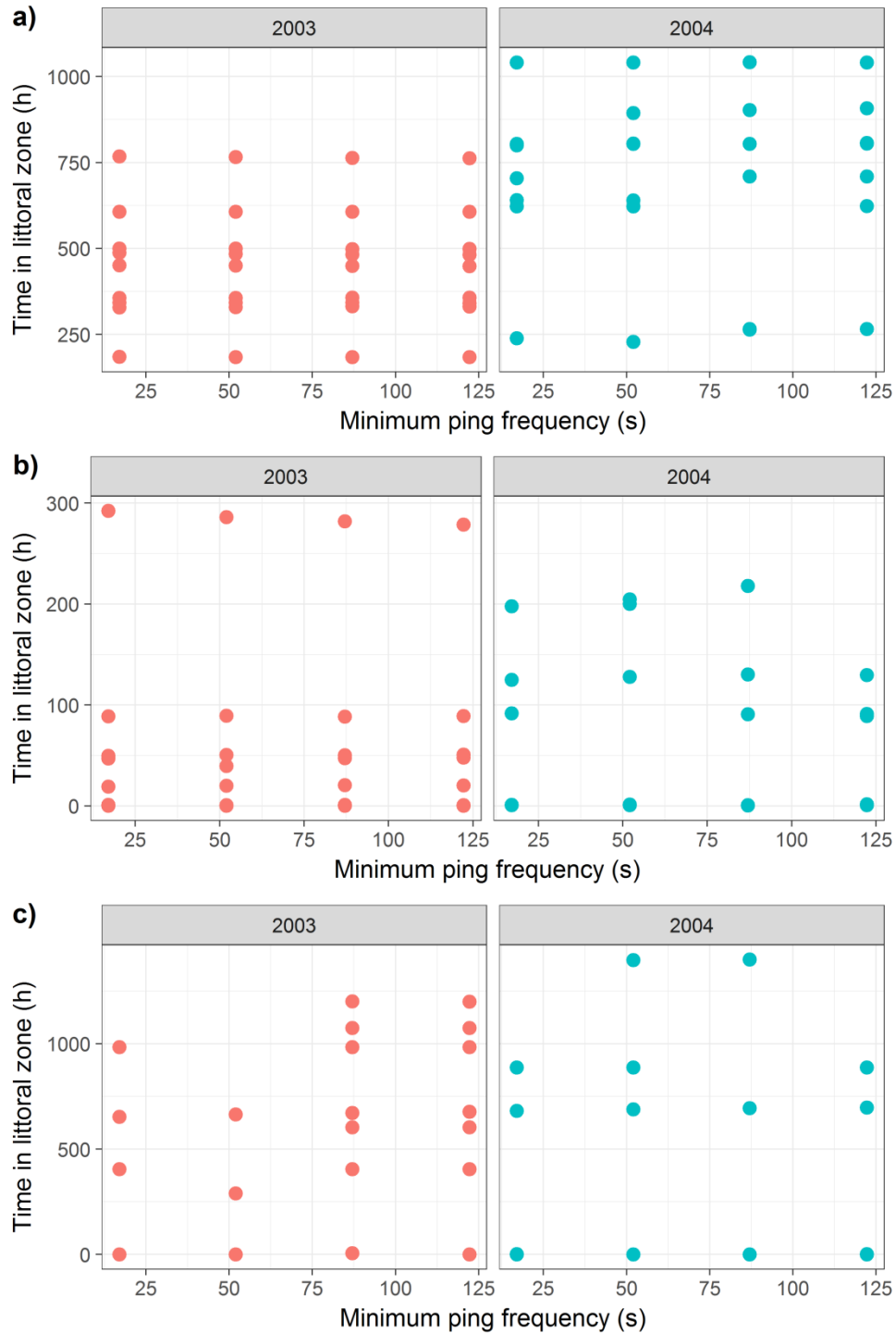
Figure S2 – The amount of time (h) spent in the littoral zone by individual lake trout implanted with acoustic transmitters in L373 during the (a) spring, (b) summer, and (c) fall periods of 2003 (n = 20) and 2004 (n = 16) under various minimum ping frequencies. Estimates of the time spent in the littoral zone were not influenced by the minimum ping frequency of transmitters for any season, but did differ by year for spring and summer, but not fall.

CHAPTER 3

Changes in the growth and size structure of a cold-water fish population during a period of warming

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Contributions of Authors: All data in this chapter were collected as part of the long-term monitoring program at the Experimental Lakes Area. I analyzed all data and wrote the manuscript. P.J.B. and M.D.R. provided insight into analyses and provided comments and edits.

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Abstract

Declines in the adult body sizes of ectotherms has been proclaimed as the third universal response to climate change, but the mechanisms behind this phenomenon are not well known, especially for fishes. Using 28 years of monitoring data from a pristine small Boreal Shield lake, we determined if an unexploited population of the cold-water fish, lake trout (*Salvelinus namaycush*), underwent changes in age- and size-structure during a period when air temperatures rose by ≈ 1 °C. We also performed bioenergetics simulations driven by empirical data on changing seasonality to determine the mechanisms behind any observed changes in body size. Over the study period, the growth of immature (age 3-4) lake trout increased, while the size-at-age of mature (age 10-11) fish, and maximum size of the population decreased. We also found evidence that the age-at-maturity of the population decreased by two years (from age 6 to age 4) and that the body condition of both immature and mature lake trout decreased over this time. The number of adults in the population increased over the study, while biomass did not change. As a result, the adult population became comprised of greater number of smaller, skinnier, younger individuals over time. Over this same period, the relative abundance or mean size of the prey fish population remained unchanged. Bioenergetics simulations that included declining age-at-maturity and expected shifts in diet and temperature occupancy most closely matched empirical data. Overall our results suggest that impacts of warming resulted in a shift towards faster life histories (i.e. rapid early growth, earlier maturation, smaller adult sizes, and decreased survival).

Introduction

Rising air temperatures experienced over the past century have had widespread impacts on biodiversity. The most recognized biological responses to warming have been shifts in species distributions toward the poles (Perry et al. 2005) and higher elevations (Chen et al. 2011), and changes in phenology, such as advancements in the timing of spring reproductive events (Stenseth and Mysterud 2002, Walther et al. 2002, Parmesan and Yohe 2003). More recently, widespread reports of declines in mean body size across a variety of species (Daufresne et al. 2009, Gardner et al. 2011, Sheridan and Bickford 2011) have prompted researchers to suggest these phenomena may be a third universal response to warming (Gardner et al. 2011); however, the mechanisms causing these trends are not well understood (Ohlberger 2013). Given that body size affects nearly all biological properties (Peters 1983, Schmidt-Nielsen 1984) and influences food web dynamics (Petchey et al. 2008, McCann and Rooney 2009), a more thorough understanding of the causes of warming-induced declines in mean body size declines is sorely needed.

Temperature-related reductions in animal body size have been observed in both endotherms and ectotherms (Ashton et al. 2000, Yom-Tov and Geffen 2011, Gardner et al. 2011, Sheridan and Bickford 2011), but the latter are thought to be especially susceptible to future warming. This is because the body temperatures and consequently the metabolic rates of ectotherms track that of their ambient environment (Fry 1947, Brett and Groves 1979). The direct impacts of warming on ectotherm body size generally follow the temperature-size rule (TSR), which describes an individual's phenotypic response to warming throughout ontogeny (Atkinson 1994). The TSR predicts that warmer temperatures should cause ectotherms to have a higher early growth rate (somatic growth), but smaller maximum adult body size (Atkinson 1994, Van der Have and De Jong 1996, Angilletta et al. 2004, Kingsolver and Huey 2008). Therefore, the consequence of the TSR is a shift in size-at-age, and the observed changes in body size of an ectotherm would depend on what stage of ontogeny is examined (Ohlberger 2013). Although support

for the TSR has been well-documented across a wide range of taxa, the mechanisms behind this phenomenon are still under debate (Atkinson et al. 2006, Lefevre et al. 2017, Lefevre et al. 2018, Pauly and Cheung 2018). In fact, some studies have suggested that there may not be a single mechanism, and that the TSR could be a result of proximate adaptations through different causes in different taxa (Angilletta and Dunham 2003, Ghosh et al. 2013).

For ectotherms that exhibit indeterminate growth, including most fish species, maximum adult body size is a balance between energy intake and metabolic demands, where net energy is allocated to growth (somatic and reproductive). Fish accumulate somatic tissue rapidly during early life; however, following sexual maturation, somatic growth slows due to energy allocation to growth of reproductive tissue and increased cost of base metabolism (Lester et al. 2004). Therefore, post-maturation somatic growth requires a surplus of energy over that necessary for metabolism and reproduction. The growth performance of fish as a function of temperature follows a right-tilted bell-curve, whereby growth at cold temperatures is low and increases with temperature up to an optimum and then rapidly declines as the thermal maximum for growth is exceeded due to increased metabolic demands (Fry 1947, Jobling 1997, Pörtner and Farrell 2008). Therefore, it would be expected that increases in lake water temperatures should have impacts on the growth of fish, especially cold-adapted species.

There have only been a small number of empirical studies that have documented declines in the body size of wild fish populations in a manner consistent with the TSR. Baudron et al. (2014) found that six of eight commercial fish species studied in the North Sea exhibited declines in maximum body size by an average of 16 %, over a 40-year period where water temperatures increased by 1-2 ˚C. Similarly, Daufresne et al. (2009) showed evidence for reductions in the mean size and size-at-age of several marine and freshwater fish species sampled over periods ranging from 14-31 years. Cheung et al. (2013) used a modelling approach to predict that marine fish species would become 14-24 % smaller by 2050 due to warming water temperatures. The modelling employed by Cheung et al. (2013) assumed that

reductions in fish growth and maximum body size were attributed to the inability of the gills to meet

increasing whole-body oxygen demand of fish experiencing warming, known as the gill-oxygen limitation

(GOL) hypothesis (Pauly 2010). The results of Cheung et al. (2013) were used to explain empirical

observations in Baudron et al. (2014) and to underpin expectations that warming will drive evolution of

smaller body sizes in fish (Waples and Audzijonyte 2016). Recently, however, the physiological

underpinnings of the GOL hypothesis have been called into question (Lefevre et al. 2017), and this

physiological explanation for shrinking fish body size remains a contentious topic (Lefevre et al. 2018,

Pauly and Cheung 2018).

A key assumption of mechanisms describing the direct impacts of warming on fish body size is

that fish experience warmer water temperatures. Indeed, recent studies have demonstrated fish can

rapidly alter their habitat use in response to changing water temperatures (Goyer et al. 2014, Freitas et

al. 2015a, Freitas et al. 2015b, Aspillaga et al. 2017, Guzzo et al. 2017). These temperature-related shifts

in habitat use can have impacts on growth through changes in prey access (Guzzo et al. 2017), but this

capacity to adjust behaviour to avoid unfavourable temperatures suggests that given the availability of

refuge habitat, mobile fish may not actually experience warmer water temperatures with climate

change. Rather, changes in phenology, especially in temperate regions, may instead increase the

cumulative exposure of fish to temperature above a certain threshold (i.e. degree-days) and in turn, the

mean annual temperature experienced by fish, but not necessarily the maximum temperature

experienced (Goyer et al. 2014, Guzzo et al. 2017). This potential lengthening of growing season is like

latitudinal clines in temperature, over which fish growth rates and maximum body sizes have commonly

been found to vary (Belk and Houston 2002, Heibo et al. 2005, Rypel 2014, Weber et al. 2015). With

increasing latitude, fish typically exhibit slower growth, mature later, live longer, and achieve larger

maximum sizes (Rypel 2014, Weber et al. 2015). Therefore, if warming has similar impacts on fish body

size as latitude, we would expect that warming would cause cold-water fish populations to have "faster"

life-histories (Waples and Audzijonyte 2016) characterized by greater early growth, earlier maturation, and reduced maximum body sizes and life-spans (Pauly 1980, Atkinson 1994, McDermid et al. 2010, Rypel 2014).

Cold-water fish populations that inhabit freshwater lakes are particularly useful for understanding warming-related impacts on fish body size because the option for fish to emigrate is often limited or removed, forcing resident fish to respond to changes in thermal habitat through physiology or behaviour, or a combination of the two. One such fish is the predatory lake trout (*Salvelinus namaycush*), a species whose native range encompasses oligotrophic lakes of northern North America (Martin and Olver 1980). Lake trout require cold-water (≤ 15 °C) for optimal metabolic function (Martin and Olver 1980, Ryan and Marshall 1994, Evans 2007) making it a suitable species for studying the effects of warming in freshwater lakes. Lake trout populations are especially concentrated near the southern extent of its geographic distribution within the Boreal Shield ecozone, where they typically inhabit small (75 % of lakes < 500 ha, median size 169 ha) thermally-stratifying lakes (Gunn and Pitblado 2004). These small Boreal Shield lakes have been found to respond to increases in air temperatures experienced over the past half-century through increases in summer surface water temperatures and shifts in phenology that include reductions in duration of ice-cover (i.e. winter) and longer spring periods (Keller 2007, Guzzo and Blanchfield 2017). In response to these shifts in phenology, lake trout have been found to adjust their behaviour to avoid water temperatures exceeding 15 ˚C, which has implications to their diet and growth (Plumb and Blanchfield 2009, Guzzo et al. 2017). Moreover, lake trout populations are known to exhibit plasticity in body size with environmental factors, with maximum body size increasing with latitude (Shuter et al. 1998, McDermid et al. 2010, Rypel 2014). Therefore, it would be expected that changes in lake trout growth in Boreal Shield lakes over the past half-century should reflect shifts in temperature-dependant phenology.

The objective of this study was to test the hypothesis that because of the direct impacts of temperature on fish growth, an unexploited lake trout population should have undergone changes in growth and size-structure consistent with the TSR and faster life-histories during a period of warming. We predicted that due to longer growing seasons, lake trout should grow faster at younger ages, mature earlier but achieve a reduced maximum size. We also tested the prediction that reductions in the maximum size of predatory fish is cause by bottom-up scaling of shrinking prey size. To test these predictions, we used 28 years of monitoring data from a lake trout population located in a region of the Boreal Shield where annual air temperatures increased ≈ 2 °C since 1970. The explicit objectives of the study were to: (1) use long-term mark-recapture data to quantify changes in the mean size and age, maximum size, growth, condition, and life-history and population characteristics of lake trout; (2) relate changes in the lake trout population to variations in prey density and size; (3) examine changes in lake trout abundance and biomass to test for potential impact of density effects on growth; and (4) use existing bioenergetic models with diets, water temperature, and age-at-maturity informed by empirical data from objectives 1-3, to simulate growth and consumption of lake trout in the study lake to determine mechanisms leading to changes in lake trout growth.

Methods

Study site

We used long-term monitoring data collected within the IISD-Experimental Lakes Area (IISD-ELA), located in northwestern Ontario, Canada (49˚40'N, 93˚44'W). The IISD-ELA is a set of 58 small Boreal Shield lakes and their watersheds set aside for conducting aquatic research (Blanchfield et al. 2009). Our study system was Lake 373 (L373), a long-term reference lake used to monitor natural variation that is closed to angling. L373 is a small (surface area 27.3 ha, maximum depth 20.8 m), single basin lake that contains a native, resident, self-sustaining lake trout population. In addition to lake trout, the fish

community of L373 consists of northern redbelly dace (*Phoxinus eos*), finescale dace (*P. neogaeus*), pearl dace (*Margariscus margarita*), slimy sculpin (*Cottus cognatus*), and white sucker (*Catostomus commersonii*). The lake also contains the freshwater shrimp (*Mysis diluviana)* and various zooplankton and benthic invertebrate species.

Climate and lake temperatures

Daily air temperature and precipitation data have been collected at the Environment and Climate Change Canada Rawson Lake weather station located within the IISD-ELA since 1969. We used these meteorological data to calculate mean annual air temperature for each study year. Annual dates of winter ice-formation and break-up (hereafter ice-on and ice-off dates, respectively) were monitored at Rawson Lake (also known as Lake 239, surface area 54 ha) and were assumed to be the same for L373, as the lakes are relatively similar in size and located within ≈ 10 km from one another.

Water temperatures in L373 were monitored every 2-4 weeks during the open-water seasons of 1986-2013. Because lake trout sampled in the initial years of the study would have lived through years previous, we also used water temperature data from nearby Lake 239 to extend our water temperature dataset for L373 back to 1970 (see among-lake comparison below). Water temperatures were measured using a handheld probe at 1 m depth intervals from the lake surface to bottom. We used this temperature profile data to estimate the mean daily temperatures of the littoral zone (depths < 6 m; Sandstrom et al. 2013), which along with the presence or absence of ice-cover was used to divide each year into four seasons (Fig. 1a) (Guzzo et al. 2017). We used mean littoral zone temperatures instead of surface temperatures (e.g. Guzzo and Blanchfield 2017) to delineate seasons because the behaviour, diet, and growth of lake trout in L373 were found to closely follow this categorization (Guzzo et al. 2017). The period of ice-cover was denoted "winter". The period between ice-off and the date before the mean littoral zone temperature exceeded 15 ˚C was denoted "spring". The period starting when

mean littoral zone temperature reached and maintained 15 ˚C was denoted "summer". "Fall" was the period between when lakes cooled to ≤ 15 ˚C until ice-on. We chose 15 °C to define seasonal transitions during the open-water season because this temperature has been shown to best describe the upper limit of daily depth distribution occupied by lake trout in L373 (Plumb and Blanchfield 2009, Guzzo et al. 2017) and because the aerobic scope of lake trout declines at water temperatures > 15 °C (Evans 2007, Kelly et al. 2014). We calculated the season lengths using both the L373 and Lake 239 datasets and compared overlapping years (1986-2013) and found that the estimates were strongly correlated using Pearson's correlations (Spring: n = 28, r = 0.82, P < 0.01; Summer: n = 28, r = 0.76, P < 0.01; Fall: n = 28, r = 0.91, P < 0.01). Therefore, we assumed that the season length estimates for Lake 239 for 1970-1985 would represent conditions in L373 during this period.

Fish population monitoring

The lake trout and prey fish communities in L373 were examined bi-annually using standardized collection methods as part of the long-term fish monitoring program at the IISD-ELA during 1986-2013. Fish were collected using the same methods for most of the 28 years of monitoring. Fish capture included catch-and-release methods with Beamish-style trap nets (spring and fall; lake trout and prey fish) and short (< 30 min) evening small-mesh gill net sets on spawning shoals (fall; lake trout only) (Mills et al. 1987, 2000, 2002a, 2002b).

The weights (g) and fork lengths (mm) of each lake trout captured were recorded and tag numbers were recorded from previously captured fish. Age-at-capture was determined by adding years to previously estimated ages at first capture, which were estimated from pectoral fin-rays by a single reader for the entire study period (Mills and Beamish 1980, Mills et al. 2002b, Mills and Chalanchuk 2004). Fish not previously captured had the leading fin-ray of the pectoral fin removed for ageing and were tagged with a PIT, Carlin-style sew on or VIE tags for future identification (Mills et al. 1987).

Together size- and age-at-capture data allowed for an estimation of fork length-at-age and weight-at-age for each sampled lake trout. The body condition of lake trout was estimated as a percentage of standard weight specific for lake trout (i.e. relative weight), with only fish with total lengths > 280 mm included in the calculation (Piccolo et al. 1993). We present the mean fork length, weight, and relative weight of all fish captured each fall during sampling. Additionally, we present the mean length-, weight- and relative weight-at-age for lake trout aged 3 and 4 and aged 10 and 11, to show the differential changes in growth among younger immature and older mature fish, respectively. We used these groups of ages (i.e. aged 3 and 4 and aged 10 and 11) to ensure we achieved sufficient sample sizes for each year. To examine changes in size and age makeup of the population over time we grouped the data into five-year time periods (to obtain sufficient data) that represent the start (1986-1990), middle (1996-2000), and end (2009-2013) of the study to examine shifts in the size and age distributions. Annual age distributions can be found in Fig. S3.

We calculated point estimates of asymptotic (i.e. maximum) fork lengths ($L\infty$) and weights ($W\infty$) of the L373 lake trout population at the start (1986-1990) and end (2009-2013) of the study using the von Bertalanffy growth model (Ricker 1975): $L(t) = L\infty(1 - e^{K(t-t0)})$ and $W(t) = W\infty\big(1 - e^{K(t-t0)}\big)^3$, where $L(t)$ and $W(t)$ are the fork length (mm) and weight (g) at age t (years), $L\infty$ and $W\infty$ are the asymptotic fork length and weight, K is the growth coefficient, and t_0 is the theoretical age when the fish would have had a fork length or weight of zero, which was assumed to be zero. Point estimates of the parameter omega (ω), which is a measure of early growth rates (ω Fork length: mm year^{-1}; ω Weight: g year^{-1}), was calculated as the product of $L\infty$ or $W\infty$ and K (Gallucci and Quinn 1979). The von Bertalanffy growth curves were fit using data only for lake trout aged 1-15 captured in the first and last five years of the study to prevent inclusion of the same fish in each fit. These growth curves provided a snapshot of how the key life history traits $L\infty$, $W\infty$, and ω differed near the start and end of the study period. We

also calculated the upper 5th percentile of lake trout fork lengths and weights captured on spawning

shoals each fall as an additional measure of maximum body size.

To obtain a proxy for age- and weight-at-maturity we calculated the lower 5th percentile of lake

trout ages and weights captured on the spawning shoals during fall sampling each year. Prior to

calculation of the lower 5th percentile for each year we excluded fish aged < 3 years, as these fish were

unlikely to be mature based on preliminary analysis of the data.

We estimated the annual abundance of lake trout by capture-recapture techniques based on

individual fish capture histories using the POPAN formulation of the Jolly-Seber model (Jolly 1965, Seber

1965, Schwarz and Arnason 1996) in the R package *RMark* (White and Burnham 1999, Laake 2013). This

model assumed that marked and unmarked fish had equal catchability and survival, that tags were not

lost or misread, sampling is instantaneous, and that the study area does not change over the study. The

POPAN Jolly-Seber is an open model, which for our study lake meant that fish could leave the study

through death or be recruited through births. We used a fully parameterized model to provide time-

varying parameter estimates for apparent survival, catchability, and entry to the population, and used

these to derive abundance estimates. For abundance, spring and fall sampling events were treated as

separate capture events within the same year; however, to obtain annual survivorship estimates, we

assumed all spring captures (which only accounted for ≈ 7.5 % of all lake trout captured) occurred during

the subsequent fall and ran the model using only fall capture events. We then used survivorship

estimates from the fall-only model to estimate (i.e. mortality = 1 - survivorship) interval mortality for

each year. We tested for overdispersion and underdispersion in model fits using goodness of fit tests,

where variance inflation factors ($\hat{c}$) > 1 indicated overdispersion and $\hat{c}$ < indicated underdispersion

(Cooch and White 2017). Estimates of $\hat{c}$ were 1.22 and 1.16 for spring and fall and fall-only models,

respectively, indicating some overdispersion. We therefore applied a $\hat{c}$ correction to each model prior to

extracting abundance and survivorship estimates (Cooch and White 2017). Annual estimates of lake

trout biomass were calculated as the product of annual fall abundance estimates and mean weight of

fall captures, standardized by lake area.

The fork lengths (mm) of each prey fish captured during spring sampling were recorded and the

relative abundances (species combined), were estimated from trap-net captures using catch-per-unit

effort (CPUE). Annual estimates of spring CPUE were calculated by dividing the total number of prey fish

caught by the number of net days (i.e. # trap nets x # fishing days; Guzzo et al. 2014). We also calculated

mean body sizes (via fork length) of the prey fish community for each year of the study to determine if a

decline in prey fish body size occurred over time. Slimy sculpin was not included in CPUE or mean size

calculations because this species is not well sampled by the method; as they are captured in very low

numbers, their exclusions has little impact on calculations.

Bioenergetics

To determine if observed variations in seasonal phenology and age-at-maturity contributed to observed

changes in the body size of lake trout, we simulated the annual growth of lake trout in L373 during the

study period. We did this using the existing lake trout parameterization of the Wisconsin Bioenergetics

Model (Stewart et al. 1983) in the program Fish Bioenergetics 4.0 (Deslauriers et al. 2017). The

bioenergetics model is a mass-balance model based on the assumption that all food consumed (C) is

used for metabolism (R) and specific dynamic action (SDA), lost through egestion (F) and excretion (E),

or accumulated as growth (G): $C \approx R + SDA + F + E + G$, where components can be converted between

units of mass and energy. For details on equations and parameters for each component see Stewart et

al. (1983) and Deslauriers et al. (2017).

We performed three sets of bioenergetics simulations to test (a) the relative effects of age-at-

maturity and alterations in (b) habitat occupancy and (c) diet due to changes in seasonal temperature

phenology. The conditions imposed during each simulation were that mean daily temperature

occupancy was the same each day within a given season, but the length of each season varied from year to year, based on our estimation of each season length from empirical lake temperature and ice-cover data (described above). We further assumed that each prey item was similarly available for each year of the simulation as we found no changes in prey fish density over time (see Results) and that the seasonal diets and thermal occupancies were similar across years; however, because the length of seasons varied over time, so did the number of days lake trout would be exposed to different water temperatures and therefore diets (Table 1). Each simulation started with a 110 g lake trout, assumed to be age 1 (captured in fall), with an energy density of 5,510 J g wet mass^{-1} and used a theoretical start date of October 15 (the day before estimated spawning) of each year. We qualitatively estimated October 15 as the typical date of lake trout spawning using all years of fall netting data and telemetry data from L373. The lake trout energy density value was determined using bomb calorimetry of mortalities collected from L373 sporadically over the study period (n = 33, M. Guzzo, *unpublished data*).

The first simulation (Simulation 1) estimated growth and consumption of lake trout over three years, from age 1 to age 4 (Table 2). Simulation 1 was iteratively repeated starting with each study year (e.g. run 1: Fall 1986-Fall 1989; run 2: Fall 1987-Fall 1990, and so forth), to provide modelled weight-at-age 4 estimates for a fish captured in 1989 and each year following up to 2013. No reproductive losses (i.e. reproductive organ weight) were imposed during Simulation 1, as lake trout in L373 do not begin to invest into reproduction until at least age 4 (see Results), and our simulations assumed fish weights obtained in fall were prior to spawning and the loss of reproductive mass. Simulation 2 used the estimated weight for age 4 fish from Simulation 1, and estimated an additional six years of growth, from age 4 to age 10 (e.g. a fish that was age 1 in fall 1986 and was age 10 in 1995) to provide weight estimates for age 10 fish for 1995-2013 (Table 2). In Simulation 2, reproductive losses of 10 % were imposed each year, but the age at which these losses were imposed was changed to match observed reductions in age-at-maturity (see Results). We choose 10 % as the weight lost to reproduction as this

was the mean gonadosomatic index estimated (combining males and females) for lake trout based on data accumulated from mortalities collected from several IISD-ELA lakes of similar size and food web structure (Michael Rennie, *unpublished data*). For these simulations with variable age-at-maturity, we assumed lake trout that were born in 1986 and 1987 first spawned at age 6, born 1987-1998 first spawned at age 5, and those born in 2003 and onwards first spawned at age 4 (see Results). In Simulation 3, we also estimated the growth of lake trout from age 4 to age 10 assuming a constant age-at-maturity of age 6 to show how this metric influenced simulated weights (Table 2). We then compared observed weight-at-age data for age 4 and age 10 lake trout to those final weights from bioenergetics simulations.

For the simulations, we used lake water temperature data from profiles and ice-on and ice-off dates to assign a season to each day during the study period Fall 1986 through Fall 2013 (spring, summer, fall, or winter; details above). Each study day was then assigned a corresponding diet and temperature occupancy based on diet and acoustic telemetry data, respectively (Table 1; details below).

The seasonal diets of lake trout were estimated using a combination of stomach contents collected from L373 (spring, summer and fall; Guzzo et al. 2017) and literature values from lakes of similar size and food web structure to L373 (winter; Martin 1954). Mean daily temperature occupancies of lake trout were determined using 13-year means of acoustic telemetry data collected in L373 during 2003-2013. We chose to use 13-year means because telemetry data was not available for the entire study period (see SI). Input values for seasonal diets and temperature occupancies are in Table 1.

We calibrated the consumption input to the bioenergetics model using observed growth data (see SI for details) and the diet and temperature occupancy described above and found that a constant proportion of maximum consumption of 0.6435 allowed bioenergetics outputs to closely match observed weight-at-age data.

Statistics

We used Mann-Kendall tests (Mann 1945, Kendall 1955) to determine if long-term, monotonic trends

occurred in time series of annual air temperature, season lengths, and lake trout (except point estimates

of $L\infty$, $W\infty$, and ω) and forage fish data. Where Mann-Kendall tests indicated significant time-series

trends, corresponding slopes were estimated using Sen's slope (Sen 1968). Mann-Whitney tests were

used to test whether changes in the size (fork length and weight) and age distributions occurred over

time.

Results

Air and lake temperatures

Mean annual air temperatures at the study site increased by nearly 2 °C during 1970-2013, from ≈ 1.77

°C in 1970 to ≈ 3.61 °C in 2013 (Fig. 1b). In response to this increase in air temperature, seasonality in

thermal habitat of L373, based on the mean temperature of the littoral zone (< 6 m depth), changed

over time. Winters became shorter (n = 44, *tau* = -0.30, P < 0.01) and were just over two weeks shorter

in 2013 than in 1970 (Fig. 1b). The lengths of spring (n = 44, *tau* = 0.02, P = 0.88) and fall (n = 44, *tau* = -

0.002, P = 0.99) did not change over time (Fig. 1c). Shorter winters were offset by longer summers (n =

44, *tau* = 0.30, P < 0.01), which were also about two weeks longer in 2013 relative to 1970 (Fig. 1c).

Lake trout

The mean body size of lake trout captured in L373 declined over the study period (fork length: n = 28,

tau = -0.64, P < 0.01; mass: n = 28, *tau* = -0.74, P < 0.01). Mean annual fork lengths decrease by 1.8 mm

year[-1] over the study period, from ≈ 450 mm in 1986 compared to 400 mm in 2013 (Fig. 2a). Similarly,

mean weights were nearly 500 g less in 2013 (≈ 700 g) than in 1986 (≈ 1100 g), decreasing by 16.1 g year[-]

[1] over this period (Fig. 2b). These declines in body size were congruent with a decline in mean age (n =

28, *tau* = -0.42, *P* < 0.01), as lake trout captured in the latter years of the study were on average 2-3 years younger than at the start of the study (Fig. 2c). Decreases in mean size and age were, in part, due to shifts in the distributions of size (fork length: *U* = 6863, *P* < 0.01; weight: *U* = 7215, *P* < 0.01) and age (*U* = 4900, *P* < 0.04) in the population over time. Precipitous declines of the largest (fork length > 500 mm, weight > 1000 g) and oldest (age > 20 years) classes of lake trout resulted in smaller, younger fish accounting for a greater proportion of the population over time (Fig. 3). In fact, lake trout exceeding 500 mm and 1000 g were nearly absent from collections occurring during the last five years of the study (Fig. 3a, b).

Shifts in the mean annual size-at-age and relative weight-at-age of lake trout were also observed, but the direction of these changes, specifically for size-at-age, varied depending on fish age. Immature lake trout (ages 3 and 4 combined) exhibited amplified size-at-age over time as both mean fork length-at-age (*n* = 24, *tau* = 0.40, *P* < 0.01) and weight-at-age (*n* = 24, *tau* = 0.33, *P* < 0.03) for these fish increased (Fig. 4a, b). Age 3-4 lake trout averaged about 75 mm longer (increase of 2.75 mm year^{-1}) and 150 g heavier (increase of 0.75 g year^{-1}) in 2013 compared to 1986. In contrast, the relative weight of immature lake trout decreased by ≈ 40 % or 0.75 % year^{-1} over the study (*n* = 24, *tau* = -0.48, *P* < 0.01; Fig. 4c). On the other hand, mature (ages 10 and 11 combined) lake trout displayed reductions in each of fork length-at-age (*n* = 28, *tau* = -0.60, *P* < 0.01; Fig. 4d), weight-at-age (*n* = 28, *tau* = -0.68, *P* < 0.01; Fig. 4e), and relative weight (*n* = 28, *tau* = -0.40, *P* < 0.01; Fig. 4f). The average age 10-11 lake trout exhibited reductions in fork length of ≈ 50 mm or by 1.45 mm year^{-1} (450 to 400 mm), weight-at-age of ≈ 500 g or 13.15 g year^{-1} (1200 to 700 g), and relative weight of ≈ 10 % or 0.40 % year^{-1} (95 to 85 %). Similar trends in growth and condition were found for other classifications of immature (age 1-3) and mature (age 5+) lake trout in L373 (Fig. S4).

Point estimates of asymptotic fork length ($L\infty$), weight ($W\infty$) and early growth rates ($\omega_{\text{Fork length}}$ and ω_{Weight}) obtained from von Bertalanffy growth models mirrored those of size-at-age data (Fig. 5a, c).

$L\infty$ decreased from 453.1 mm (95 % CI: 446.6-460.2 mm) to 410.0 mm (95 % CI: 406.9-413.2 mm) in the

roughly two decades between the initial and final five years of the study (Fig. 5a). Over the same period,

estimates of $\omega_{Fork\ length}$ increased, from 172.2 to 228.8 mm year^{-1} (Fig. 5a). Similarly, $W\infty$ also decreased

from the first to the final five years of the study, from 1214.3 g (95 % CI: 1137.3-1307.4 g) to 755.7 g (95

% CI: 739.0-772.9 g), while estimates of ω_{Weight} increased, from 388.6 to 430.8 g year^{-1} (Fig. 5c). Annual

estimates of maximum fork lengths and weights using the upper 5th percentile of all lake trout captured

during fall decreased by 15 % and 50 %, respectively, over the course of the study (fork length: n = 28,

tau = -0.79, P < 0.01; weight: n = 28, tau = -0.81, P < 0.01; Fig. 5b, d).

In the most recent years, first time spawners were 2 years younger and ≈ 20 % smaller by

weight, but similar in fork length compared to at the start of the study. The youngest lake trout captured

on the spawning shoals, which was used as proxy for age-at-maturity, declined at a rate of -0.07 years

old year^{-1} (n = 28, tau = -0.35, P < 0.01) over the study, representing an average decrease of almost 2

years (from age 6 to age 4) (Fig. 6c). Similarly, the smallest lake trout by weight captured on spawning

shoals, declined at a rate of -6.0 g year^{-1} over time (n = 28, tau = -0.39, P < 0.01), while the smallest the

lake trout by fork length did not change over time (n = 28, tau = -0.23, P = 0.11). The weight-at-maturity

of lake trout decreased by an average of 150 g over the study, from 700 to 550 g (Fig. 6b). Together

these data indicated that lake trout began to mature at younger ages and smaller weights, but similar

lengths (i.e. lower body condition) over time. Qualitative examination of von Bertalanffy growth curves

provides additional evidence that age-at-maturity occurred at a younger age over time (Fig. 5a, c).

The abundance of lake trout in L373, though variable, increased over time from just over 200

adults in the first few years of the study up to ≈ 275 adults in the latter years of the study (n = 28, tau =

0.31, P = 0.02; Fig. 7a). Biomass of adult lake trout did not exhibit a directed trend over time (n = 28, tau

= -0.06, P = 0.65), but did vary over the study, increasing from < 6 kg ha^{-1} in 1986 to ≈ 10 kg ha^{-1} in 1995,

and then declining steadily to early levels by the end of the study (Fig. 7b). Natural mortality of lake

trout estimated from the mark-recapture model was highly variable over time and did not exhibit a

trend (n = 28, *tau* = 0.22, *P* = 0.11, often ranging between 0-25 % year^{-1} (Fig. 7c).

Prey fish

Relative abundance (CPUE) of prey fish, the preferred diet item of lake trout, was variable throughout

the study, averaging about 17 fish net^{-1} day^{-1} and exhibiting no single trend throughout the study (n = 24,

tau = -0.27, *P* = 0.08) (Fig. 8a). The mean size of prey fish, measured as fork length, did not exhibit a

single trend over time (n = 24, *tau* = 0.01, *P* = 0.94). Instead, the mean size of prey fish displayed a

hump-shape trend, increasing from a low of ≈ 40 mm in 1986 to its peak of > 75 mm in 2001 and then

decreasing back down to ≈ 40 mm in the last 7 years of the study (Fig. 8b). We also found no evidence

that any prey fish species exhibited a reduction in body size over the course of the study (pearl dace: n =

25, *tau* = 0.27, *P* = 0.08; finescale dace: n = 22, *tau* = -0.01, *P* = 0.99: northern redbelly dace: n = 23, *tau* =

-0.15, *P* = 0.32).

Bioenergetics

Simulation of growth based on a constant (but specific to each season) daily temperature occupancy and

diet makeup but varying in the length of each season (based on empirical data), indicated that an age 1

(110 g) lake trout eating at 64.35 % of its maximum consumption, could achieve a greater size-at-age 4

over time compared to at the start of the study (Simulation 1, Table 2). On average, the modelled weight

of an age 4 lake trout increased by roughly 100 g, from 1989 to 2013 (Fig. 9a). To achieve the observed

changes in growth in Lake 373, the model predicted a required 20 % increase in annual consumption,

which equated to an average increase in daily consumption of ≈ 1 g, from 4 to 5 g (Fig. 9c). As we

continued to model the growth of these age 4 fish through to age 10 assuming the same 64.35 % of

maximum consumption and an age-at-maturity that decreased from 6 to 4 years over time (Simulation

2, Table 2, Fig. 6a), we found that simulated weights of age 10 lake trout declined over time (Fig. 9b),

agreeing with observed weight-at-age data. Corresponding consumption estimates declined by ≈ 15 %

over time (Fig. 9d). In contrast, when we assumed a constant age-at-maturity of age 6 over time

(Simulation 3, Table 2), the simulated weights of age 10 lake trout increased by about 100 g over time,

despite an annual cost of reproduction (10 % mass) being imposed (Fig. S5a). These continued increases

in mass of mature lake trout when assuming a constant age-at-maturity did not match observed data

and the corresponding consumption values were likely impractical (Fig. S5b).

Discussion

We found that during a period of warming, an unexploited lake trout population exhibited clear changes

in size structure that are consistent with the TSR. Congruent with reductions in maximum adult body

size, we observed increases in juvenile body size, decreases in mean size, mean age, condition of both

juveniles and adults, as well as a loss of the oldest and largest fish. Our data suggest that the older fish

died out over time, presumably because of natural causes, but subsequent cohorts were not able to

reach the size or age of their predecessors because of changing conditions, such as reduced access to

high quality littoral prey due to changing seasonality and earlier maturation. Our bioenergetic

simulations support the idea that changing phenology, particularly shorter winters, improves the

conditions for growth of juvenile fish, and that this led to age-at-maturity decreasing by two years over

time. This earlier onset of maturation in addition to longer summers experienced over time, has

negative impacts on the growth of adult lake trout by limiting their access to littoral prey for longer

periods, and was likely the cause of reductions in maximum adult body size. Lastly, we show that during

this size-structure shift, the abundance of the population increased, while its overall biomass stayed

constant. As a result, the lake trout population is now comprised of a greater number of smaller,

skinnier, younger individuals compared to 28 years ago.

Although our mark-recapture data did not indicate a significant increase in mortality over time, those estimates did seem to increase after 2005. Moreover, we found that the mean age of the population, which is often used as an index of lifespan (Brown et al. 2004, Munch and Salinas 2009) decreased over time. Observed advances in maturation may reflect phenotypic plasticity, where early growth increases with warming due to shorter winters and in turn a longer period when optimal temperatures for growth existed each year (i.e. growing seasons). This finding of plastic maturity with warming is supported by studies that have found that maturation is linked to temperature and growth rate, rather than being set by age (Alm 1959, Policansky 1982, 1983). An alternate explanation is like that of fisheries induced evolution, whereby increased adult mortality through fishing mortality increases the fitness benefits of maturing earlier and leads to a compression of life cycles (Gadgil and Bossert 1970, Ernande et al. 2004, Olsen et al. 2004). Although our study population was not fished, results suggest that adult mortality may have increased over time, potentially due to reduced energetic efficiency at larger body sizes caused by reduced access to littoral energy with longer summers. Assuming lake trout spawned somewhere between age 4-6, only five generations of new spawners would have occurred by 2013 since monitoring began in 1986. This would be a short period for evolution for earlier maturation to occur, especially if only small (and variable) increases in mortality occurred. While rapid evolution in response to mortality is plausible, studies have suggested that the potential for actual fishing practices to cause fisheries induced evolution in wild populations may be modest (Brown et al. 2008, Hilborn and Minte-Vera 2008). Moreover, evolution for earlier maturation would depend on variation in age-at-maturity to exist among individuals within the population, which may be limited due to the small size of the lake and limited number of spawners. Lastly, results of Mills et al. (2004) suggest that juvenile recruitment in some ELA lake trout populations may be density-independent and in these populations, compensation for adult mortality occurs primarily through increased growth of juveniles,

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leading to lower age of first maturity, which further supports the idea that advances in lake trout

maturation were due to physiological plasticity.

The longer open-water period experienced over time has positive effects on the feeding and

growing conditions for lake trout in L373. Generally, longer open-water seasons extend the period when

lake water temperatures are within the optimal range for lake trout growth (10 ± 2 °C; Christie and

Regier 1988, Ryan and Marshall 1994, Evans 2007), while reducing the period when lake trout growth is

nil or negative (i.e. winter; Shuter et al. 2012). However, longer summers may have counteractive

effects on growth for adult and juvenile fish. For adults, longer summer will negatively impact growth by

restricting access to littoral prey fish for longer periods (Guzzo et al. 2017), thereby reducing growth

efficiency for this life-stage by forcing it to feed on smaller prey (i.e. *Mysis*). In contrast, longer summers

should not directly impact the ability of juvenile fish to feed on their main prey item *Mysis* (Trippel and

Beamish 1993, France and Steedman 1996), which are confined to the hypolimnion during this season

(Paterson et al. 2011). Therefore longer summers could potentially increase the capacity for growth of

juvenile lake trout, although there is the possibility that increased competition for *Mysis* between

juveniles and adults may occur during longer summer periods. Overall, the shorter winters and longer

summers will benefit the growth of juvenile lake trout. If this increased growth at immature stages leads

to earlier maturation, this added cost of reproductive investment at younger ages and reduced growth

potential due to longer summers would decrease the maximum size of adults, as found in the long-term

data.

Our bioenergetics simulations produced annual weights for immature lake trout that closely

followed the observed increases in the weight of age 4 lake trout in L373 over time. However, as we

continued to simulate the growth of age 4 lake trout through to age 10 and incorporated the observed

reduction in age-at-maturity from age 6 to age 4, we found that the simulated weights of age 10

decreased over time, also matching trends in the empirical data. In contrast, simulations for age 10 fish

that assumed a constant age-at-maturity (age 6) produced weights that increased over time. Together, these results suggest that early growth and shifts in age-at-maturation are playing a key role driving warming-induced changes in maximum body size (Charnov 1993, Waples and Audzijonyte 2016). The observed changes seen in this study of earlier maturation and reduced maximum size over a period of warming are similar to what one would expect when looking at differences in populations across latitude, where both age-at-maturity and maximum size are reduced with decreasing latitude (Rypel 2014, Weber et al. 2015). The results of our bioenergetic simulations are in line with those of Kao et al. (2015) who modelled the growth of lake trout in Lakes Huron and Michigan under base and warming scenarios. In the scenario where consumption could increase, assuming sufficient prey availability, Kao and colleagues showed that the growth efficiency of lake trout increased with warming. However, when consumption was forced to be constant in warming scenarios, the growth efficiency of young fish increased compared to base conditions, but as these fish grew their growth efficiency began to decline and were eventually lower than in base conditions. These results further support our findings that warming may be beneficial to the growth of young lake trout, but not older, larger individuals.

It is imperative to note that our simulations did not increase the actual temperatures experienced by lake trout, but only the number of days they experienced each seasonal water temperatures, which were all well below their metabolic optimum of 15 °C (Ryan and Marshall 1994, Evans 2007, Kelly et al. 2014). Although lake trout are known to make rapid forays into warm water during summer (Bergstedt et al. 2003, Morbey et al. 2006), these were likely very rapid and limited or non-existent during the hottest parts of summer (Guzzo et al. 2017). All in all, our results point to phenotypic plasticity in age-at-maturity due to increased juvenile fish growth and development rather than the inability of the gills to meet increasing whole-body oxygen demand (Pauly 2010, Pauly and Cheung 2017), as the cause of changes in maximum body size found in our study lake.

Over a period when there was the loss of the largest, most fecund, and most experienced spawners, there was an increase in abundance, while biomass stayed relatively constant. Our biomass estimates were in line with those of (Mills et al. 2004) who estimated the mean biomass of L373 population during 1986-1999 to be 7.8 kg ha^{-1}, providing confidence in our estimates. Because our study population is unexploited, these results support the idea that an ecosystem's carrying capacity for lake trout is a function of biomass. This is supported by the findings of Fry (1939), who noted that lake trout populations with smaller mean sizes were in higher abundance than those with great mean sizes. This idea of biomass-based carrying capacity makes sense from a bottom-up perspective (i.e. prey supply) because lake trout is the only top predator in the study lake and its gross consumption increases with mass (Brett 1971, Stewart et al. 1983).

Trends in prey fish densities and mean size also failed to provide explanation for reductions in adult body size found here as both metrics did not show any trend over time. Additionally, the mean size of prey fish was relatively constant over time, suggesting that bottom-up scaling, where smaller prey sizes induced by warming contribute to smaller consumer body sizes (Sheridan and Bickford 2011), was not a cause of the declines in lake trout body size in this lake. However, it is possible that increases in the number of small lake trout and longer summers experienced over time could have increased this lake trout population's consumption of *Mysis*, which could provide an explanation for reductions in *Mysis* densities observed in L373 during 2002-2008 (Paterson et al. 2011). If true, this would suggest that warming-induced shifts in coupling between littoral and pelagic lake habitats may have implications for food web stability (Post et al. 2000, Kondoh 2003, Rooney et al. 2006).

While we acknowledge our study focused on a single population, we note that data from other lakes within the IISD-ELA show similar trends. Lake trout in Lake 224, which is like L373 both biologically and physically, also showed increases in the size-at-age of immature fish and decreases in the size-at-age of mature fish during 1976-2000, when active baitfish harvest occurred. However, post-2000,

baitfish harvest stopped, and adult lake trout size rebounded to levels found in the late 1970s (Fig. S6).

Similarly, in Lake 468, which is much larger than L373 and contains the pelagic prey fish, cisco

(*Coregonus artedi*), the maximum size of lake trout captured decreased from 1981 to 2006 (Fig. S7).

Although, we chose not to focus on these lakes in the study because of various issues, including the lack

of prey water temperature data in Lake 468 and the potential impact of minnow harvest in Lake 224, the

general agreement in trends among data from L373 and Lakes 468 and 224 provides support to our

findings that adult body size of lake trout declines with warming

An additional factor that may be influencing the size-structure of the lake trout population in

L373 is the interactions among age classes over time. The age distributions of lake trout populations

often show temporal fluctuations due to sporadic recruitment. However, once a strong cohort becomes

established, it can dominate the population until it is either fished out or dies off — a phenomenon

known as the "storage effect" in marine systems (Secor, 2007, 2000; Warner and Chesson, 1985).

Therefore, it is possible that as a dominant age class establishes and moves through the population over

time, its cannibalistic and competitive interactions may alter the growth rates, sizes at maturity, and

maximum sizes of younger cohorts (De Roos and Persson, 2013). For example, there is the possibility

that as summers become longer, increased reliance on *Mysis* by adult lake trout could lower availability

of this prey item for juvenile lake trout. Assuming a strong cohort existed in the population at the start

of sampling, as this strong cohort dies out *Mysis* availability for young fish should increase resulting in

enhanced juvenile growth. However, based on the annual age distribution of the L373 lake trout

population (Fig. S3), there is no indication of a dominant age class (i.e. strong cohort) moving through

the population over time. Moreover, temporal trends in both mean size and age of lake trout in L373

(Fig. 2) suggest that cycles in size and age distributions may occur, but these are to a much lower

magnitude compared to reductions in size-at-age observed over time (Fig. 4). A more rigorous analysis

of the role of the storage effect on changes in size-structure over time is warranted.

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Table 1. Seasonal temperature occupancies (˚C) and diets used in bioenergetics simulations of lake trout growth in Lake 373 over time.

Season	Thermal conditions	Temperature occupancy	Proportion in diet			
			Invertebrates	Fish	*Mysis*	Zooplankton
Winter	Ice-covered	2.0	0.35	0.40	0.20	0.05
Spring	After ice-off and when littoral zone ≤ ˚15 C	8.3	0.60	0.37	0.03	0.00
Summer	Littoral zone > ˚15 C	6.7	0.02	0.45	0.27	0.26
Fall	Before ice-on and when littoral zone ≤ ˚15 C	7.6	0.00	0.22	0.72	0.06

Table 2. Summary of the bioenergetic simulations of the growth of lake trout in L373 performed in this study.

Simulation	Start age	End age	Start weight	Reproductive age
1	1	4	110 g	NA
2	4	10	End weights from Simulation 1	Variable, declining from age 6 to age 4 over time (see Results)
3	4	10	End weights from Simulation 1	Constant, age 6
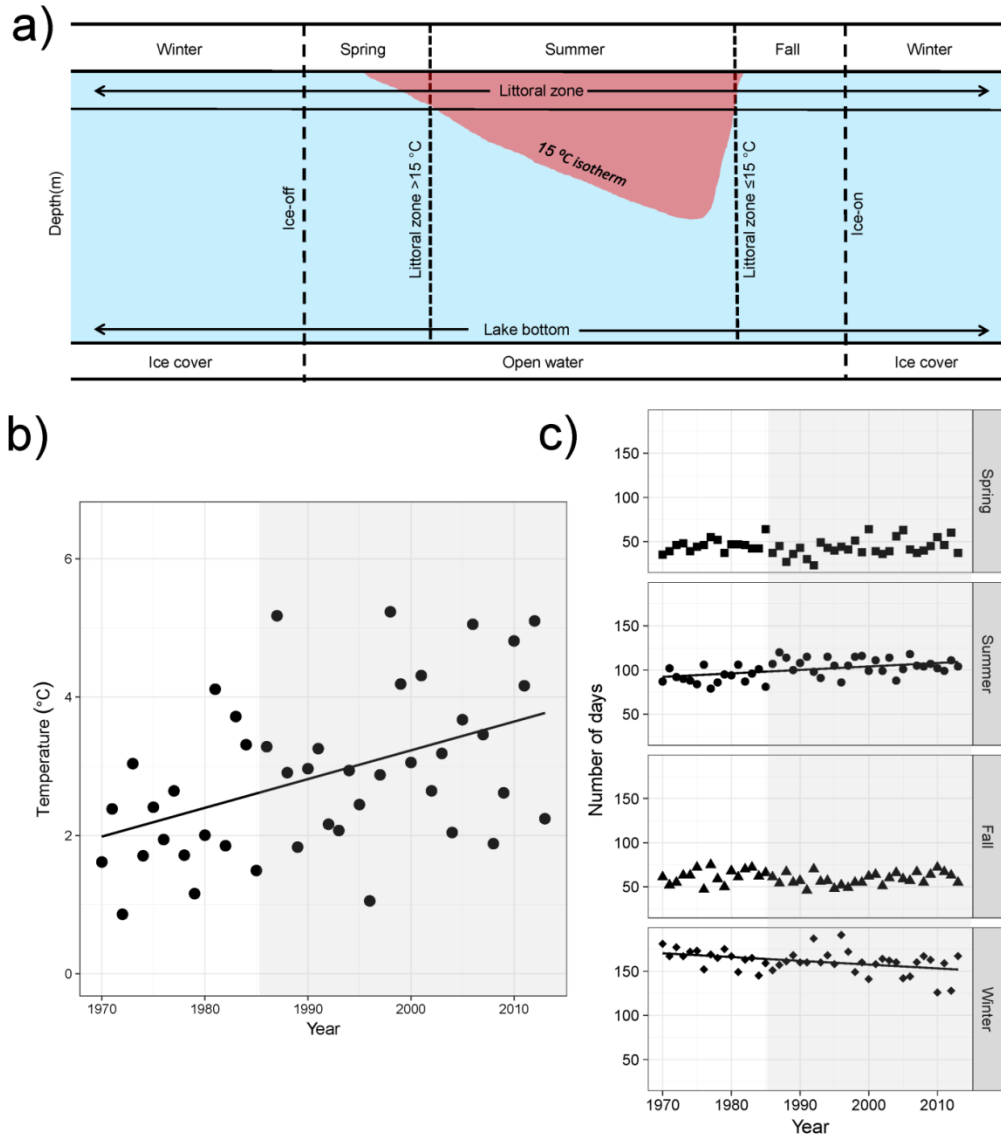
Figure 1 – (a) Schematic illustrating the seasonality of lake thermal habitat in thermally-stratifying Boreal Shield lakes and (c) how the phenology of this thermal habitat in our study lake changed over time as a function of (b) increasing mean annual air temperatures experience during 1970-2013. In panel a, winter is the period of ice-cover, fall and spring are the periods before and after ice-cover when the mean littoral zone (depths < 6 m) temperature was ≤ 15 °C, summer is the period when the littoral zone was > 15 °C. Trend lines in panel b-c are presented where Mann-Kendall tests indicated significant monotonic trends over time. The grey shaded area in panels b-c indicate the period (1986-2013) when monitoring data was collected from L373.
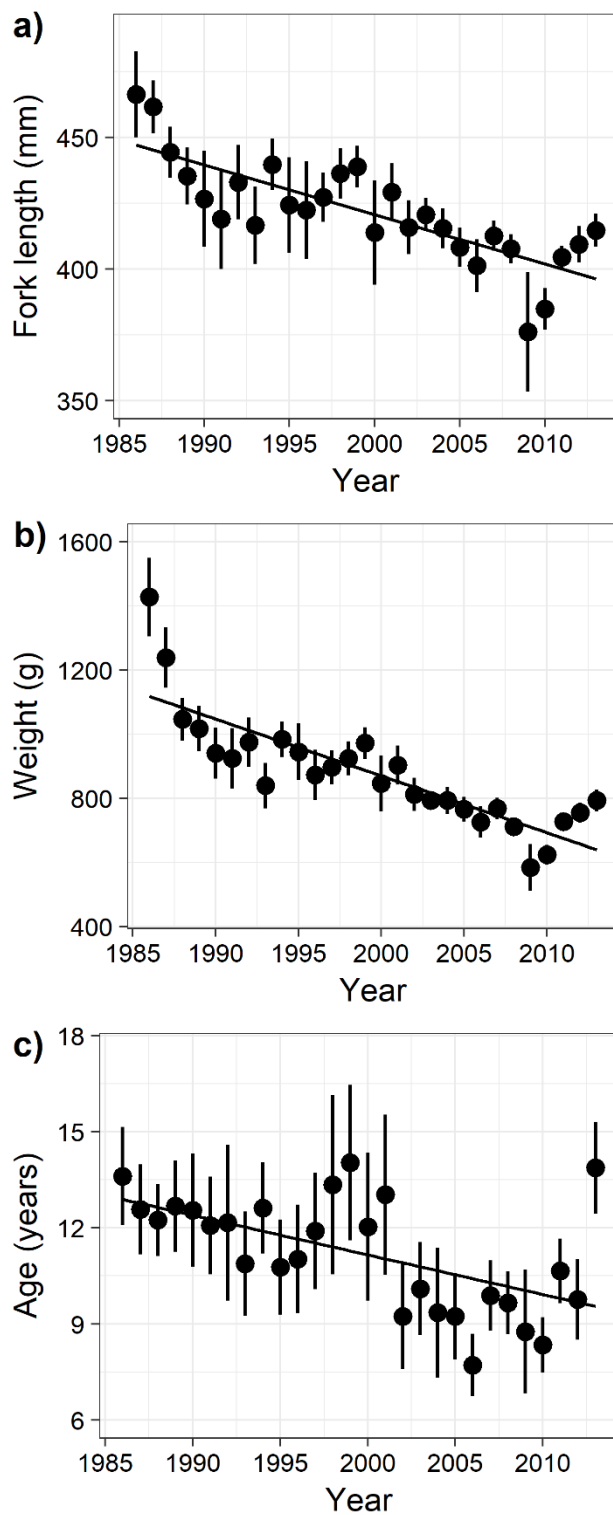
Figure 2 – Annual variations in mean (± SD) (a) fork length, (b) weight, and (c) age of lake trout sampled each year in L373. Trend lines are presented where Mann-Kendall tests indicated significant monotonic trends over time.
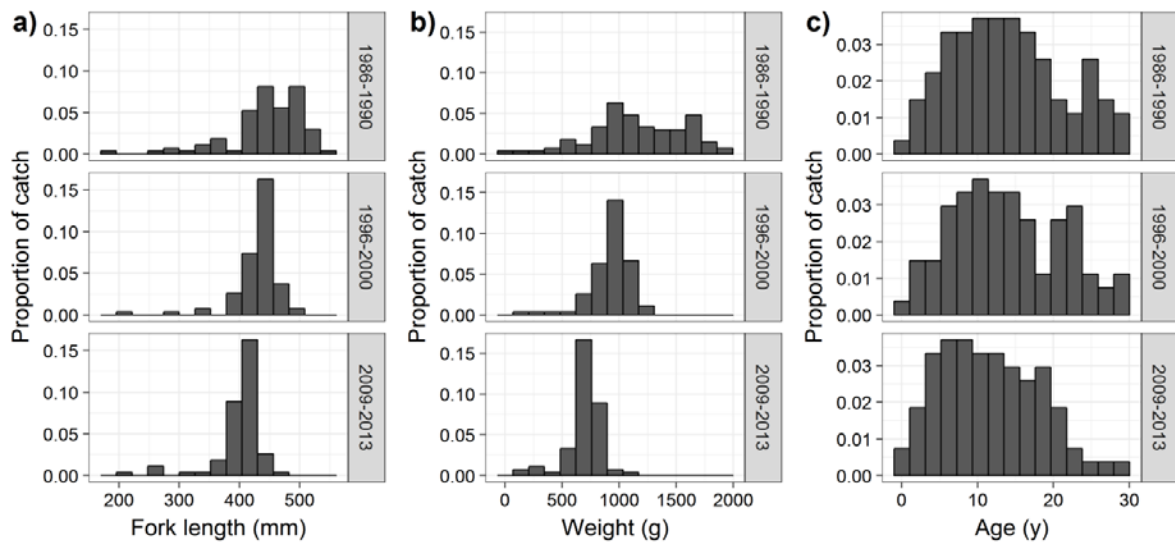
Figure 3 – Variations in the (a) fork length, (b) weight, and (c) age distributions of lake trout sampled from L373 during 1986-2013.
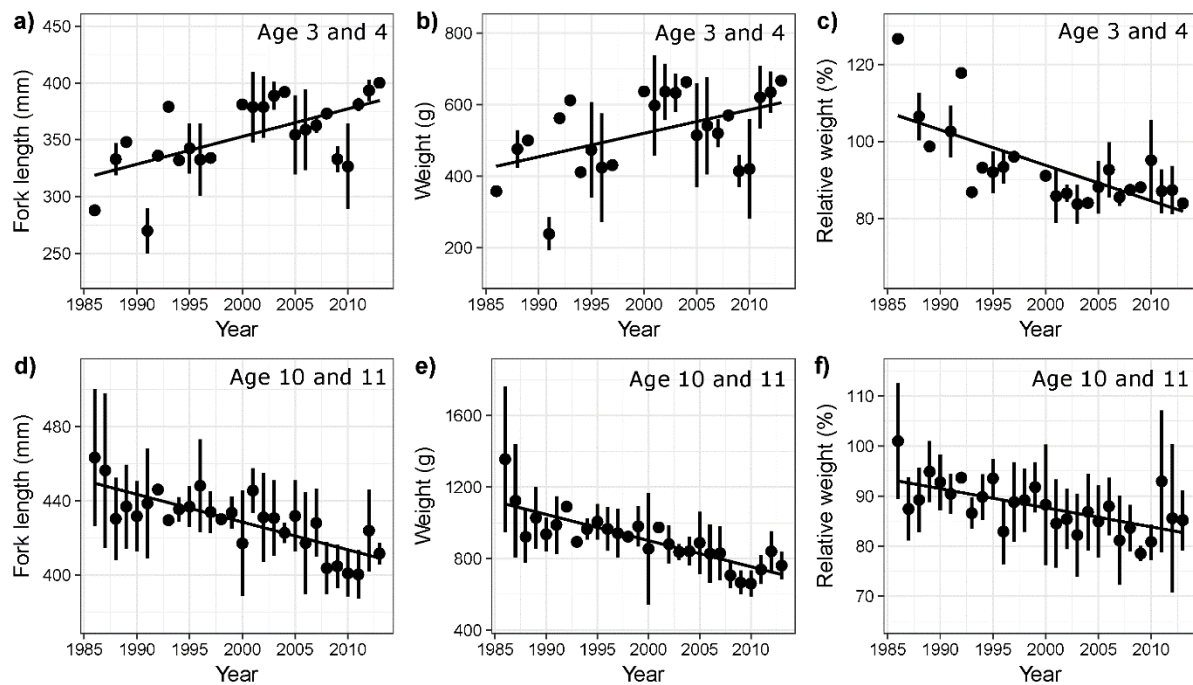
Figure 4 – Annual variations in mean (± SD) (a, d) fork length-at-age, (b, e), weight-at-age and (c, f) relative weight of immature (age 3-4, top row) and mature (age 10-11, bottom row) lake trout sampled L373. Trend lines are presented where Mann-Kendall tests indicated significant monotonic trends over time. Points without error bars indicate that only one fish of that age class was sampled that year and therefore SD could not be estimated.
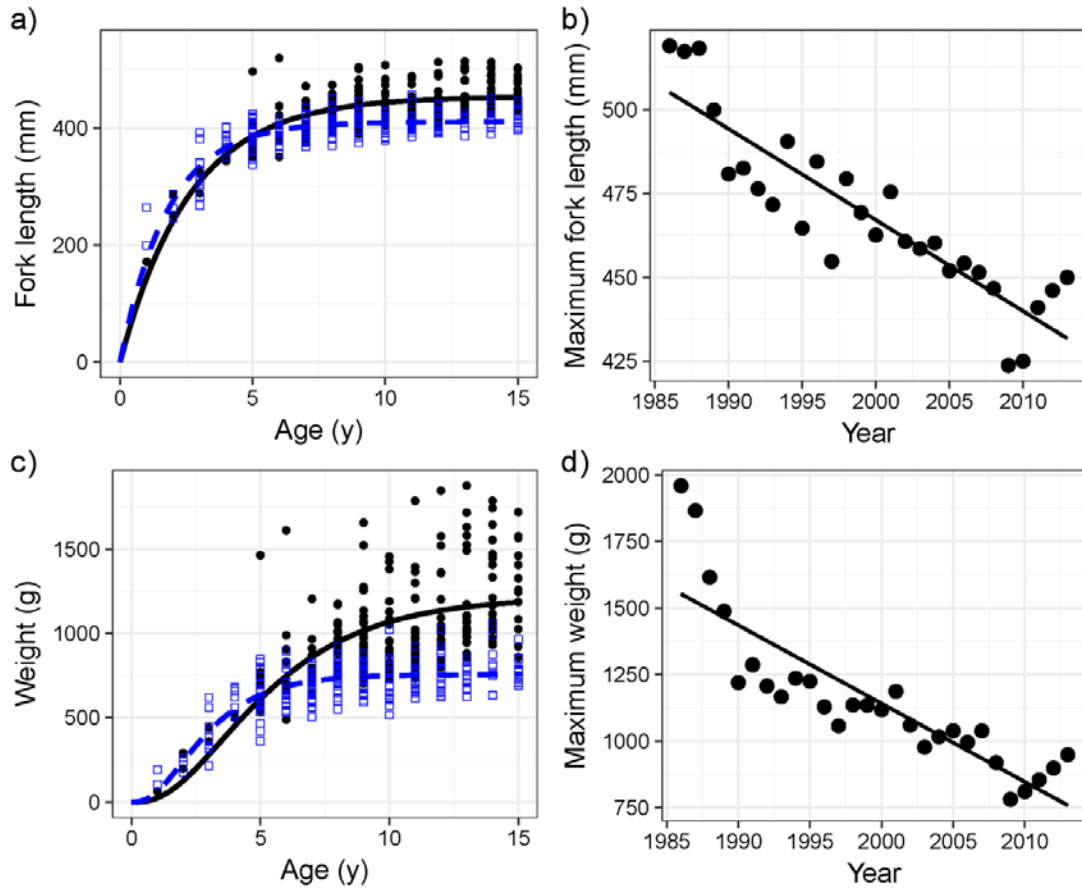
Figure 5 – Comparison of von Bertalanffy growth curves based on (a) fork length and (c) weight of lake trout collected in L373 for the first and last five years of the study. Additional estimates of maximum (b) fork length and (d) weight were calculated as the 95th percentile of all lake trout captured during annual fall sampling. In panels a and c, each data point is an individual fish and trend lines are best fits of the growth curves, with black solid lines and black dots indicating data from 1986-1990 and blue dashed lines and hollow squares indicating data from 2009-2013. In panels b and d, trend lines are presented where Mann-Kendall tests indicated significant monotonic trends over time.
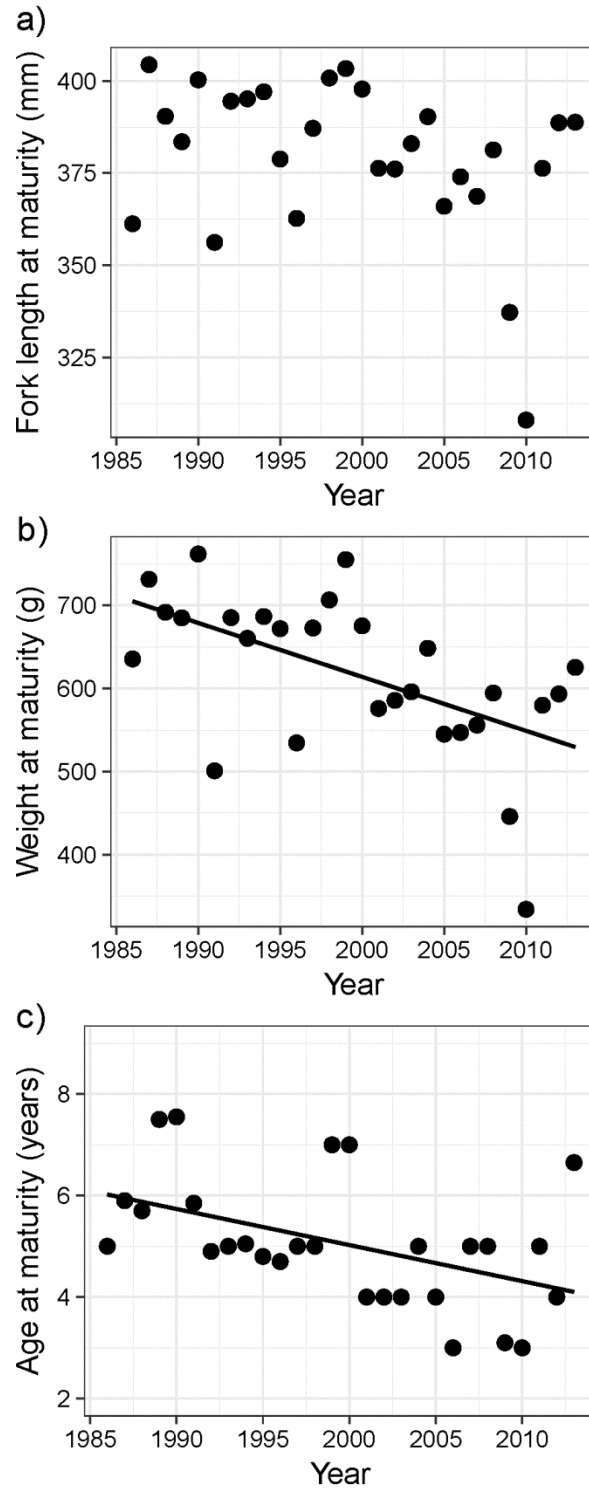
Figure 6 – Annual variations in lake trout (a) fork length-, (b) weight-, and (c) age-at-maturity in L373 observed during 1986-2013. The lower 5th percentile of lake trout fork lengths, weights, and ages were used as proxies for size- and age-at-maturity (see Methods). Trend lines are presented where Mann-Kendall tests indicated significant monotonic trends over time.

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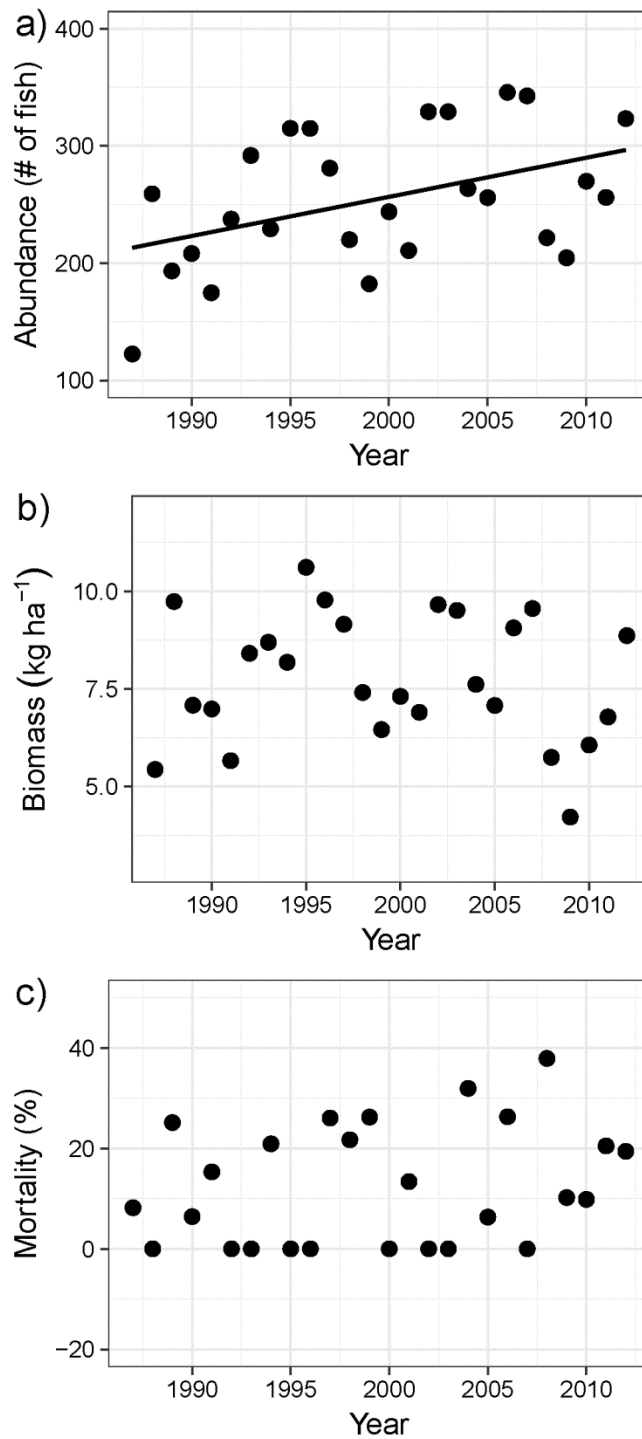
Figure 7 – Annual variations in lake trout (a) abundance, (b) biomass, and (c) natural mortality in L373 during 1987-2012. Note: abundance estimates for the years 1986 and 2013 were not reliable due to the time-varying mark-recapture model parameterization. Trend lines are presented where Mann-Kendall tests indicated significant monotonic trends over time.
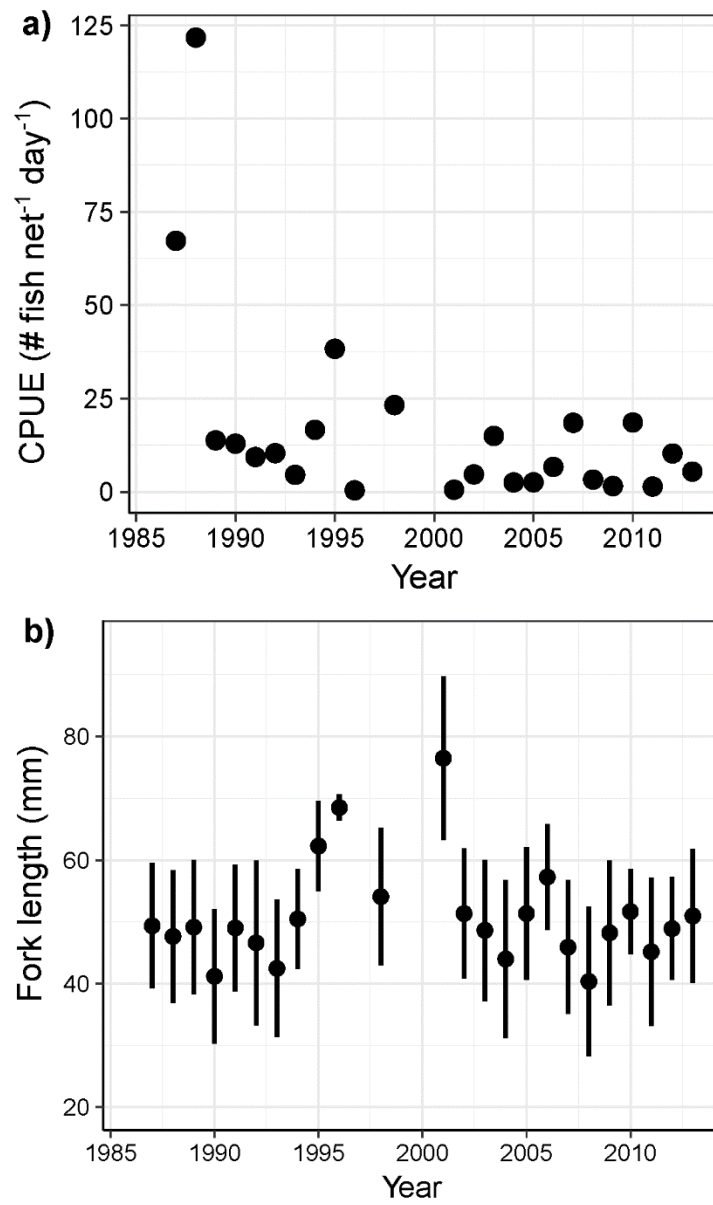
Figure 8 – Annual variations in spring (a) catch-per-unit-effort (CPUE) and (b) mean (± SD) fork length of prey fish captured in the L373 captured during 1987-2013.
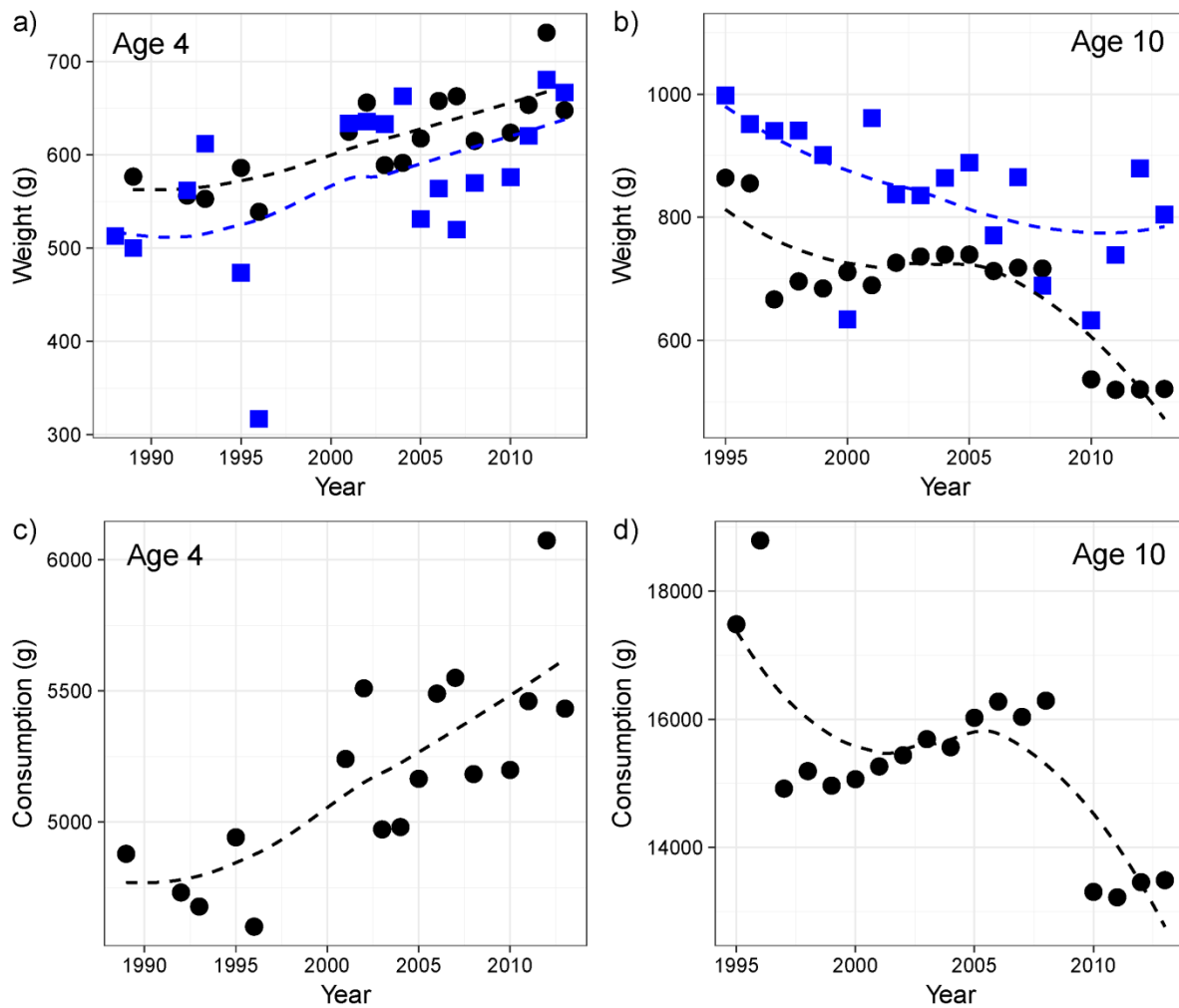
Figure 9 – Comparison of mean annual lake trout weights for (a) age 4 and (b) age 10 as observed in L373 (black circles) and modelled using bioenergetics models (blue squares). Corresponding total consumption estimates (i.e. from age 1 to age 4 or age 1 to age 10) for (c) age 4 and (d) age 10 bioenergetics simulations are also provided. Note differences in axis scales for age 4 and age 10 plots. Dashed lines are loess curves to help show trends over the entire time series.

Bioenergetics parameterization

Daily temperature occupancy

The daily temperature occupancy values used in bioenergetics simulations were determined using acoustic telemetry data collected in L373 during 2003-2013. Telemetry data were collected from a total of 41 individual fish (fork length 380-501 mm) implanted with depth-sensing transmitters (V16P-4L or V13P-1L, VEMCO Ltd., Bedford, NS) that randomly transmitted a coded signal every 16-64 s (V16) or 120-300 s (V13). The depths of transmitter-implanted fish were monitored year-round using 4-5 omni-directional hydrophone receivers (VR2, VEMCO Ltd., Bedford, NS) with overlapping detection ranges distributed throughout the lake (see Blanchfield *et* al. 2009b, Plumb & Blanchfield 2009 for details on transmitter implantation and the receiver array).

Raw telemetry data were filtered to remove dead fish, malfunctioned tags, detections outside the depth range of the lake, and multiple detections/false detections. Data from the first two weeks after a transmitter was implanted were removed to reduce potential effects of tagging on behaviour (Rogers and White 2007). Because two different transmitter types were used during the study period — V16 transmitters that emitted pings about five times more frequently than V13 transmitters — we "thinned" the detection data of fish implanted with V16 transmitters to be comparable to those of the V13 transmitters (Guzzo et al. 2017). A water temperature was then assigned to each remaining depth detection using a daily lake temperature profile (0.1 m resolution). Lake profiles were obtained using *in situ* water temperature measurements obtained from a string of data loggers (HOBO Temp Pro H20-001, Onset Computer Corp., Cape Cod, MA, USA) deployed over the deepest point of L373 at 1 m intervals from 1-8 m and at 10 m, 15 m, 19 m (Plumb and Blanchfield 2009). Logger data from 29 April to 20 June 2003 were not available and data from bi-weekly temperature profiles were supplemented. Loggers

were removed from the lake during ice-cover during 2009-2013, so winter temperature occupancy could not be estimated for these years. Our final filtered and corrected telemetry dataset to estimate seasonal temperature occupancies consisted of 7,079,107 detections (range 449,505-957,223 detections year^{-1}) from xx individual fish (range 7-18 detections year^{-1}).

Using the dataset described above, we calculated the grand mean (± SD) seasonal temperature using mean daily temperature occupancies for all tagged lake trout during each study year. Given that mean seasonal temperature occupancies were relatively similar among years (Fig. S1), we decided to take the grand mean (± SD) of these annual seasonal temperature occupancies (Fall: 7.7 ± 0.6 °C, Spring 8.3 ± 0.6 °C, Summer 6.9 ± 0.8 °C, Winter 2.8 ± 0.2 °C) and use these values as daily temperature occupancies in our bioenergetics simulations.

Daily diets

We used stomach contents to quantify the seasonal diets of lake trout in L373. Stomach contents were obtained using non-lethal dietary lavage in spring (23 and 28 May 2014, *n* = 14) and summer (12 August 2014, *n* = 4) and whole stomachs were collected from mortalities during fall sampling (various dates between 1-21 October 1986-2012, *n* = 24). Items from each stomach were identified and grouped into the following groups: benthic invertebrates and terrestrial and aquatic insects, prey fish, zooplankton, *Mysis*, indigestible, and unidentifiable/digested. Following identification, we calculated the proportion of the total identifiable stomach content mass for each diet item. Winter diets were approximated from literature values from lakes with similar food webs (Martin 1954): benthic invertebrates 0.35; prey fish 0.40, *Mysis* 0.20; and, zooplankton 0.05.

Bioenergetic calibrations

We used the lake trout parameterization of the Wisconsin bioenergetics model (Stewart et al. 1983) in

Fish Bioenergetics 4.0 (Deslauriers et al. 2017) to simulate observed growth (i.e. weight) of lake trout in

L373 during 1986-2013. To calibrate our inputs to the lake trout bioenergetics model we started using

the linear (immature) growth period between ages 1-4 where net energy from food (after sufficing

metabolic costs) is converted to somatic mass (negligible reproductive investment). We first performed

a linear regression on all weight-at-age data for fish ≤ age 4 collected during 1986-2013 to determine

the mean annual increase in weight. The linear regression indicated that the weight of immature lake

trout increased by 160.46 g y^{-1} on average during this time period, translating to an increase in growth of

481.38 g between ages 1 to 4 ($F_{1, 96}$ = 169.3, P < 0.01, r^2 = 0.64; Fig. S2). Using the resulting linear

relationship, we predicted that the average weight of an age 1 and age 4 lake trout in L373 during 1986-

2013 was 110 g and 591 g, respectively. We used these values of 110 g and 591 g as the start and end

weights in bioenergetics simulations of the linear growth period. We used the average length of each

season (winter, spring, summer, fall) during 1986-2013, average water temperature occupancies in each

season (estimated using telemetry, see above), and seasonal diets (estimated with stomach contents,

see above) as inputs to the model (Table 1). The starting energy density of lake trout was set to 5510 J g^{-1}

^{1}. Energy densities of prey items were taken from literature values (Table 2). Reproductive investment

was set to zero. Our simulations indicated that to achieve growth from 110 to 591 g and given our daily

temperature and diet inputs, an age 1 lake trout would need to eat at 64.35 % of its maximum

consumption. This equated to an average daily ration of 4.5 g (range 1.3-13.9 g day^{-1}) over the three-

year simulation. This p-value was within those reported elsewhere for lake trout (0.42-0.75; (Stewart et

al. 1983) and was applied to all other simulations in order to estimate growth under scenarios listed in

Table 2.

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Table S1 – Daily temperature and diet inputs into a three-year (age 1-4) bioenergetics simulation of lake trout growth representing average conditions from 1986-2013.

Days	Season	Temperature [1]	Proportion of diet [2]			
			Invertebrates	Fish	*Mysis*	Zooplankton
1-30	Fall (post spawn)	7.6	0	0.22	0.72	0.06
31-189	Winter	2.0	0.35	0.40	0.20	0.05
190-234	Spring	8.3	0.6	0.37	0.03	0
235-338	Summer	6.7	0.02	0.45	0.27	0.26
339-365	Fall (pre-spawn)	7.6	0	0.22	0.72	0.06

[1] Estimated using telemetry data collected during 2003-2013, [2] Based on stomach content data (Chapter 2) and literature values (Martin 1954)

Table S2 – Prey and starting predator energy densities used in all bioenergetic simulations.

Species	Category	Energy density (joules g wet mass^{-1})
Lake trout	Predator	5510 [1]
Benthic invertebrates	Prey	3285 [2]
Prey fish	Prey	4198 [2]
Mysis diluvania	Prey	3642 [3]
Zooplankton (copepoda)	Prey	2792 [3]

[1] Average data from L373 lake trout mortalities, [2] Martens 2013, [3] Cummins and Wuycheck 1971
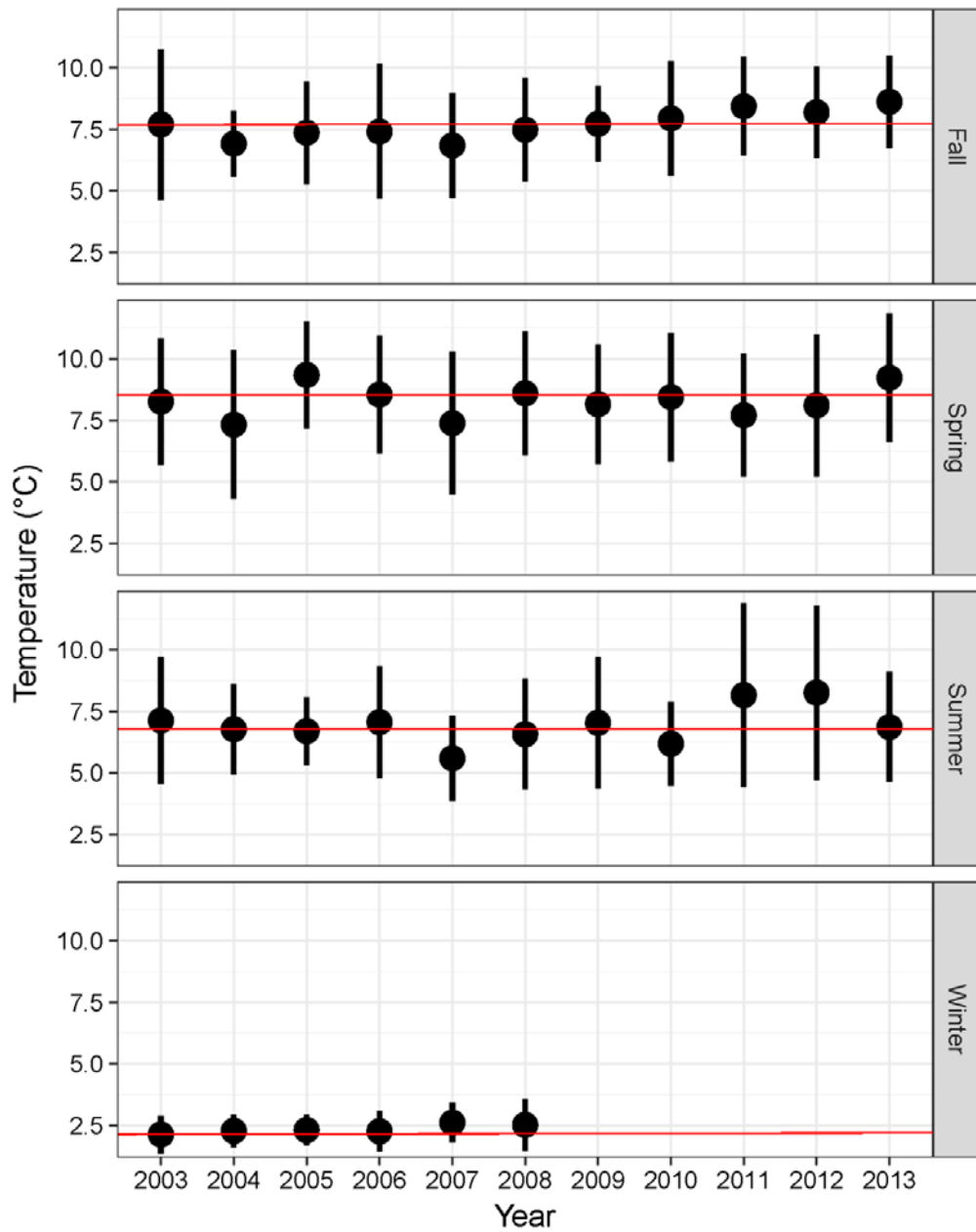
Figure S1 – Mean seasonal temperature occupancy of lake trout implanted with acoustic recievers during each study year. Red lines are the grand means for each season (see Table 1).

$$y=160.46x - 50.00$$
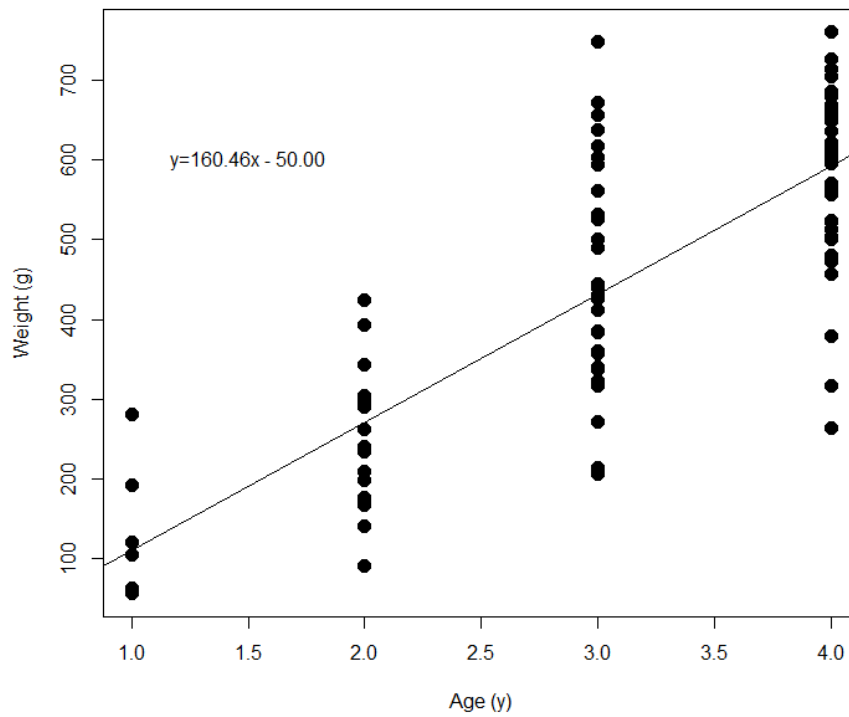
Figure S2 – Weight-age relationship for immature lake trout (age 1-4) collected during fall (1986-2013) from L373 as part of the ELA fish monitoring program.
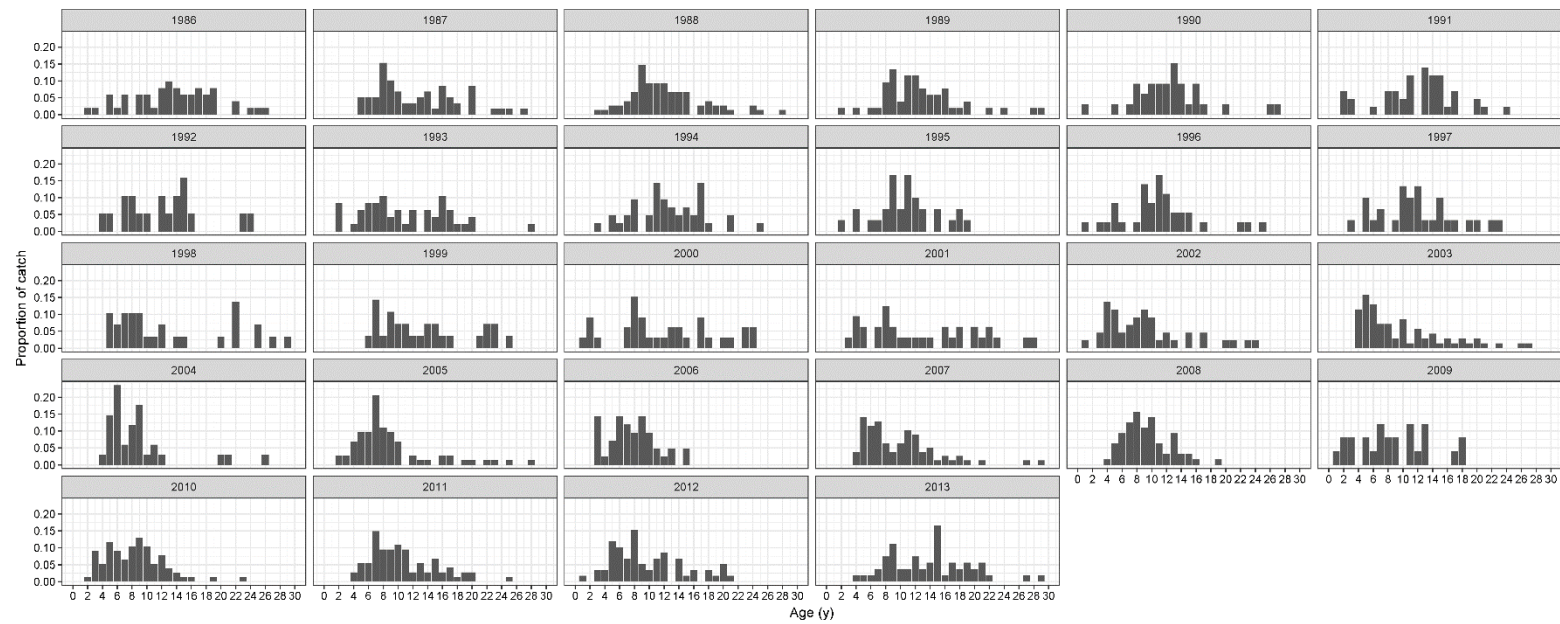
Figure S3 – Annual age distributions of lake trout captured in L373 during fall sampling events occuring during 1986-2013.
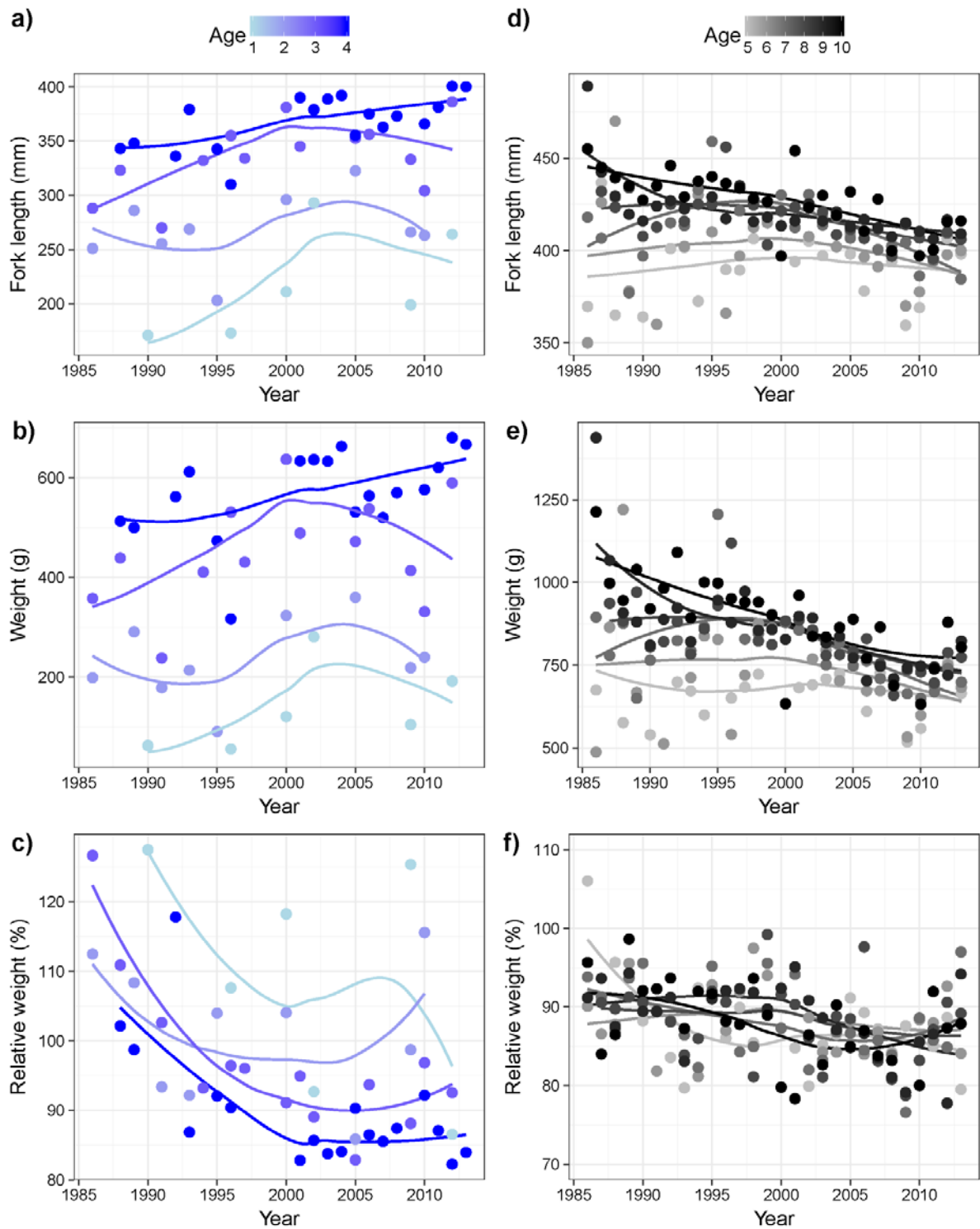
Figure S4 – Annual variations in (a, d) fork length-at-age, (b, e) weight-at-age, and (c, f) relative weight of aged 1-4 (left) and aged 5+ (right) lake trout sampled L373.
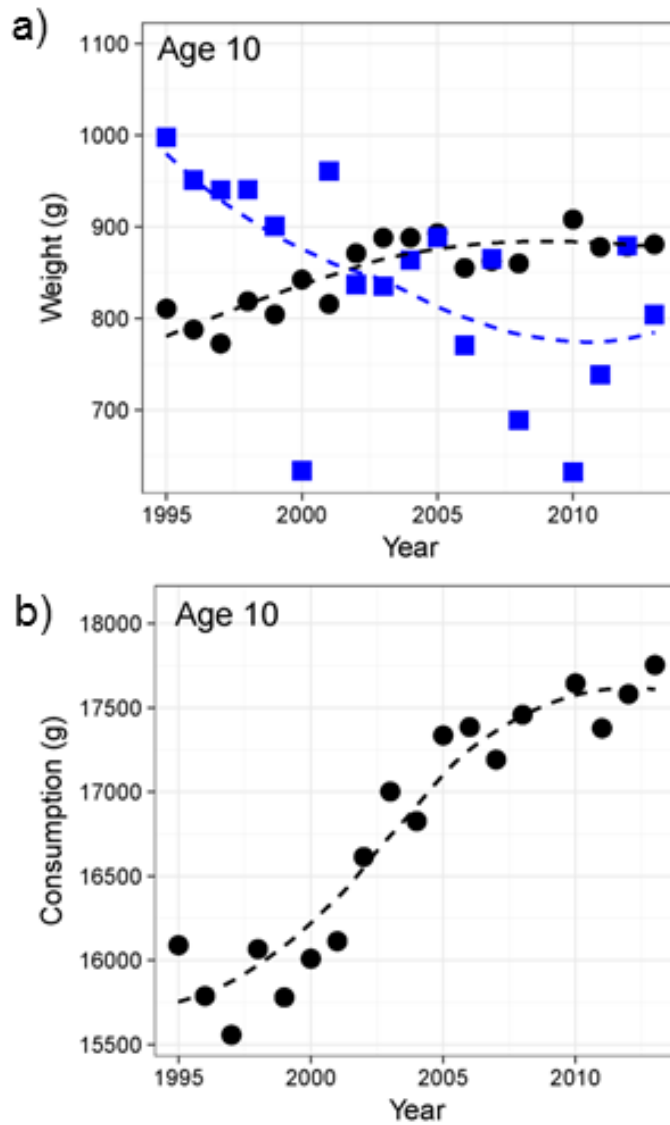
Figure S5 – Comparison of mean annual lake trout weights for (a) age 10 as observed in L373 (blue squares) and modelled using bioenergetics models (black circles) assuming a constant age-at-maturity of age 6 over time. Corresponding total consumption estimates from simulations are provided in (b). Dashed lines are loess curves to help trends over the entire time series.
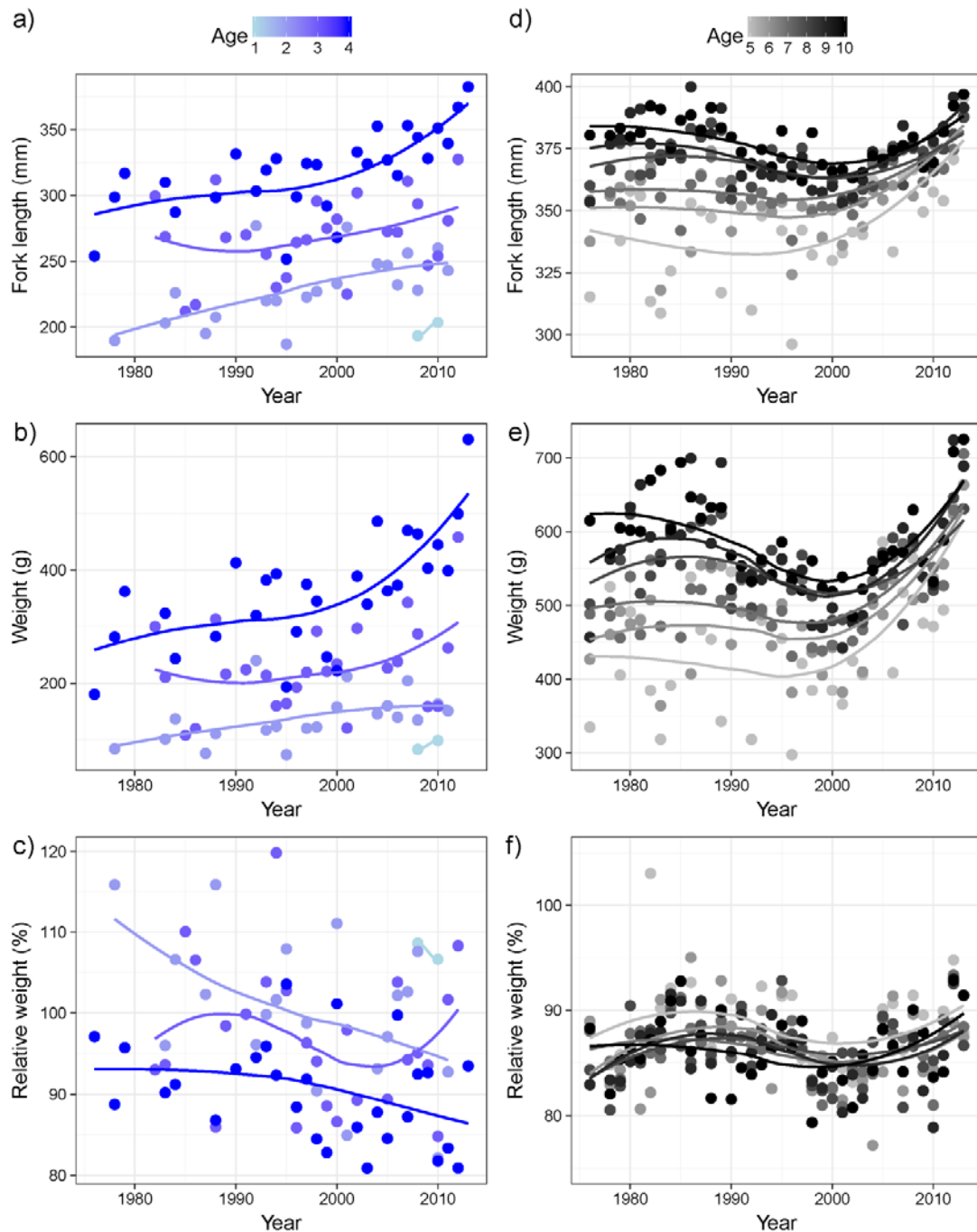
Figure S6 – Annual variations in (a, d) fork length-at-age, (b, e) weight-at-age, and (c, f) relative weight of aged 1-4 (left) and aged 5+ (right) lake trout sampled ELA Lake 224. Minnow harvest was known to occur prior to the year 2000 in Lake 224. Trend lines in each plot are LOESS curves to help visualize trends in the data for each age.
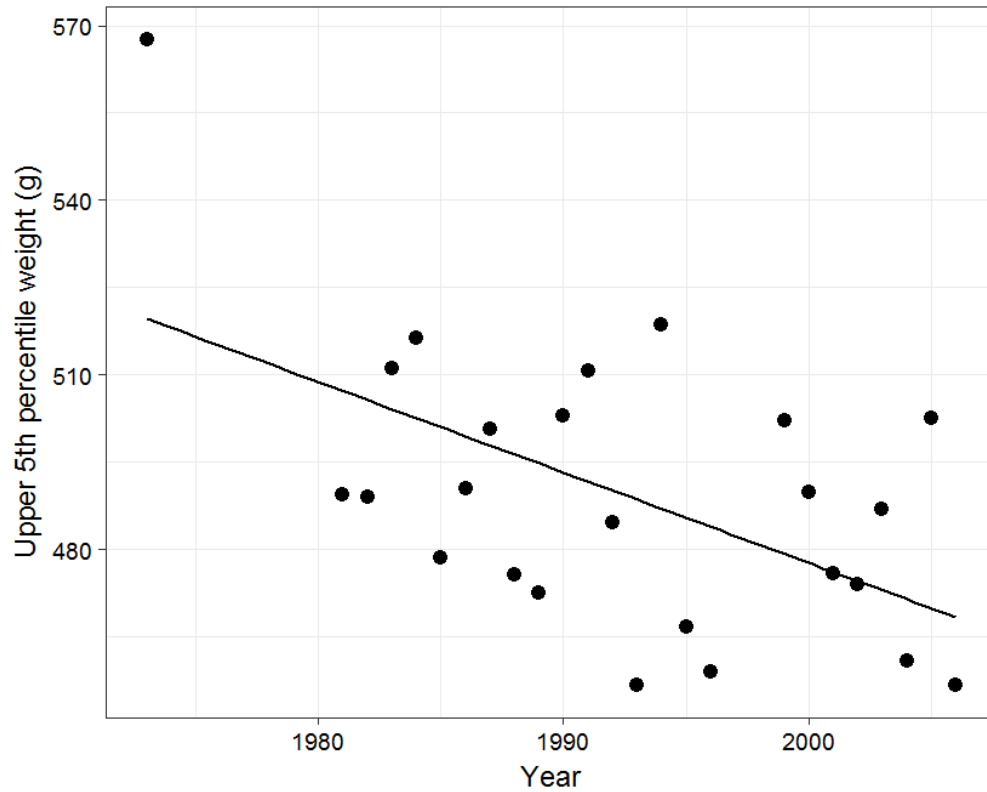
Figure S7 – Annual variations in lake trout maximum body size in ELA Lake 468. Maximum size was estimated as the upper 5th percentile of lake trout captured each year, with only years with a minimum sample size of 20 included. Trend line indicates a significant monotonic trend over time determined by a Mann-Kendall test (n=25, tau=-0.32, P=0.03, slope=-1.38 g y^{-1}).

CHAPTER 4

The seasonal ecology of lake trout (*Salvelinus namaycush*) in a northern lake and the bioenergetic implications of warming

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Contributions of Authors: I collected and analyzed data and wrote the paper. P.J.B. edited the paper. A.J.C. made the project database and helped with field and lab work. P.J.B and P.A. C. helped with field work, field logistics, and secured project funding. P.A.C. provided stable isotope data and lake trout otoliths.

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Abstract

The Canadian North has warmed at a rate nearly double that than the rest of country and this trend is expected to continue. The warmer temperatures anticipated may alter the behaviour and growth of cold-water fish species that inhabit the freshwater lakes of northern Canada; however, our ability to predict these changes is limited given the scarcity of data on the seasonal ecology of fish populations in this region. We conducted a detailed study of lake trout (*Salvelinus namaycush*) in a northern lake to document the seasonal habitat use, diet, and activity of lake trout in response to annual cycles in temperature. We found that the behaviour and diet of lake trout was governed mainly by a combination of ice-cover and the existence of water temperatures > 15 ˚C. During summer when littoral zone temperatures were > 15 ˚C, lake trout occupied mainly deep offshore water, rarely entered the littoral zone, and were the least active. Lake trout's occupancy of the littoral zone was higher in spring, fall, and winter relative to summer, but littoral habitat use was still reduced compared to small southern lakes without pelagic prey fish, likely due the availability of cisco (*Coregonus artedi*) and the predation risk of large northern pike (*Esox lucius*). Lastly, bioenergetics simulations indicated that the annual growth and consumption of lake trout would increase under a 2 ˚C warming scenario. The findings here provide a first attempt at evaluating the year-round behaviour of lake trout in a northern lake and predicting they may respond to climate change.

Introduction

Globally, freshwater lakes are concentrated at northern latitudes, a region where warming related to climate change is most severe (IPCC 2014). In Canada, air temperatures in the north have risen at a rate more than double that of the country's landmass, and this trend is anticipated to continue (IPCC 2014, Warren and Lemmen 2014). Based on a conservative scenario, in which greenhouse gas emissions become stabilized (RCP4.5), the Canadian Regional Climate Model 4 (CanRCM4; Scinocca et al. 2016) predicts that by the end of the century mean annual air temperatures in northern Canada (> 60 °N latitude) will be 2-4 °C greater than those experienced during 1986-2005. As a result, freshwater lakes in the Canadian North are expected to undergo some of the most rapid and striking physical and biological changes because of warming by the end of the century (Prowse et al. 2006a, 2006b, Wrona et al. 2006). Increases in air temperatures are expected to reduce the duration of ice-cover, increase surface water temperatures, and alter thermal structure and seasonal phenology of lakes (Prowse et al. 2006a, 2006b, Keller 2007, O'Reilly et al. 2015, Guzzo and Blanchfield 2017). While these physical responses of lakes to warming are fairly well-known, how fish will respond to these changes is poorly understood, particularly in northern lakes.

The food webs of northern lakes are typically characterized by cold-water fishes (Magnuson et al. 1979), which often support subsistence, as well as commercial and recreational fisheries. Cold-water fishes have a narrow thermal window for optimal metabolic function, therefore the warmer temperatures expected with climate change may impact the behaviour and growth of these species in northern lakes more than at southern latitudes (Fry 1947, Magnuson et al. 1979). One cold-water species commonly found in the oligotrophic lakes of northern Canada is the lake trout (*Salvelinus namaycush*; Johnson 1976, Martin and Olver 1980, Wilson and Mandrak 2004). To survive in cold, unproductive ecosystems, lake trout have evolved a life-history characterized by slow growth, late maturation, and low reproductive output (Martin and Olver 1980). Lake trout are top predators in most

lakes, and although their preferred prey is fish, they can be opportunistic depending on environmental

conditions such as temperature (Fry 1939, Martin 1954, Tunney et al. 2014, Guzzo et al. 2017) and food

web structure (Martin 1952, Vander Zanden and Rasmussen 1996). Lake trout have optimal growth at

temperatures 10 ± 2 °C (Magnuson et al. 1990) (Connor et al. 1981, Christie and Regier 1988a) and

optimum aerobic scope ≈ 15 °C, above which their aerobic scope rapidly declines (Evans 2007, Kelly et

al. 2014). Together, its requirement for cold water and vulnerable life history make lake trout

susceptible to the warmer conditions expected with climate change.

Despite the center of lake trout's latitudinal distribution being in the north (> 60 °N) and many

populations existing in this region (Sawatzky et al. 2007, Sharma et al. 2009), most research on lake

trout has focused on populations near the southern extent of its distribution (Gunn et al. 2004).

Furthermore, those studies that have occurred in the north on lake trout diet and habitat use have

almost exclusively focused on the open-water season (i.e. summer), thereby failing to capture

seasonality, which is important for understanding how lake trout may be impacted by warming (e.g.

Mackenzie-Grieve and Post 2006, Cott et al. 2011, Guzzo et al. 2015, Hulsman et al. 2016). However,

data from southern research provides some insight as to how the seasonal ecology of lake trout may be

impacted by warming.

Based on southern studies, the main impact of warming on lakes that will influence lake trout

ecology and growth is likely the reduction in the length of the ice-covered period and resultant

lengthening of the growing season — the period when water temperatures near the optimal for growth

exist within the lake (Keller 2007, Guzzo and Blanchfield 2017, Chapter 3). Although lake trout have been

found to remain active during winter (Blanchfield et al. 2009) and feed mainly on fish during this period

(Martin 1954, Vander Zanden and Rasmussen 1996), winter is typically viewed as a maintenance period,

where growth is minimal (Shuter et al. 2012). Some studies from southern lakes have suggested that the

most important season for lake trout growth is spring. During this period, when surface waters are cool,

lake trout spend long periods within the nearshore-littoral zone of lakes, where prey is abundant (Fry 1939, Martin 1952, Guzzo et al. 2017). In contrast, during summer, littoral water temperatures exceed the optimal for lake trout and they seek refuge in deep water, resulting in a seasonal diet shift to offshore prey, which can be more energetically costly to obtain if in low density or of inferior energetic value (Fry 1939, Martin 1952, Tunney et al. 2014, Guzzo et al. 2017). As a result, lake trout growth has been found to be greatest in years when the spring period is long and or summer is relatively short (King et al. 1999, Plumb et al. 2014, Guzzo et al. 2017). Although fall is a period when lake temperatures are cool promoting feeding in the littoral zone, this is also when lake trout spawn and may be a less important time for feeding and growth relative to spring (Fry 1939, Guzzo et al. 2017). In fact, Guzzo et al. (2017) show that the seasonal habitat use and diet of lake trout during the open-water season clearly transitioned as mean littoral zone (< 6 m depth) water temperatures exceeded 15 ˚C. The close association between lake trout habitat use and littoral zone temperatures found in Guzzo et al. (2017), suggests that if with warming, northern lakes undergo chances in seasonality like those found in southern lakes , it would be plausible to expect this may alter the habitat use and growth of lake trout in these systems. Because the winter encompasses such a long proportion of the year at northern latitudes, an increase in growing season like that found in ELA lakes should be beneficial to lake trout growth. Indeed, Hill and Magnuson (1990) used bioenergetics models to demonstrate that lake trout growth in the Laurentian Great Lakes should increase with warming.

The objectives of this study were two-fold. First, we conducted a detailed study of the seasonal limnological conditions, habitat use, activity and diet of lake trout in a northern lake over a period of two-years to provide much needed information on the ecology of this species in northern climes. For this objective, we hypothesized that due to their underlying physiological need for cold temperatures (< 15 ˚C; Evans 2007), lake trout should exhibit similar seasonal patterns in habitat use and diet as found in southern lakes. Therefore, we predicted that during spring, when littoral zone temperatures are cool,

lake trout would use this habitat the most and most reliant on prey from this region. In contrast, lake

trout should be least reliant on littoral habitat and prey during summer, when littoral temperatures

exceed 15 ˚C (Martin 1952, Evans 2007, Guzzo et al. 2017). The second objective was to forecast how

the growth of lake trout from this population may change with future warming. Given the impacts of air

temperature on the thermal phenology of north-temperate lakes and the direct impacts of temperature

on fish metabolism, we hypothesized that the annual growth of lake trout would be altered by warming.

Assuming warming increases the length of the open-water period, as in southern lakes, we predicted

that annual growth and consumption of lake trout would increase with warming due to a longer growing

season. We tested this prediction using bioenergetics models to estimate the annual growth and

consumption of lake trout in our study lake under current conditions observed during our study, and

then examine how this would change if seasonal conditions were to change based on a warming

scenario of 2 ˚C, where summer length increased by 14 days and winter length decreased by 14 days

(Chapter 3). Bioenergetic simulations for current and warming scenarios were informed by results of

objective 1 (i.e. daily temperature occupancy and diet and season lengths) and lake trout size-at-age

data collected during the study.

Methods

Study site

The study took place from June 2012 to October 2015 at Alexie Lake (62°40'36.59" N, 114° 4'22.76" W),

a scientific research lake located in the Canadian Shield, ≈ 30 km north east of Yellowknife, NT, Canada

(Fig. 1). Alexie Lake is a medium-sized (surface area: 402 ha; mean depth: 11.7 m; maximum depth: 32

m), oligotrophic lake that thermally-stratifies during summer months and is ice-covered for roughly

seven months of the year (Healey and Woodall 1973). Alexie Lake is in the middle of lake trout's

latitudinal distribution (Muir et al. 2016) and its size and physical and limnological characteristics are

typical of most Canadian lake trout lakes (Healey and Woodall 1973, Gunn and Pitblado 2004). The adult

lake trout population of Alexie Lake is native and self-sustaining, consisting of roughly 2,500 fish during

the study, based on a preliminary multiple mark-recapture estimate (Lorrain Brekke, *unpublished data*).

The lake trout population was previously exploited as part of harvest experiments (Healy 1973), but the

population had since recovered. In addition to lake trout, the fish community of Alexie Lake consists of

the piscivores burbot (*Lota-lota*) and northern pike (*Esox lucius*), as well as lake whitefish (*Coregonus*

clupeaformis), cisco (*Coregonus artedi*), lake chub (*Couesius plumbeus*), ninespine stickleback (*Pungitius*

pungitius), trout-perch (*Percopsis omiscomaycus*), slimy sculpin (*Cottus cognatus*), spoonhead sculpin

(*Cottus ricie*), and deepwater sculpin (*Myoxocephalus thompsoni*) (Cott et al. 2011). The lake also

contains the freshwater shrimp, *Mysis diluvania* and plankton and invertebrate communities common to

northern oligotrophic lakes (Healey and Kling 1975, Healey 1977).

Lake bathymetry

The bathymetry of Alexie Lake was recorded in June 2012 using high-resolution hydroacoustic sensing

(Milne Technologies, Keene, ON, Canada). Hydroacoustic data were collected using a 120 kHz Simrad

EK60 7.0 ° x 7.0 ° split-beam echo-sounder system and following a systematic parallel survey design with

transects spaced 25 m apart (for details see Cott et al. 2015).

Air and lake temperatures

A weather station (HOBO micro station data logger: model H21-002, Onset Computer Corporation, Cape

Cod, MA, USA) was installed at Alexie Lake on 19 September 2012 that recorded air temperature (HOBO

12-bit temperature smart sensor: model S-TMB-M-002) and wind direction (± 3 °C) and speed (± 0.3 m

s^{-1}) (R.M. Young wind monitor: model 05103, R.M. Young Company, Traverse City, MI, USA) every half

hour for the remainder of the study (Fig. 1). The gap in air temperature from 5 July 2012 until

installation of the weather station was filled using data from the Environmental Canada and Climate

Change (EC&CC) Yellowknife meteorological station "A". To confirm that data from the two sites were

comparable, we correlated the mean daily air temperatures for each day of 2013 and 2014 from the

Yellowknife and Alexie Lake weather stations and found a strong correlation (Pearson correlation: n =

738, r = 1.00, P < 0.01). Therefore, we generated a relationship using linear regression between mean

daily air temperature data from EC&CC station "A" and our weather station so that daily air

temperatures at Alexie Lake could be predicted from EC&CC stations "A" data. The resulting equation

was: Alexie air temperature = Station "A" air temperature x 1.03 + 0.13; $F_{[1, 736]}$ = 1.03 x 10^5, P < 0.01, r^2 =

0.99).

Dates of fall ice-formation (ice-on) and spring ice break-up (ice-off) were determined using

photographs from two trail cameras (Bone Collector 8 MP, Bushnell Corp, Overland KS, USA),

programmed to take a picture each hour. We installed the cameras to overlook the two major basins of

Alexie Lake (Fig. 1). Ice-on and ice-off dates were denoted as the day on which ice completely formed or

melted from the area of the lake visible on the photographs from both trail cameras.

Water temperatures were recorded from 5 July 2012 through September 2015 using a string of

data loggers (HOBO Pendant Temp/Light, 64k model: UA-002-64, Onset Computer Corporation) installed

over the deepest point of Alexie Lake (Fig. 1). Data loggers were set at 0.5 m, at 1 m depth intervals from

1 m to 20 m, and at 25 m and 30 m below the surface of the water. Water temperatures were recorded

hourly. We calculated a mean daily temperature for each depth followed by linear interpolation to

obtain mean daily temperatures for every 0.1 m depth interval from the water surface to bottom.

We used a combination of littoral zone (< 6 m depth) water temperature and the presence or

absence of ice-cover to characterize each season for lake trout (Table 1) (Guzzo et al. 2017). The period

of ice-cover was denoted "winter". The period between ice-off and the date before the mean littoral

zone temperature exceeded 15 °C was denoted "spring". The period starting when mean littoral zone

temperature reached and maintained 15 °C was denoted "summer". "Fall" was the period between

when lakes cooled to ≤ 15 °C until ice-on. We chose 15 °C to define seasonal transitions because this

temperature has been shown to best describe the upper limit of daily depth distribution occupied by

lake trout in smaller lakes (Plumb and Blanchfield 2009, Guzzo et al. 2017) and because the aerobic

scope of lake trout declines at temperatures > 15 °C (Evans 2007, Kelly et al. 2014).

Habitat use and movement

The habitat use and movement of lake trout in Alexie Lake were monitored using acoustic telemetry. We

implanted 30 lake trout (fork length range: 427-651 mm; weight range: 870-2570 g) with acoustic

transmitters during 12-15 June 2012 (see Guzzo et al. 2016). Lake trout were captured during daytime

hours by trolling over shallow water (≈ 3-10 m) around the perimeter and islands of the lake with

barbless lures that targeted the top few meters of the water column. Once captured, fish were brought

to shore in a holding container, lightly anesthetized in a solution of 90 mg L^{-1} Tricaine Methanesulfonate

(MS-222) buffered with sodium bicarbonate, and implanted with a with a coded, acoustic, pressure-

sensing (depth) transmitter (V13P-1L, VEMCO Ltd., Bedford, NS, Canada). See Blanchfield et al. (2009)

for a detailed description of surgical procedures. Transmitters were 13 mm in diameter, 33 mm in

length, weighed 6 g in water and did not account for more than 2 % of a fish's body weight; as such it

was assumed that it did not affect swimming ability (Winter 1983). Prior to implantation, each

transmitter's pressure sensor was individually calibrated at 4 m depth intervals from surface to bottom

in Alexie Lake, and were accurate to ± 1.7 m at depths of 34 m or less with a resolution of 0.15 m.

Transmitters randomly emitted an acoustic signal every 80-160 s.

The depth and spatial positions of individual acoustic-implanted fish were monitored using an

array that consisted of 72 underwater omni-directional acoustic receivers (VR2W, 69 kHz, VEMCO Ltd.)

with overlapping detection ranges (as determined by a range test performed prior to the study) that

were anchored to the lake bottom, and allowed for near complete positioning coverage of transmitter-tagged fish throughout Alexie Lake (Fig. 1; Cott et al. 2015, Guzzo et al. 2016). Each receiver was outfitted with an acoustic transmitter ("sync tag"; V16-1L, 69 kHz, code transmission every 1200 s ± 100 s), located 1-2 m above the receiver, to allow for internal clock synchronization during data processing. An additional 11 reference tags were distributed throughout the acoustic array to aid in system synchronization and positioning accuracy (Fig. 1). The positions of transmitter-implanted lake trout were then calculated using the detection data collected from all receivers within the array using a proprietary algorithm based on time-difference of arrival (TDOA) methodology, known as the VEMCO Positioning System (VPS) (Espinoza et al. 2011, Biesinger et al. 2013, Smith 2013).

Prior to analyses, we filtered telemetry data to ensure only high-quality positions were obtained. First, time-series plots of fish depth and spatial positions were used to eliminate positions from fish that had died, shed their tag, or had tag malfunctions. Second, where positions with successive timestamps were less than the minimum transmission rate of the transmitters we removed the second detection as these data were assumed to be false detections. Third, we removed positions outside of the shoreline and outside the possible depth range of the lake — above the surface of the lake or below the bottom (but within tag accuracy of ± 1.7 m) of the lake at the position determined by VPS (total of 34,682 positions or ≈1 % of all positions). Fourth, we used the estimated positions of sync tags relative to their known locations to determine data filters based on hyperbolic positioning error (HPE; Smith 2013) that balanced the retention of positions and minimized the mean positioning error (see SI). The HPE filtering removed an additional 12 % of fish positions remaining after the first three filter methods. Finally, we omitted all data collected within the first 14 days from the date of the final tag implantation (i.e. data prior to 29 June 2012) to reduce the chances that our analyses included days when fish behaviour may have been altered (Rogers and White 2007). The filtered telemetry dataset consisted of

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3,879,511 positions from 26 individual lake trout, with a median time between consecutive positions of 156 s (5th percentile = 92 s, 95th percentile = 722 s).

Using the filtered telemetry dataset, we then translated the depth of each position to a corresponding water temperature using the temperature logger data described above. We then calculated the mean daily depth, temperature, bathymetric depth (i.e. vertical position above bottom), and the three-dimensional total distance travelled of each lake trout for each day of available data. Three dimensional estimates of total distance travelled were obtained by summing the horizontal and vertical distances travelled between successive positions and dividing this sum by the time difference between those successive positions to produce an estimate of swimming speed (m s^{-1}) for all daily positions. All speeds recorded within a day for a given fish were averaged and then multiplied by 84,600 s (i.e. total number of seconds in a day) to give an estimate of total daily distance travelled, which was converted to km. Daily estimates of the total time spent in the littoral zone by each fish were calculated as the ratio of littoral zone positions: total positions scaled to a 24-h period. A position was considered littoral when both its bathymetric depth (i.e. from spatial location) and water column depth (i.e. from tags depth sensor) were < 6 m, indicating the fish was both nearshore and shallow. We also calculated the number of littoral forays and the average duration of littoral forays. To help illustrate seasonal changes in spatial habitat use by lake trout, we used kernel estimated utilization distributions (UD; Worton 1989) using the R package *adehabitatHR* (Calenge 2006). Individual spatial positions were used to estimate a UD, which was used to estimate the size (ha) and shape (coordinates) of spatial UDs using 50% of the data, known as a "core area". We choose to use core areas to visualize changes in seasonal habitat use because they are representative of habitat used often by a species, which is linked to foraging (Guzzo et al. 2016).

Linear mixed effects models (LMM) were used to model variation in seasonal habitat use metrics among the four seasons with marginal *F*-tests used to test the significance of the fixed factor

season. Separate LMM were run for each of the daily habitat metrics calculated for each fish (depth, temperature, bathymetric depth occupancy, horizontal, vertical and total distance travelled, number of littoral forays, average duration of littoral forays, and time spent in littoral zone), with each LMM having season treated as a fixed factor (levels = spring, summer, fall, and winter), and individual fish nested within study year treated as random intercepts. Assumptions of linear mixed effect models (LMMs) including normality and heteroskedasticity and were evaluated following Zuur et al. (2010). Where necessary, data were transformed to meet assumptions of LMM, reported in Table 2. LMM were performed in the statistical computing package R (R Core Team 2017) using the function *lme* from the package *nlme*. Marginal *F*-tests were performed using the *anova* function. Where the fixed effect of season was found to be significant we calculated least squares means (± 95% CI) estimates of each metric for each season. Temporal autocorrelation in each response variable was accounted for by incorporating autoregressive (AR), moving average (MA), or a combination of AR and MA (ARMA) correlation structures into the LMM. The appropriate correlation structures were chosen by examining autocorrelation function plots of the normalized residuals of each model and R^2 (Zuur et al. 2009). The best correlation structures chosen for each response variable are provided in Table 2.

Diets

We quantified the seasonal diets of lake trout using a combination of stomach contents and stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotopes collected at various times throughout the study (Table 3). Stomach contents were collected during winter, spring, and fall to assess the diets of lake trout during these seasons. Because no sampling trips occurred during the summer months (July-August), stable isotope mixing models based on lake trout dorsal muscle tissue collected in late summer were used to assess summer diet (Table 3). A previous study in Alexie Lake had shown that the isotope values of these

samples closely matched the summer habitat use of lake trout, supporting our assumption that these samples would depict summer diet (Guzzo et al. 2016).

Stomach contents were collected using a combination of dead sampling and gastric lavages during spring, fall, and winter seasons of various study years. Dead-sampled fish were euthanized immediately upon capture in an overdose bath of MS-222 or sharp blow to the head. Euthanized lake trout were placed on ice and processed shortly after, which included collection of fork lengths, weights, and removal of whole stomachs, which were immediately frozen for later quantification. Lake trout obtained for gastric lavages were captured by barbless angling and were lightly anesthetized in a buffered solution of 90 mg L^{-1} MS-222 immediately following capture. A thin (≈ 0.5 mm diameter) 0.5 m long tube attached to a 1 L water bottle was gently slid down the fish's throat into their stomach, which was determined by feeling the tube move through the belly of the fish. The fish was then inverted over an empty bucket and the water bottle was squeezed firmly for ≈ 5 s, flushing water into the inverted stomach and washing out its contents into the bucket below. This flushing procedure was repeated three times to ensure all contents were obtained. The fish was then placed in a cooler filled with lake water to recover, and subsequently released. Contents were then transferred to a polyethylene bag (Whirl-Pak; Nasco, Fort Atkinson, WI, USA) and stored on ice until freezing. To ensure lavages were efficiently removing all stomach contents, five lake trout were sacrificed following completion of lavages using an overdose bath of buffered MS-222 and stomachs were immediately removed and cut open. In all cases, stomachs were completely empty following lavage, providing support that this method could accurately assess lake trout diets (Kamler and Pope 2001, Waters et al. 2004). For diet analysis, all stomachs were thawed, and all contents were removed and identified. Fish were identified to the species level, terrestrial insects and benthic invertebrates were combined as one prey group, and *Mysis* were identified as a separate prey item. Following identification, we calculated the proportion of the total stomach content mass for each identifiable diet item.

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Stable isotope mixing models with $\delta^{13}C$ and $\delta^{15}N$ as tracers were used to assess the summer

diets of lake trout. Values of $\delta^{13}C$ exhibit low (< 1 ‰) trophic enrichment and provide a measure of the

relative use of littoral vs. pelagic derived energy (France 1995, Vander Zanden and Rasmussen 2001). In

contrast, values of $\delta^{15}N$ are assumed to exhibit trophic enrichment of ≈ 3.4 ‰ and provide a measure of

trophic position (Vander Zanden and Rasmussen 2001). Lake trout and all prey fish species were

captured during 19-23 August 2008 using gillnets based on the Nordic community index protocol (see

Cott et al. 2011). Benthic invertebrates, aquatic insects, and *Mysis diluvania* were collected in spring and

fall of 2012 and 2013 using an Ekman sampler and vertical plankton tows, respectively. Skinless dorsal

muscle samples were immediately removed from euthanized fish and whole invertebrate and insect

samples were frozen at -20˚C. Following processing, all samples were later freeze-dried, ground by

mortar and pestle, and analyzed using standard methods at the Stable Isotopes in Nature Laboratory,

University of New Brunswick, NB, Canada. Because all lake trout had C:N ratios <3.5, we did not apply

lipid corrections on these data prior to analyses (Post et al., 2007). Prey items were not lipid extracted as

these lipids would have been consumed by lake trout, whose stable isotope data was not lipid corrected.

We quantified the likely contribution of prey items to the summer diet of lake trout using the

$\delta^{13}C$ and $\delta^{15}N$ data in a Bayesian mixing model approach performed using the package *simmr* version 0.3

(Parnell n.d., Parnell et al. 2013) in R. The mixing model used 20,000 iterations with a burn-in of 5,000

and thinning interval of 10. Within the mixing model, $\delta^{13}C$ and $\delta^{15}N$ values from 12 individual lake trout

were used as the "mix" while mean ± SD values for prey items (cisco, ninespine stickleback, slimy

sculpin, spoonhead sculpin, and deepwater sculpin were used as the "sources". The model used trophic

enrichment factors (TEF) of 0.1 ‰ for $\delta^{13}C$ and 3.4 ‰ for $\delta^{15}N$, which are specific to lake trout (Vander

Zanden and Rasmussen 2001). All mixing model runs were visually inspected to ensure that TEF-

corrected lake trout data were constrained within the bivariate iso-space formed by source data.

Diagnostic matrix plots were used to identify any strong correlations between prey sources. These plots

indicated weak to moderate correlations among the sculpin species; however, we kept the species

separate in the model. Initial mixing models (data not presented) also contained benthic invertebrates

and aquatic insects as potential sources, but these were removed to reduce the number of sources after

results indicated that these items did not account for any portion of lake trout diet in summer. Lake

chub and trout-perch were not included in mixing models as these are thought to only occur in small

numbers and were not identified in any lake trout stomachs collected.

Growth rates

Otoliths were collected from a total of 66 lake trout for age determination using a combination of gill

netting and barbless hook angling. A sample of 34 lake trout was collected on 20 August 2011 using

standardized gill net sampling protocols (Brekke 2017) and another 32 lake trout were collected

between 21 March and 28 September 2013 as part of this study. Fish collected as part of this study were

sacrificed using the same methods as for diet and stable isotope analyses, and in most cases were the

same fish. Each lake trout sacrificed for age determination had its fork length (mm) and weight (g)

recorded and sex determined by presence of reproductive organs where possible. Otoliths were

sectioned and aged using standardized methods at the Fisheries and Oceans Canada Otolith Research

Laboratory, Bedford, NS, Canada.

Fork length- and weight-at-age data were fit using the von Bertalanffy growth model (VBG)

(Ricker 1975): $L(t) = L\infty(1 - e^{K(t-t0)})$ and $W(t) = W\infty\left(1 - e^{K(t-t0)}\right)^{3}$, where *L(t)* and *W(t)* are the

fork length (mm) and weight (g) at age t (years), $L\infty$ and $W\infty$ are the asymptotic fork length and weight,

K is the growth coefficient (denoted below as K_L for fork length models, K_W for weight models), and t_0 is

the theoretical age when the fish would have had a fork length or weight of zero, which was assumed to

be zero. These VBG equations also allowed for estimates of mean annual growth from one age to the

next for bioenergetics modelling (see below). VBG models were fit using non-linear least squares

regression (function = *nls*) in R.

Bioenergetics

We used the Wisconsin Bioenergetics Model to model the growth and consumption of lake trout under

current and warming temperature scenarios. The bioenergetics model is a mass-balance approach based

on the assumption that all food consumed (*C*) is used for metabolism (*R*) and specific dynamic action

(*SDA*), lost through egestion (*F*) and excretion (*E*), or accumulated as growth (*G*):

$$C \approx R + SDA + F + E + G \tag{1}$$

where, components can be converted between units of mass and energy. We used the default

parameterization of the Wisconsin Bioenergetics Model for lake trout (Stewart et al. 1983) in the

program Fish Bioenergetics 4.0 (Deslauriers et al. 2017), except for lake trout swimming speed, which

we input as, mean daily estimates based on telemetry data (see Results). This was achieved by adjusting

the parameters RTL, RK4, RK5 and BACT to 0 and setting RK1 and ACT to a desired velocity in cm s^{-1} for

each day of the simulation (David Deslauriers, *personal communication*). For details on equations and

parameters for each component see (Stewart et al. 1983).

We performed two sets of bioenergetics simulations to test the potential effects of alterations

in habitat occupancy and diet due to changes in temperature phenology (Guzzo and Blanchfield 2017,

Guzzo et al. 2017) on the growth and consumption of lake trout of various sizes from Alexie Lake. The

conditions imposed during each simulation were that daily temperature occupancy, diet, activity (i.e.

mean swimming speed) differed among seasons but were the same each day within a given season

(Table 4). For mean seasonal temperature occupancy and diet we used the least squares daily mean

values for temperature and the seasonal diet estimates above, respectively. For activity we converted

the least squares daily mean estimate of total distance travelled estimated using telemetry data to a

speed in cm s^{-1} (Table 4). In the first simulation (typical conditions) we used the average length of each

season observed during the study (although the values varied slightly to ensure the number of days

summed to 365) to determine the length of each season in the simulation and we assumed this was a

typical year. In the second simulation, (warming scenario), we used results from Chapter 3 to define

potential changes in seasonality that may occur in Alexie Lake with warming (Table 4). Chapter 3 found

during a period where mean annual air temperature increased by ≈ 2 °C, the length of the winter period

was shortened by 14 days and the summer period was extended by 14 days, while both spring and fall

remained unchanged. We used these observed changes from southern lakes in Simulation 2 to alter the

seasonality of Alexie Lake to simulate how a ≈ 2 °C in mean annual air temperature may impact the

growth of lake trout in this lake (Table 4). Each simulation was run using starting weights of 500 g and

1,600 g to understand how the change in seasonality would differentially impact the growth of different

sized lake trout. We chose these starting weights because most lake trout in Alexie Lake were likely

immature at 500 g (Lorraine Brekke and Peter Cott, *unpublished data*) and 1,600 g is close to the

asymptotic weight of lake trout in Alexie Lake and was achieved by lake trout aged in our sample (see

results). The initial energy density of lake trout was 9000 J g^{-1} wet mass, which was the average of a 500

g and 1,600 g lake trout as predicted by the energy density-mass equation in Stewart et al. (1983). We

used the same energy density for each size to simplify the simulation and isolate the impacts of changes

in seasonality on growth and consumption. Energy densities used for prey were as follows: slimy sculpin

5000 J g^{-1} (Hondorp et al. 2005), deepwater sculpin 6000 J g^{-1} (Hondorp et al. 2005), cisco 7000 J g^{-1}

(Harding et al. 2017), ninespine stickleback 4800 J g^{-1} (Ball et al. 2007), Mysis 3642 J g^{-1} (Cummins and

Wuycheck 1971), benthic invertebrates/aquatic insects 3285 J g^{-1} (Cummins and Wuycheck 1971).

Because energy density for spoonhead sculpin could not be found, we assumed it was the same as slimy

sculpin.

Simulations started on the first day of fall and ended on the final day of summer in the following

year (i.e. 365 days). We used the fit of the von Bertalanffy growth curve on our weight-at-age data to

determine at which age lake trout in Alexie Lake were 500 g and 1,600 g and then used the fit to predict

what the change in weight was over a year period. For example, if a 500 g lake trout was on average 7

years old we would use the fit to predict its weight at age 8. We would then run the bioenergetics

simulation with each starting weight under typical conditions using the end weight set to the observed

annual change in growth based on the growth curve and solve for the daily proportion of maximum

consumption (p-value) needed to achieve this growth. Once the p-value was estimated, we ran

bioenergetics simulations with the p-value set to that value under the warming scenario inputs to

predict how the growth and consumption of lake trout would change. This same procedure was

repeated for each starting weight.

Results

Air and lake temperatures

Mean annual air temperatures differed by 1.8 °C among years, with 2012 being the warmest year (-3.0

°C), 2014 the coldest (-4.8 °C), and 2013 falling in the middle (-4.4 °C). Daily air temperatures

experienced large fluctuations each year and ranged by more than 60 °C within each of the study years

(Fig. 2a). The coldest daily temperature recorded was -41.3 °C recorded in winter 2013 and the hottest

was 25.2 °C recorded in summer 2012 (Fig. 2a). Lake temperature patterns closely followed that of

seasonal air temperatures (Fig. 2a, b), thermally stratifying each summer and being ice-covered each

winter. Surface water temperatures peaked at ≈ 22 °C temperatures each summer (2012: 21.8 °C; 2013:

22.0 °C; 2014 21.8 °C), but some differences in phenology of water temperatures existed among years.

Spring lengths were relatively similar among study years (2013: 27 days; 2014: 23 days). Although we

were not able to calculate the exact length of the 2012 summer as littoral zone temperatures were

already > 15 °C when our loggers were deployed on 25 June 2012, we know that it was at least 78 days long, which was already 7 and 12 days longer than the summers of 2013 and 2014, respectively (Table 1). Fall was 19 days shorter in warmer 2012 (51 days) than in cooler 2013 (70 days). Winter lengths were similar in 2012 (209 days) and 2013 (202 days).

Habitat use and movement

Lake trout in Alexie Lake displayed clear seasonal patterns in habitat use and movement. The depth and temperature occupancy of lake trout each varied across seasons (Depth: $F_{[2, 16070]}$ = 729.2, $P < 0.001$, R^2m = 0.12, R^2c = 0.50; Temperature: $F_{[2, 16070]}$ = 3592.7, $P < 0.001$; Table 2). On average, lake trout occupied similar depths during spring (least squares mean: 8.7 m [95 % CI: 7.4-10.2 m]), winter (8.9 m [7.5-10.3 m]), and fall (9.7 m [8.3-11.2m]) and much deeper depths during summer (13.8 m [12.1-15.6 m]) (Table 2, Fig. 3a). This seasonal depth selection translated to lake trout occupying similar water temperatures during spring (7.4 °C [7.2-7.7 °C]), summer (6.5 °C [6.3-6.7 °C]), and fall (6.7 °C [6.5-6.9 °C]), but much colder temperatures during winter (2.9 °C [2.7-3.0 °C]) (Table 2, Fig. 3b), when no water > 4 °C would have been available (Fig. 2).

The spatial location of lake trout estimated as the depth of water over which they were located (i.e. bathymetric depth) also differed by season ($F_{[2, 16070]}$ = 490.45, $P < 0.001$, R^2m = 0.15, R^2c = 0.45; Table 2), and followed observed trends in depth and temperature occupancy. Lake trout were spatially located over shallower regions of the lake in spring (least squares mean: 10.8 m [95 % CI: 9.5-12.3 m]), over the deepest regions during summer (17.6 m [16.0-19.3 m]), and over intermediate water depths during fall (13.9 m [12.5-15.5 m]) and winter (11.3 m [10.0-12.7 m]) (Table 2, Fig. 3c). These can be visualized in the spatial locations of the seasonal core areas of lake trout within Alexie Lake, where core areas in spring and winter are located over shallower regions of lake and closer to the shorelines relative to summer and fall (Fig. 4). The size of core areas coincided to lake trout occupancy of shallow water, as

core areas were largest in spring (127.8 ha) and smallest in summer (80.8 ha), while that of winter (104.3 ha) was slightly larger than fall (91.3 ha) (Figs. 3c, 4).

The amount of time lake trout spent within the littoral zone on a daily basis differed markedly among seasons ($F_{[2, 16069]}$ = 150.97, $P < 0.001$, R^2m = 0.12, R^2c = 0.50; Table 2). On average, lake trout spent the most time each day within the littoral zone during spring (6.00 h [5.24-6.75 h]) and least time during the summer (0.17 h [0.09-0.43 h]) and occupied the littoral zone similarly during fall (4.23 h [3.81-4.75 h]) and winter (4.16 h [3.76-4.64 h]) (Fig. 5a). Although the average number of daily littoral forays ($F_{[2, 5554]}$ = 11.07, $P < 0.001$, R^2m = 0.01, R^2c = 0.20) and the duration of these forays ($F_{[2, 5554]}$ = 44.26, $P < 0.001$, R^2m = 0.04, R^2c = 0.34) each differed among seasons, these behaviours were highly variable from day to day, evident from the low R^2m values (Table 2). Lake trout made the least number of daily forays into the littoral zone during summer (3.90 [3.27-4.64]) and more forays during the spring (5.81 [4.91-6.89]), fall (5.18 [4.47-5.99]), and winter (5.07 [4.41-5.82]), during which lake trout made a similar number of forays (Fig. 5b). When lake trout made forays, they were longest during fall (1.20 h [0.88-1.63 h]) and similar in duration for spring (0.60 h [0.43-0.84 h]), summer (0.64 h [0.45-0.91 h]), and winter (0.58 h [0.43-0.78 h]) (Fig. 5c)

Each of the distance travelled measures differed among seasons (Vertical: $F_{[2, 16069]}$ = 83.49, $P < 0.001$, R^2m = 0.03, R^2c = 0.28; Horizontal: ($F_{[2, 16069]}$ = 188.97, $P < 0.001$, R^2m = 0.06, R^2c = 0.42), Total: ($F_{[3, 16069]}$ = 149.97, $P < 0.001$, R^2m = 0.05, R^2c = 0.38; Table 2, Fig. 6). Lake trout were most active during spring, travelling a total (i.e. horizontal + vertical movement) of 9.7 km [8.6-10.8 km] each day, and least active during summer, when they travelled 5.9 km [5.1-6.7 km] each day (Fig. 6c). Lake trout were second and third most active during winter and fall, during which they travelled an average of 8.8 km [7.9-9.7 km] and 7.7 km [6.9-8.6 km] each day, respectively (Fig. 6c). Horizontal movement contributed most of the total distance travelled and as a result, differences in horizontal movement among seasons were similar to total distance travelled (Spring: 8.9 km [7.8-10.3 km]; Summer: 5.0 km [4.3-5.6 km]; Fall:

6.4 km [5.7-7.3 km]; Winter: 7.9 km [7.0-8.9 km] (Fig. 6a). Vertical distance travelled by lake trout was highest in spring (0.23 km [0.20-0.26 km]) and lowest in winter (0.12 km [0.10-0.15 km]). Daily vertical activity in summer and fall averaged 0.19 km [0.16-0.21 km] and 0.15 km [0.12-0.17 km], respectively (Fig. 6c). Although the differences in vertical distance travelled seemed small (i.e. difference between spring and summer being only 0.11 km) there is on average only ≈ 12 m and at maximum 32 m of vertical habitat to traverse in Alexie Lake. Therefore, a difference in vertical activity of 0.11 km would equate to a lake trout moving from the surface to the bottom of the deepest point of Alexie Lake about four times each day.

Diet

Lake trout diets in Alexie Lake varied seasonally (Table 3). Lake trout stomachs collected in winter, spring, and fall contained similar amounts of prey (Table 3). Stomachs from winter contained mostly stickleback (76 %) and cisco (21 %) with spoonhead sculpin and benthic invertebrates/terrestrial insects accounting for 2 % and 1 % of stomach contents by mass, respectively (Table 3). In spring, lake trout stomachs contained mainly benthic invertebrates/terrestrial insects (80 %) and cisco (12 %), with *Mysis* and stickleback accounting for the remaining 1 % and 5 % of contents by mass, respectively (Table 3). The stable isotope mixing models advised that the summer diet of lake trout did not contain benthic invertebrates/terrestrial insects and was mainly comprised (94 %) of a mix of prey fish species (stickleback: 16 %; cisco: 16 %; deepwater sculpin: 29 %; spoonhead sculpin: 14 %; and slimy sculpin: 19 %) and a small amount of *Mysis* (6 %) (Table 3). During fall, stomachs contained mainly stickleback (64 %) and benthic invertebrates/terrestrial insects (34 %), with cisco and spoonhead sculpin each accounting for 1 % of contents by mass (Table 3).

Growth rates

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The VBG models resulted in estimated (±SE) asymptotic fork length ($L\infty$) and weight ($W\infty$) of 528.4 ±

10.5 mm (t = 50.17, P < 0.001) and 1,623.3 ± 84.6 g (t = 19.18, P < 0.001), respectively, each with

corresponding growth coefficients (K) of 0.16 ± 0.01 (K_L: t = 19.18, P < 0.001; K_W: t = 19.18, P < 0.001).

The resultant VBG equations were as follows: $(t) = 528.4(1 - e^{0.16(t-t0)})$; $W(t) = 1,623(1 - e^{0.16(t-t0)})^3$ (Fig. 7).

Bioenergetics

Based on the VBG equation for weight, a 500 g lake trout in Alexie Lake would have been age 7 and

would have grown to 606 g by age 8. To achieve this annual growth of 106 g under current climate

conditions, as measured empirically in this study, a 500 g lake trout would have needed to feed at 44 %

of its maximum consumption each day and consumed a total of 1,358.6 g of food (Fig. 8a). Under

simulated conditions with changes in season length under the 2 °C warming scenario, the same

size/aged lake trout would need to only eat at 42 % of its maximum capacity to achieve the same annual

growth. This means that if that fish were to eat at the same rate in warming conditions as typical

conditions (44 % of maximum), it would consume an additional 28.6 g of food and in turn grow 8 g larger

(Fig. 8a). For a mature lake trout at roughly asymptotic weight (1,600 g) to gain 7 % of its weight, the

minimum for spawning (Eschmeyer 1955) it would have to eat at least 41 % of its maximum capacity

each day or a total of 2,714.9 g, reaching a final body weight of 1,715.5 g over one year (Fig. 8b). The

same lake trout eating at 41 % of its maximum capacity under the warming scenario would grow an

added 12.3 g and eat an additional 53 g of food. Under warming a 1,600 g lake trout would only need to

eat 40 % of its theoretical maximum consumption to reach 7 % annual growth (Fig. 7b). Overall, lake

trout growth was ≈ 5 % more efficient under warming conditions compared to current conditions for

both 500 g and 1,600 g fish.

Discussion

We found that the habitat use, movement, and diet of lake trout in a northern lake varied with large

seasonal fluctuations in air and water temperatures that are synonymous with high-latitude regions.

Specifically, we show that the behaviour and diet of lake trout was governed in part by a combination of

ice-cover and the existence of water temperatures > 15 ˚C. Lastly, bioenergetics simulations indicated

that the growth, consumption, and growth efficiency of lake trout would all increase under a 2 ˚C

warming scenario relative to current conditions observed during this study. The findings here provide a

first attempt at evaluating the year-round behaviour of lake trout in a northern lake and predicting how

its bioenergetics may be altered by climate change.

During the open-water season, the behaviour and diet of lake trout was associated with the

presence of water temperatures exceeding 15 °C in this northern lake. Each year following ice-off when

lake temperatures were cool, lake trout occupied the shallower regions of the lake, were highly active,

and spent long periods in the littoral zone, presumably feeding mainly on emergent insects and benthic

invertebrates, which dominated stomach contents. This occupancy of shallow water and high feeding

rate of littoral prey has been found in many southern lakes (Martin 1952, Plumb and Blanchfield 2009,

Guzzo et al. 2017) and has been found to be a critical period for lake trout growth in both lakes with and

without pelagic prey fish (King et al. 1999, Guzzo et al. 2017). Although lake trout in Alexie Lake used the

littoral zone often during spring, its reliance on this area was much lower than observed by Guzzo et al.

(2017), who monitored lake trout using telemetry in a small southern lake with no pelagic prey fish.

However, the size and food web of Alexie Lake are more characteristic of what would be considered a

typical temperate lake trout lake compared to the smaller lakes that lack pelagic prey fish, which have

been the focus of most telemetry studies (Morbey et al. 2006, Blanchfield et al. 2009, Plumb and

Blanchfield 2009, Wall and Blanchfield 2012, Guzzo et al. 2017). The reduced occupancy of the littoral

zone by lake trout in Alexie Lake is likely due to a general lack of cyprinid prey fish species, and the fact

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that stickleback in Alexie Lake were rarely observed or captured near the shoreline and were often observed shoaling at the edge of steep drop-offs. The presence of large northern pike in the nearshore area (Guzzo et al. 2016), which had been observed attacking adult lake trout during the study, and the availability of pelagic prey fish species including cisco likely also contributed to the reduced littoral use in Alexie Lake.

During summer, lake trout seemingly avoided the littoral zone. In addition to the threat of northern pike predation, littoral zone water temperatures during summer exceeded 15 °C. Thus, lake trout avoidance of this region in summer is consistent with physiological studies that have shown a rapid decline in aerobic scope for lake trout when in waters that exceed 15 °C (Evans 2007, Kelly et al. 2014). Similar behaviour by lake trout has also been found in small southern lakes (Plumb and Blanchfield 2009, Guzzo et al. 2017). However, the average daily temperatures occupied by lake trout during summer in Alexie Lake were typically below those optimal temperatures for aerobic scope and growth (10 ± 2 ˚C; Connor et al. 1981, Christie and Regier 1988b). This occupancy of lake depths where water temperatures are below the optimal range for lake trout have been observed in previous studies of lake trout habitat use (Snucins and Gunn 1995, Mackenzie-Grieve and Post 2006, Plumb and Blanchfield 2009). This use of habitat with sub-optimal temperature could be because in heterogeneous environment fish grow faster when energetics is optimized with respect to many key factors (e.g. temperature, food availability, and activity) rather than temperature alone (Crowder and Magnuson 1983, Plumb et al. 2014). Indeed, during summer lake trout occupied deep offshore waters within the hypolimnion where they fed exclusively on prey fish. The low activity and small core area of lake trout during summer were likely a result of reduced volume of optimal thermal habitat, including reduced access to the littoral zone. As littoral zone temperatures cooled to ≤ 15 °C signifying the start of fall, the depth and space use of lake trout quickly shifted to shallower nearshore water, activity increased, and they began to spend more time in the littoral zone, presumably to spawn (Redick 1967, Muir et al. 2012, Callaghan et al. 2016).

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After this initial shift to the nearshore, lake trout activity and their presence in littoral regions declined as they recovered from spawning (Fry 1939).

During winter (i.e. ice-covered period), which lasted nearly 7 months each year, lake trout were highly active despite cold water temperatures < 4 ˚C. Lake trout moved both vertically and horizontally around the lake and often used the littoral zone during this period, likely to capture stickleback, which comprised a large portion of their winter diets. These findings of high activity during winter are like those of Blanchfield et al. (2009) who found that activity levels of lake trout in a small southern lake were similar between summer and winter. However, Blanchfield et al. (2009) showed that lake trout mainly occupied the upper 3 m of the water column near the deepest part of the lake, suggesting that lake trout were making many small movements in a localized area, possibly due to light limitation. In contrast, we show that on average lake trout occupied much deeper habitat (≈ 9 m depth), displayed high degrees of both vertical and horizontal activity, made movements in and out of the littoral zone, and had large core area sizes, suggesting that lake trout in Alexie Lake used larger portions of the lake in winter. This difference in activity between lakes could be due to the broader prey fish community of Alexie Lake, but may also be because winters are 1-2 months longer in Alexie Lake relative to more southern lakes (Guzzo and Blanchfield 2017).

Using the same criteria as Guzzo et al. (2017), we found that the spring and summer periods in Alexie Lake were much shorter, by 14 d and 49 d, respectively, than observed in the small southern Boreal Shield Lake used in that study. Although the length of fall was similar between these two lakes, the winter was over one month longer in Alexie Lake compared to the southern lake studied by Guzzo et al. (2017). We also found that the length of spring, summer, and winter were relatively similar among years in Alexie Lake; however, the between-year difference in fall length was quite large. This finding of differences in fall length between years of differing annual temperatures contrasts with studies of smaller ELA lakes which found that fall length did not change with warming (Guzzo and Blanchfield 2017,

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Chapter 3). This difference in fall length among study years may indicate that changes in seasonal

phenology may be different in the north. While we did only have data for two consecutive years

representing the fall season, at the very least, this result suggests that more data from northern lakes

are necessary to better understand how these systems may respond to warming and perhaps cautions

extrapolating data from southern lakes to infer changes to northern lakes.

We used empirically-informed bioenergetics simulations to model the growth and consumption

of lake trout under current and warming scenarios. Our model simulating the change in growth and

consumption under warming conditions was based on using proportions of maximum consumption (p-

values) that were calibrated using empirical data on lake trout growth, temperature occupancy, activity,

and diet from our northern study lake. Model outputs suggest that the growth, consumption, and

growth efficiency (i.e. growth per gram of food) of immature (500 g) and mature fish near asymptotic

size (1,600 g) would increase with warming compared to current conditions. Our finding that growth of

lake trout would increase with warming is like Hill and Magnuson (1990) and Kao et al. (2015) who used

bioenergetics models to show that lake trout in the Great Lakes growth would increase under various

climate change scenarios when allowing consumption to increase under warming. However, when prey

availability was assumed to be limiting and consumption was held constant, growth efficiency increased

for the youngest fish and decreased for larger fish (Kao et al. 2015). In contrast to our findings, a

bioenergetics study by McDonald et al. (1996) predicted that if July air temperatures increased by 3-6°C,

young of year (YOY) lake trout in an Arctic lake would need to increase consumption by 8-10-fold to

survive their first winter. This negative finding was because YOY lake trout in Arctic lakes occupy littoral

waters where predation risk but also food availability is low. However, these findings for this Arctic lake

may not be applicable to our study lake, as YOY lake trout are thought to occupy the deepest regions in

north-temperate lakes (Davis 1997, Davis et al. 1997). Increases in growth with warming have also been

found for other northern cold-water fish populations. Carey and Zimmerman (2014) used bioenergetic

models to show that least cisco (*Coregonus sardinella*) in an Arctic Lake would undergo increased

growth and production with warming, even when assuming constant feeding rates. Similarly, Schindler

et al. (2005) found that the growth of juvenile sockeye salmon (*Oncorhynchus nerka*) in Alaska were

greater in warmer years due to increases in zooplankton densities.

A major threat of warming to lake trout is the possibility for warm-water species currently found

in boreal regions, particularly smallmouth bass (*Micropterus dolomieu*), to expand their range north

(Sharma et al. 2007, 2009). In lakes which have been invaded by smallmouth bass, lake trout have been

shown to have a reduction in the amount of littoral prey fish in their diets due to competition for this

prey item with bass (Vander Zanden et al. 1999, Morbey et al. 2007). If smallmouth bass were to invade

Alexie Lake they would likely rely on stickleback, a main diet item for lake trout, as their main prey, as

these are in abundant numbers in proximity to the nearshore. Therefore, an invasion of smallmouth

bass would likely have impacts on the diet of lake trout by forcing them to use more pelagic prey items

which typically require more activity to capture in open-water. This increased reliance on pelagic prey by

lake trout could in turn have impacts on its growth and fitness (King et al. 1999, Guzzo et al. 2017).

However, under warming, other littoral prey fish species like cyprinids may also expand north, which

may benefit lake trout and/or potentially moderate potential impacts of a bass invasion. An additional

threat of climate change on northern lake trout is that the warmer summer water temperature and

expanded growing season may favour more thermal-tolerant cool water species such as northern pike.

An increase in the northern pike population or in their body size related to warming would increase the

threat of predation and further reduce lake trout's ability to access critical littoral resources (Werner et

al. 1983, Plumb et al. 2014).

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Table 1 – Seasonality in ice-cover and water temperatures in Alexie Lake during the study period.

Year	Ice-off date	Start of summer	Start of fall	Ice-on date	Spring length	Summer length	Fall length	Winter length
2012	NA[1]	NA[1]	2012-09-10	2012-10-31	NA[1]	NA[1]	51	209
2013	2013-05-27	2013-06-22	2013-08-31	2013-11-09	27	71	70	202
2014	2014-05-29	2014-06-20	2014-08-27	NA[1]	23	66	NA[1]	NA[1]

[1] Data required to calculate these dates and periods were not available as they fall outside of the study period

Table 2 – Result of linear mixed effects models testing for the effect of season on the behaviour of acoustic-tagged lake trout in Alexie Lake. Individual fish nested within study year were each treated as random intercepts in each model. Temporal auto correlation was corrected for using autoregressive (AR) and AR and moving average (ARMA) correlation structures. Transformations of each response variable + 1 are indicated in brackets in the first column. R^2m is the marginal coefficient of determination and is the proportion of variance accounted for by the fixed effect season. R^2c is the conditional coefficient of determination and is the proportion of variance accounted for by the fixed effect season and the random effects of individual fish nested within study year.

Response variable	Marginal F-test for Season	Correlation structure	R^2m	R^2c
Depth (square-root)	$F_{[2, 16070]}$ = 729.2, P < 0.001	AR (p = 1): ϕ = 0.90	0.12	0.50
Temperature (square-root)	$F_{[2, 16070]}$ = 3592.7, P < 0.001	AR (p = 1): ϕ = 0.88	0.59	0.60
Bathymetry depth (square-root)	$F_{[2, 16070]}$ = 490.45, P < 0.001	AR (p = 1): ϕ = 0.77	0.15	0.45
Time in littoral zone ($\log_{10}$)	$F_{[2, 16070]}$ = 150.97, P < 0.001	ARMA (p = 1, q = 1), ϕ = 0.91, ϑ = -0.31	0.12	0.50
Number of littoral forays ($\log_{10}$)	$F_{[2, 16070]}$ = 11.07, P < 0.001	ARMA (p = 1, q = 1), ϕ = 0.82, ϑ = -0.41	0.01	0.20
Average foray durations ($\log_{10}$)	$F_{[2, 16070]}$ = 150.97, P < 0.001	ARMA (p = 1, q = 1), ϕ = 0.83, ϑ = -0.32	0.04	0.34
Horizontal distance travelled ($\log_{10}$)	$F_{[2, 16070]}$ = 188.97, P < 0.001	AR (p = 1): ϕ = 0.58	0.06	0.42
Vertical distance travelled ($\log_{10}$)	$F_{[2, 16070]}$ = 83.49, P < 0.001	AR (p = 1): ϕ = 0.64	0.03	0.28
Total distance travelled (square-root)	$F_{[2, 16069]}$ = 149.97, P < 0.001	AR (p = 1): ϕ = 0.56	0.05	0.38

Table 3 – Seasonal diet composition of lake trout in Alexie Lake as quantified by stomach contents (SC) and stable isotopes (SI) with corresponding sample size (n) with number of empty stomachs in brackets and mean fork length of lake trout sampled with fork length range in brackets. Each diet value is the mean ± SD proportion that a given diet item made up of the total diet. This was quantified on a mass basis for SC and using Bayesian mixing models for SI. For SC, the mean ± SD total mass of contents from stomachs that were not empty are presented in the total mass column.

Season	Fork length	n	Total mass	Inverts/ Insects	Mysis	Stickleback	Cisco	Deepwater sculpin	Spoonhead sculpin	Slimy sculpin
Winter (SC)	480.9 (367-550)	15 (1)	5.96 ± 11.6	0.01 ± 0.02	Not found	0.76 ± 0.36	0.21 ± 0.37	Not found	0.02 ± 0.86	Not found
Spring (SC)	486.2 (415-588)	27 (4)	6.13 ± 7.23	0.80 ± 0.36	0.01 ±0.03	0.05 ± 0.20	0.14 ± 0.32	Not found	Not found	Not found
Summer (SI)	366.5 (186-606)	13	NA^2	NA^1	0.06 ± 0.04	0.16 ± 0.11	0.16 ± 0.10	0.29 ± 0.15	0.14 ± 0.09	0.19 ± 0.04
Fall (SC)	494.8 (414-556)	16 (3)	7.35 ± 10.6	0.34 ± 0.46	Not found	0.64 ± 0.44	0.01 ± 0.03	Not found	0.01 ± 0.03	Not found

[1]Diet item was not including in mixing model to reduce number of sources after an initial mixing model indicated that this item did not contribute to the summer diet of lake trout. [2] Mass of stomach contents not estimable using isotopes.

Table 4 – Conditions imposed on lake trout growth during a typical year and a year with mean air temperatures increased by 2 °C. Length (number of days) of each season was determined by water temperatures and ice presence. Daily temperature occupancy (Temp) (°C) was the least squares mean of temperature occupancy of telemetry-tagged fish. Activity is a measure of average swimming speed per day in cm s^{-1} and was estimated as the least squares mean for distance travelled using acoustic telemetry. See methods for details. Each simulation was run with starting weights of 500 g and 1,600 g.

Simulation	Fall			Winter			Spring			Summer		
	Length	Temp	Activity	Length	Temp	Activity	Length	Temp	Activity	Length	Temp	Activity
Current conditions	66	6.7	8.7	204	2.9	10.1	25	7.5	11.2	70	6.6	6.7
Warming scenario	66	6.7	8.7	190	2.9	10.1	25	7.5	11.2	84	6.6	6.7

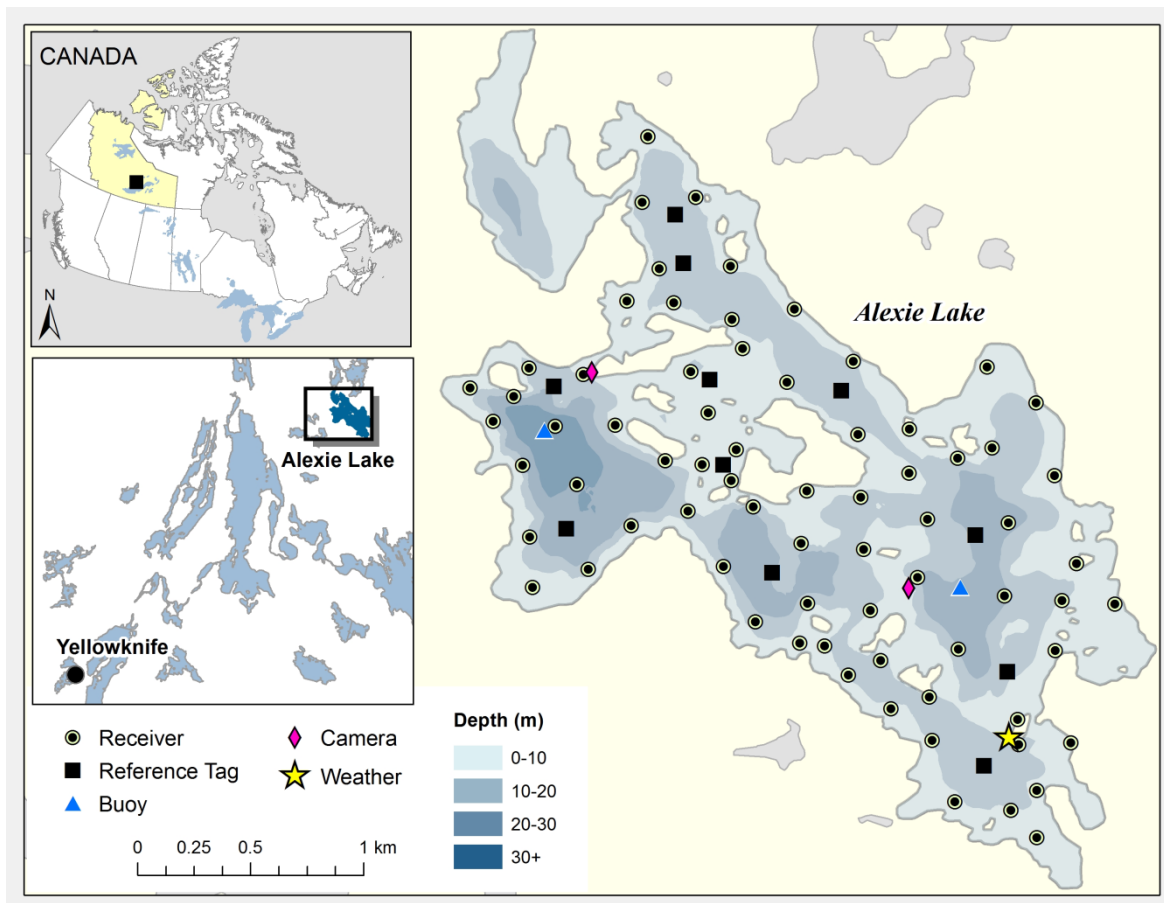**Figure 1** – Map indicating the location of Alexie Lake, NT, Canada (inset), including the locations of 72 telemetry receivers with corresponding co-located sync tags (circles), acoustic reference tags (squares), buoys to which temperature loggers were attached (triangles), ice-monitoring trail cameras (diamonds), and the weather station used to monitor air temperature and wind direction and speed (star). Depth contours are every 10 m.
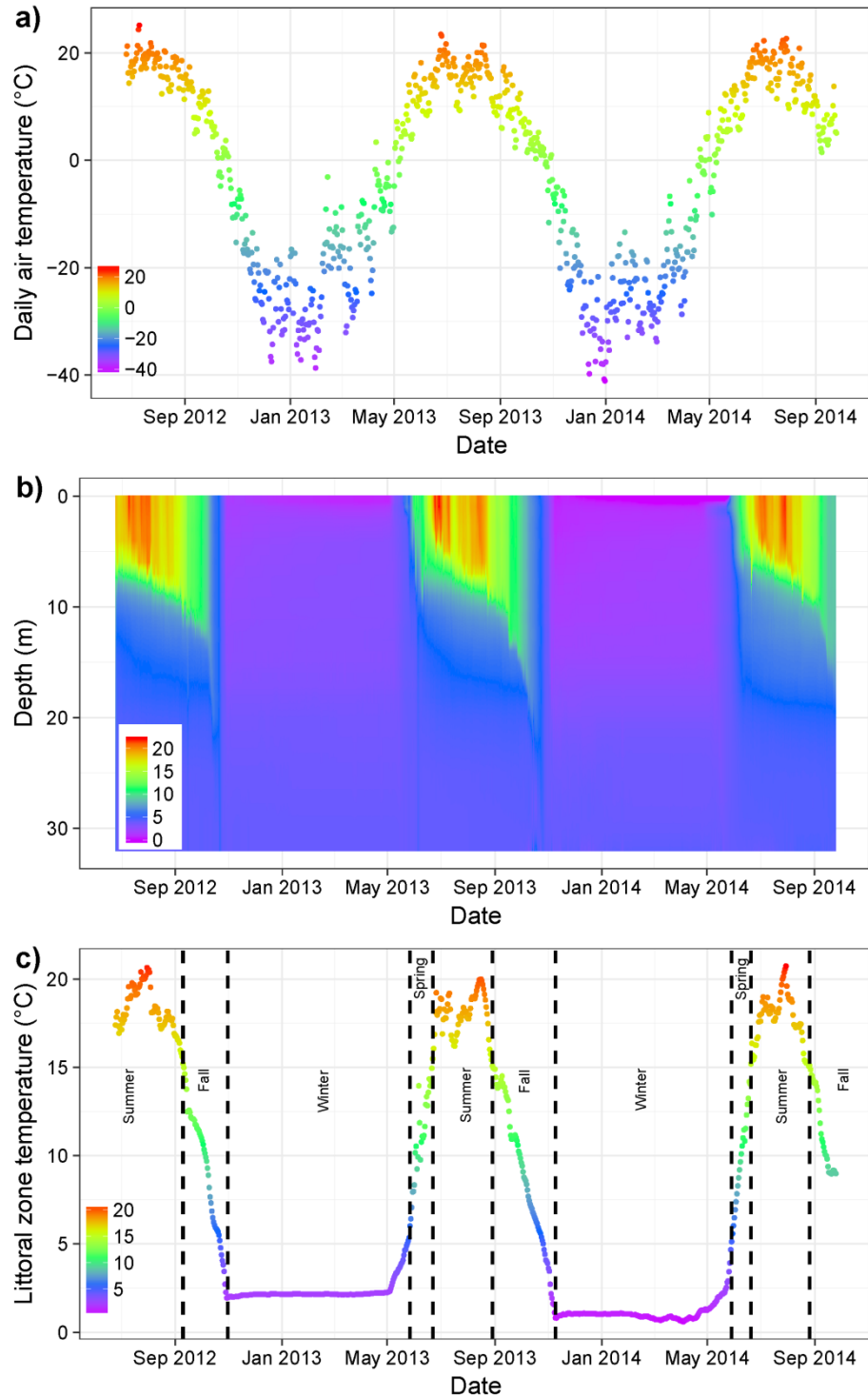
Figure 2 – Mean daily (a) air temperature, (b) lake water temperature profiles, and (c) littoral zone (depths < 6 m) water temperatures in Alexie Lake during the study period (25 June 2012-25 September 2014). Winter is the period when the lake was ice-covered. Spring is the period between ice-off and the date before the mean littoral zone temperature was > 15 ˚C. Summer is the period when mean littoral zone temperature was >15 ˚C. Fall is the period between when lakes cooled to ≤ 15 ˚C until ice-on.
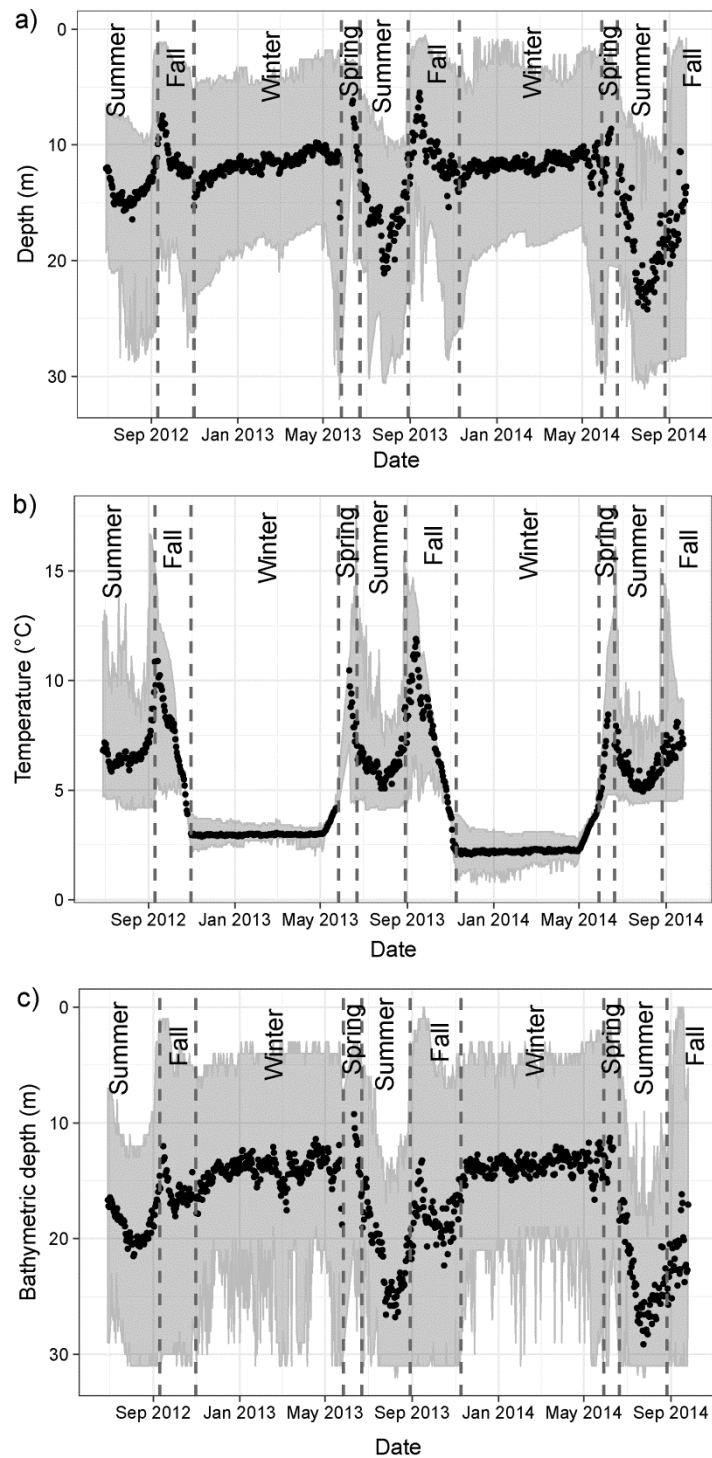
Figure 3 – Mean daily habitat use of acoustic-tagged lake trout in Alexie Lake during 2012-2014, including (a) depth within the water column, (b) temperature occupancy, and (c) bathymetric depth (i.e. depth of water over which they are located). Each black dot is the mean daily estimate for all tagged fish and the shaded gray region represents the area encompassed by the 5th and 95th percentiles.
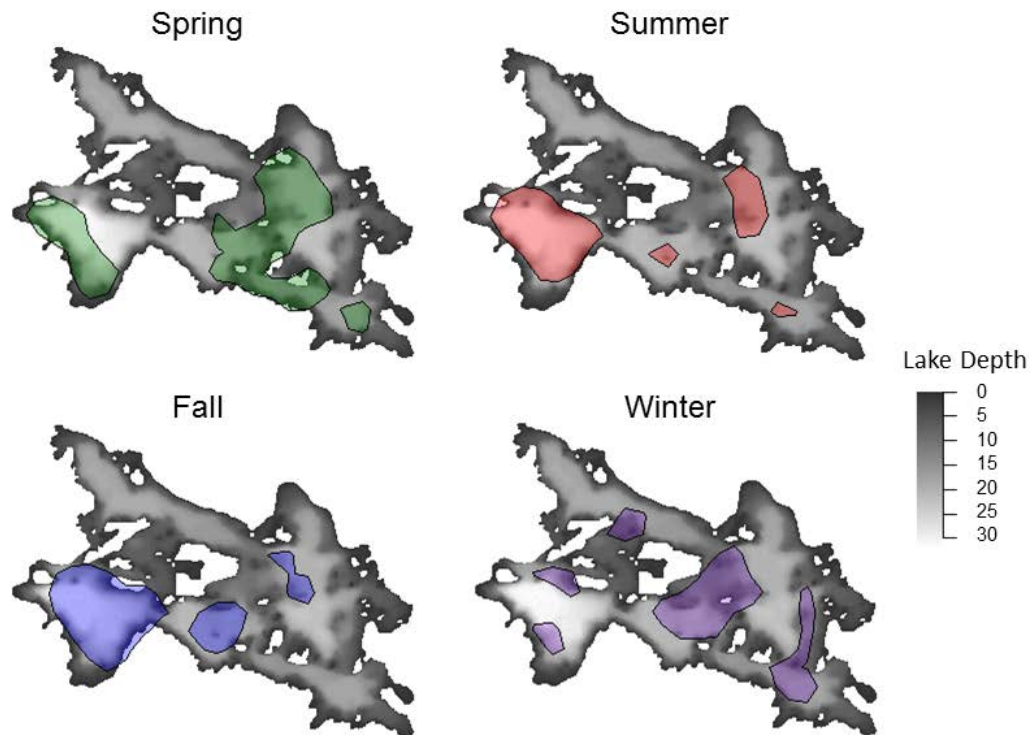
Figure 4. – Seasonal core areas (50 % kernel utilization distributions) of acoustic-tagged lake trout in Alexie Lake during 2012-2014 overlaid on a bathymetry map of the lake.
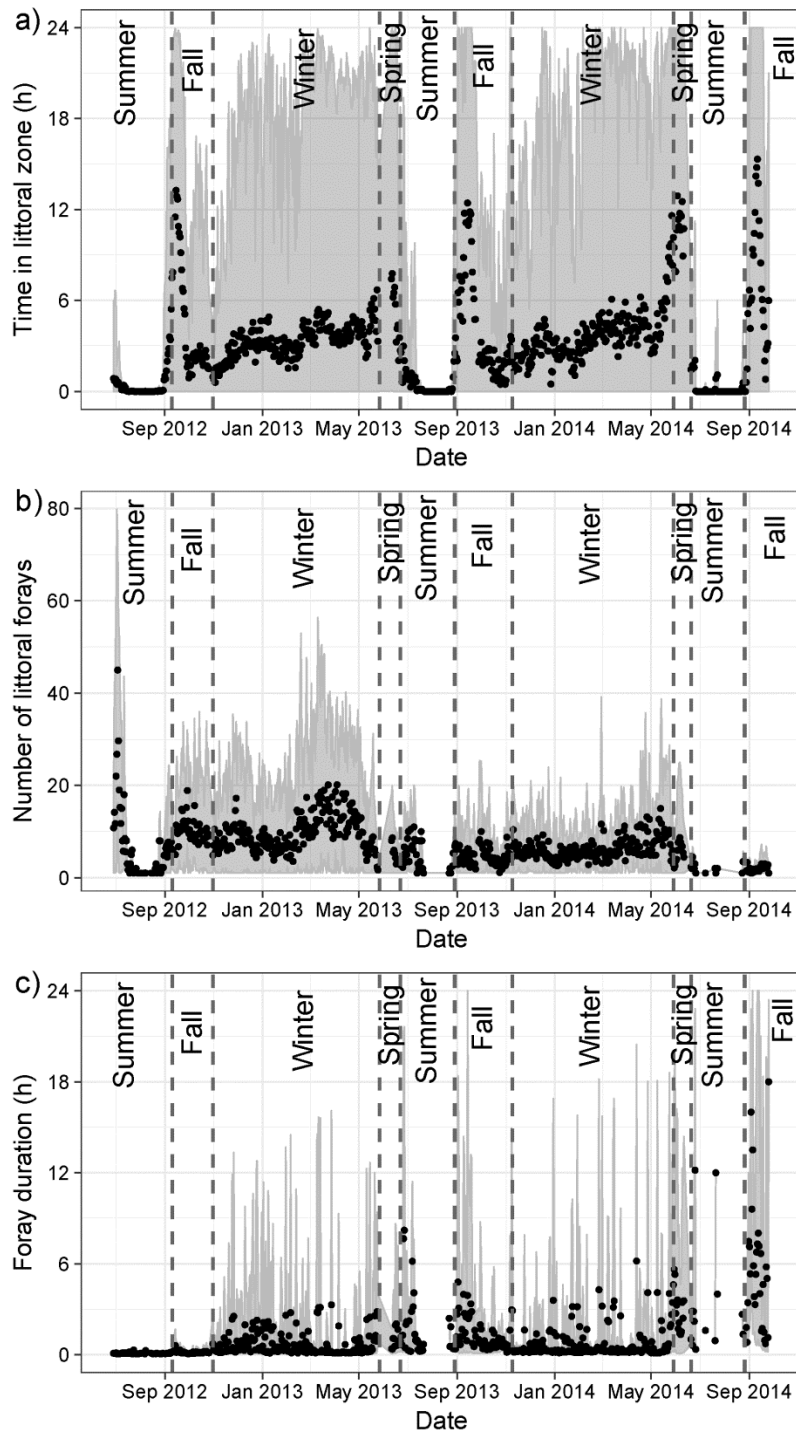
Figure 5 – Mean daily littoral habitat use of acoustic-tagged lake trout in Alexie Lake during 2012-2014, including the (a) total time spent within the littoral zone, (b) number of littoral forays, and (c) the average duration of littoral forays. Each black dot is the mean daily estimate all tagged fish and the shaded gray region represents the area encompassed by the 5th and 95th percentiles.
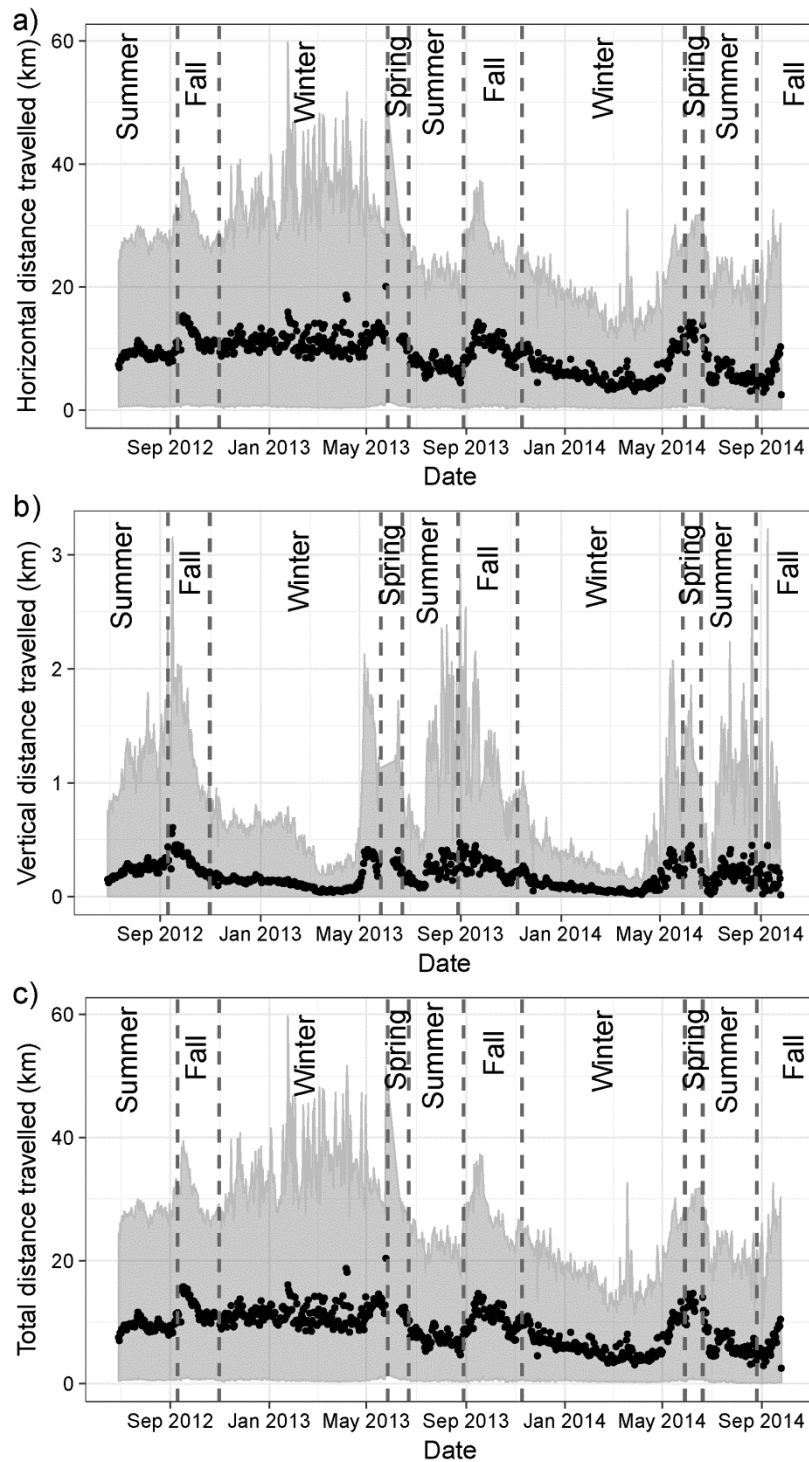
Figure 6 – Mean daily activity estimates of acoustic-tagged lake trout in Alexie Lake during 2012-2014, including the (a) horizontal distance travelled, (b) vertical distance travelled, and (c) total distance travelled (horizontal + vertical). Each black dot is the mean daily estimate for all tagged fish and the shaded gray region represents the area encompassed by the 5th and 95th percentiles.
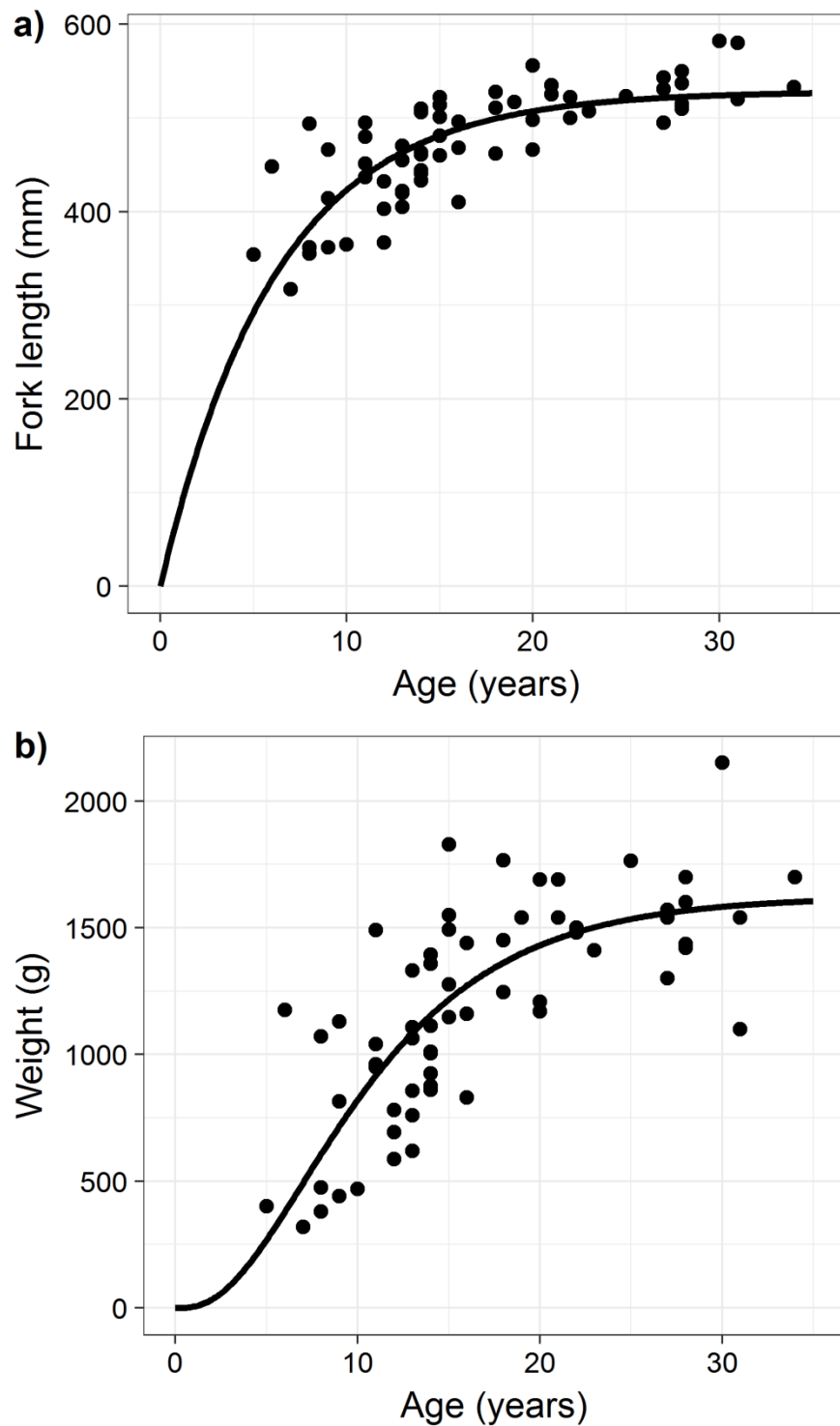
Figure 7 – (a) Fork length-at-age and (b) weight-at-age data of lake trout collected from Alexie Lake, NT during 2011-2013. Each data point is an individual fish and trend lines are best fits of the von Bertalanffy growth curves.
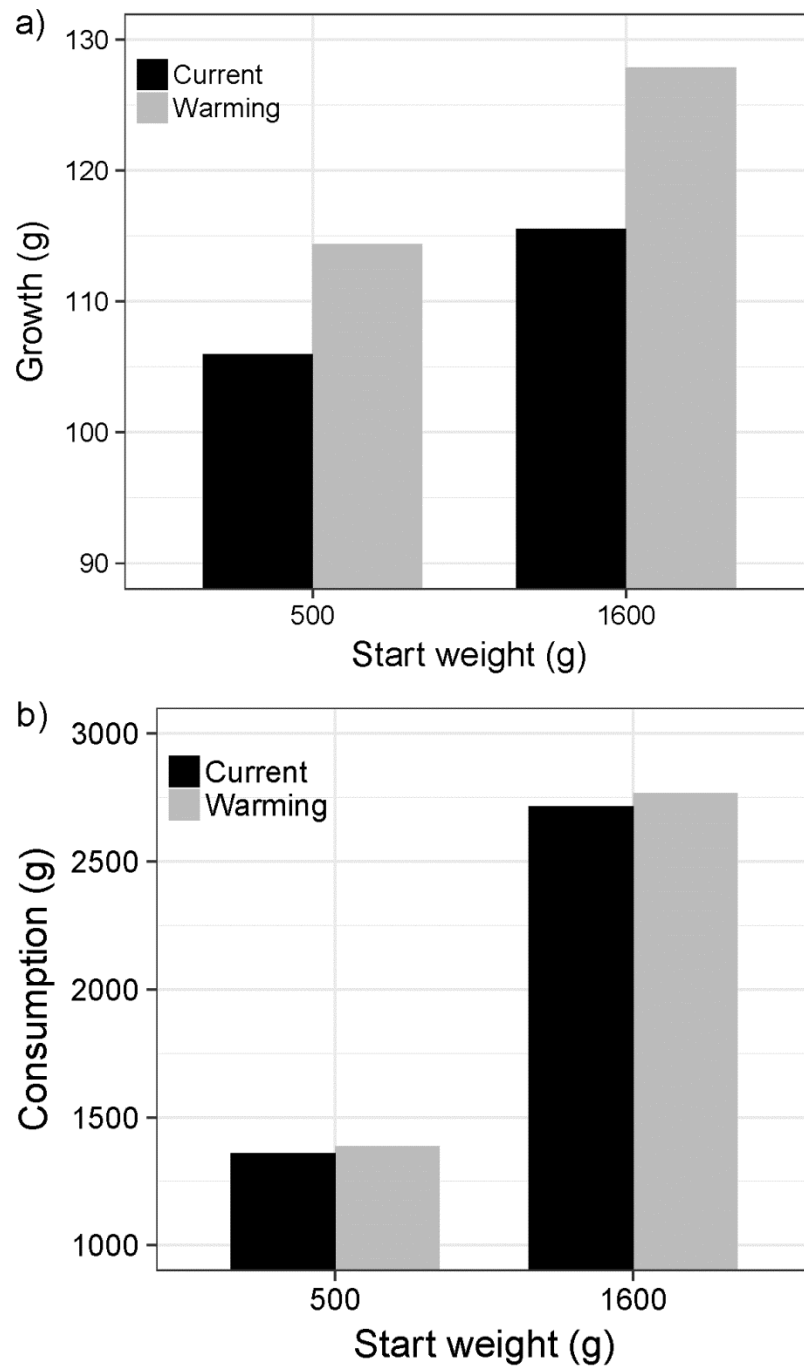
Figure 8 – Comparison of modelled annual growth and consumption of a 500 g and 1,600 g lake trout under current and simulated warming climatic conditions using the Wisconsin bioenergetic model. Model runs included average conditions during the study (2012-2014; "Current"), and a 2 °C "Warming" scenario that where summer length increased by 14 d and winter (i.e. ice cover) was reduced by 14 d (see Methods).

Telemetry Error Filtering

The fourth step in our filtering of raw positional telemetry data was to use the estimated positions of sync tags relative to their known derived locations to define data filters based on hyperbolic positioning error (HPE). HPE is a unitless position precision measure assigned to each estimated position that describes the relative error sensitivity of that position (Smith, 2013). The goal of this step of filtering was to balance the retention of positions and minimize the mean positioning error. This was achieved by first plotting out the $\log_{10}$-mean daily position measured error (i.e. estimate position location vs. known location of a sync tag) vs. the $\log_{10}$-mean daily HPE over time (Fig. S1). Because there were seven download and data analysis periods, the HPE values vary over the study period; this pattern in clear in Fig. S1. Importantly, we see that HPE and measured error closely match one another over the entire study period, providing confidence in our use of HPE to filter fish position data. We then calculated the mean measured error of sync tag positions within each one unit interval bin of the HPE for each data period separately for each download/analysis period (Fig. S2). A break-point regression was then applied to each measured error-HPE curve to determine at which point an HPE cut off would no longer improve the measured error. The estimated break points (i.e. estimated HPE cut offs) were typically just prior to the asymptote of each curve (Table 1, Fig. S2). After applying the HPE cut offs to all seven datasets, we retained 88 % of the original positions that entered this phase of data filtration. The seven datasets were then combined and used for the next step of data filtering before being used in analyses.

Table S1 – Results of hyperbolic positioning error (HPE) data filtering for the acoustic telemetry dataset. The dataset was broken up into seven period corresponding to the various receiver downloads and spatial position estimation by VEMCO.

| Period	Date range	Raw measured error	HPE cut off	Filtered measured error	Proportion remaining
1	28 June 2012 – 11 Sept 2012	7.01 ± 22.63	35.14 ± 0.19	4.45 ± 5.12	0.97
2	14 Sept 2012 – 27 Oct 2012	10.41 ± 35.13	34.90 ± 0.27	4.95 ± 5.97	0.95
3	28 Oct 2012 – 25 May 2013	36.78 ± 79.84	115.28 ± 0.53	19.14 ± 23.25	0.93
4	11 June 2013 – 24 Sept 2013	9.48 ± 24.95	52.67 ± 0.40	5.97 ± 7.63	0.97
5	28 Sept 2013 – 1 Nov 2013	12.17 ± 38.44	12.63 ± 0.13	3.84 ± 3.35	0.85
6	1 Nov 2013 – 11 June 2014	22.66 ± 73.67	30.55 ± 0.23	6.64 ± 6.94	0.89
7	20 June 2014 – 25 Sept 2014	20.07 ± 46.38	56.71 ± 0.59	10.30 ± 11.11	0.93
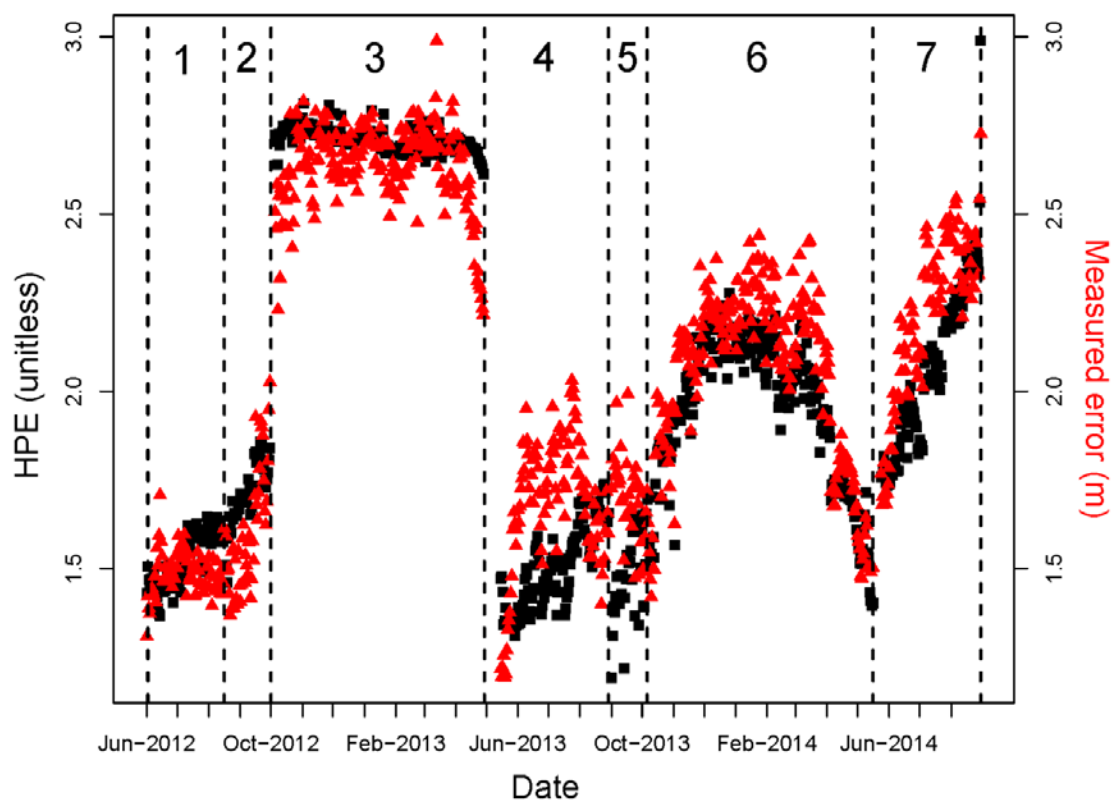
Figure S1 – Variations in mean daily $\log_{10}$ HPE (black squares) and $\log_{10}$ measured error (red triangles) for sync tag positions estimated by VPS over the course of the study.
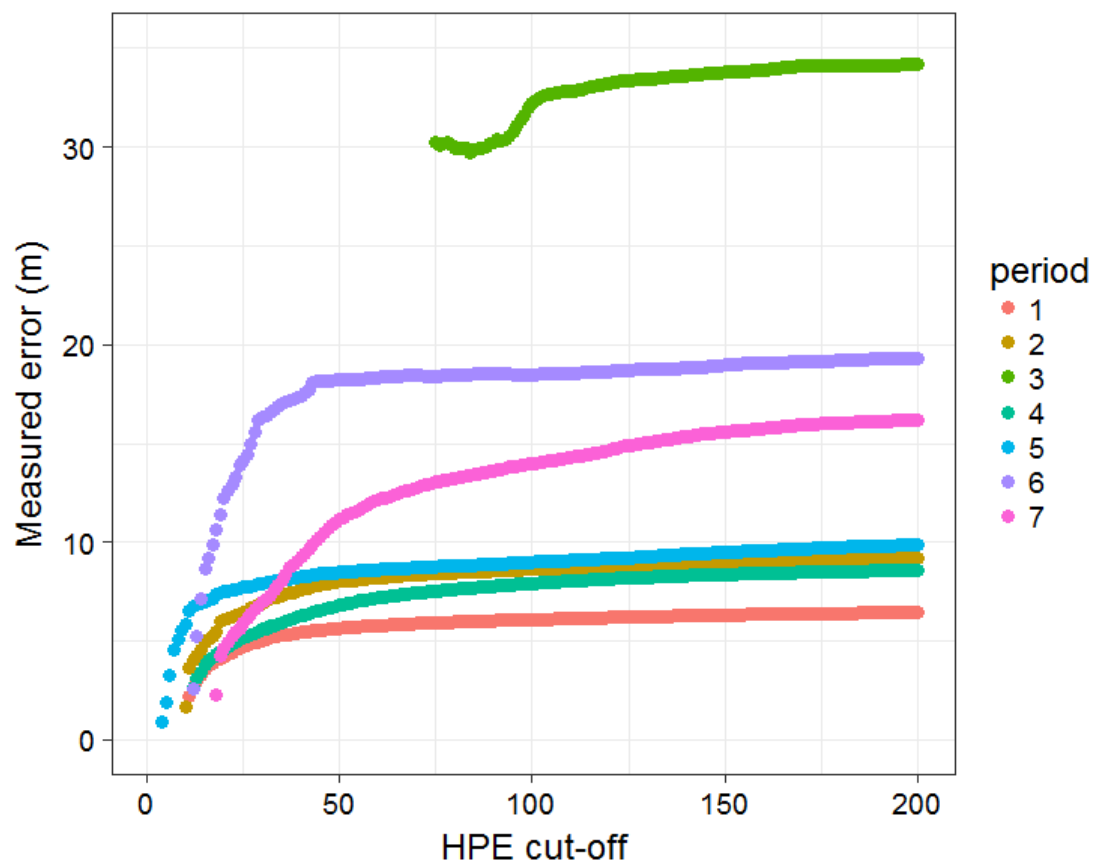
Figure S2 – Changes in mean measured error of estimated sync tag positions as a function of various HPE cut-offs.

EPILOGUE

Lake trout has been considered a sentinel species for understanding the impacts of climate change on north-temperate lake ecosystems because the warmer temperatures expected in this region directly impact cold-water habitat that is vital to its survival. Yet, despite a rich literature describing the ecology of lake trout in north-temperate lakes (e.g. Gunn et al. 2004), surprisingly few studies have quantified the impacts of climate change on lake trout in these systems, particularly at the northern extent of this climate zone. Existing research on the climate effects on north-temperate lake trout populations mainly stems from lakes near the southern portion of lake trout's distribution, with information on northern systems being sparse. Climate-related research on lake trout from southern lakes has focused heavily on the volume of oxythermal habitat available during the open-water season (Schindler et al. 1996, Herb et al. 2014), with little focus on how the phenology of thermal habitat may be changing in response to warming (but see Jansen and Hesslein 2004), and how this altered phenology may modify prey availability, behaviour and growth. Studies by Plumb and Blanchfield (2009) and Plumb et al. (2014) represent an initial attempt to understand how changes in thermal habitat related to warming translate to lake trout habitat use, diet, and growth. These studies examined lake trout habitat use in a warm and cool year and concluded that in warmer years, longer periods of warm water existing during the open-water season restrict lake trout's access to littoral energy, particularly during spring, and according to bioenergetics modelling should result in reduced growth. Although these studies occurred in a lake without pelagic prey fish, where the importance of littoral energy for growth is magnified, their conclusion that spring is a critical period for annual growth is supported by studies from larger lakes containing pelagic prey fish, where lake trout growth was also found to be reduced in years with earlier onset of thermal stratification (King et al. 1999). However, these studies led by Plumb were unable to include empirical growth data to test whether lake trout growth was indeed lower in warmer years. Moreover, no studies to date have used long-term data to test if the growth and size structure of lake

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trout populations have changed over time in response to warming. My research addresses this

knowledge gap by combining long-term habitat, behaviour, and growth data to further understand how

north-temperate lake trout populations are impacted by climate change.

The primary goal of my thesis was to understand how climate change, specifically warming,

impacts north-temperate lake trout populations. My research was divided between two geographical

areas and lake types comprising two sections of my thesis. Much of my thesis focused on examination of

long-term datasets from small, well-studied, near-pristine research lakes at the Experimental Lakes

Area, which is located near the southern extent of lake trout's distribution at this longitude (Section A;

see Prologue). This dataset allowed for a detailed understanding of how climate change alters the

phenology and amount of habitat for lake trout and how these changes in habitat transcend to alter lake

trout behaviour, growth, and life-history. The second area of focus was on lake trout from a northern

lake (> 60 °N latitude), where climate change is predicted to have strong influence on cold-water habitat

(Prowse et al. 2006a, 2006b, Wrona et al. 2006) (Section B; see Prologue). For this research I conducted

a detailed examination of lake trout diet, activity and habitat use over a period of 2 years in a northern

lake, and used the findings from my earlier thesis chapters to direct analysis of the seasonal ecology of

lake trout in this system and predict how its growth may be impacted by warming.

Research focused on long-term datasets from southern lakes draw clear links between

increasing air temperatures and lake trout habitat, behaviour, and growth. Chapter 1 showed that the

main impact of warming on lake trout habitat is through seasonal shifts in phenology, specifically

reductions in the duration of ice-cover, increases in the number of days that surface water temperatures

were cool (≤ 15 °C) in spring, and delayed timing of cooling in fall. The chapter also showed that in the

longest studied lakes, the complete elimination of optimal oxythermal habitat for lake trout was

becoming more common over time. Chapter 2 showed that lake trout use of the littoral zone (< 6 m

depth) during the open-water season was greatest in spring, and lake trout use of this habitat became

limited when the mean temperature exceeded 15 °C. This criterion was based on the mean temperature of the entire littoral zone to define seasons during the open water period, and was different than in Chapter 1, which used surface temperatures. Together these findings suggest that the use of only surface water temperatures, which are commonly collected instead of detailed profile data, may overestimate the length of the period when littoral zones are accessible for lake trout. In fact, a reanalysis of data presented in Chapter 1 performed in Chapter 3 instead found that the summer period, when littoral zone temperatures were > 15 °C, actually become longer over time, while the length of spring did not change. Chapter 2 also showed that littoral habitat and energy use by lake trout were both positively related to spring length and negatively related to summer length, but showed no trend with fall length or prey fish density. Consequently, annual changes in the growth and condition of lake trout were positively correlated to littoral habitat and energy use. This supports previous research suggesting that the littoral zone disproportionately (relative to the littoral zone size vs. rest of lake) contributes to the energy sources of fish (Hampton et al. 2011, Vander Zanden et al. 2011). Together these results suggest that in more stressful years, those with shorter springs and longer summers, lake trout have reduced access to littoral habitat and therefore assimilate less littoral energy, resulting in reduced growth and condition. These findings also highlight the importance of the spring period for lake trout growth in thermally-stratifying lakes.

Chapter 3 found that during 1986-2013, the growth and size structure of a lake trout population within a long-term monitoring lake had shifted. The size of premature fish increased while mature fish have decreased in size, resulting in a reduced mean size and maximum body size of the population. Additionally, age of maturity has decreased by two years and the population is now made up of a larger number of younger, smaller fish of lower condition compared to at the start of population monitoring. Concomitant with these reductions in adult size and condition, the abundance of lake trout has increased, but since they are of smaller average size, the biomass of the population has remained

constant; supporting the idea that carrying capacity is based on biomass, not abundance. No obvious

trends in the size or density of littoral prey fish, lake trout's main prey were observed over time,

suggesting this was not the main cause of body size changes. Instead, the observed changes in the

growth and size-structure of the population are consistent with the concept that longer growing seasons

cause by warming will result in "faster" life histories (Waples and Audzijonyte 2016) and is supported by

an increase in maximum size of lake trout found with increasing latitude (Rypel 2014) and other studies

that have found similar trends toward faster life histories of fish populations with decreasing latitude

(Weber et al. 2015). Indeed, my bioenergetic modelling simulations based on empirical data of season

length, temperature occupancy, and diet closely matched the observed trends for premature fish. For

adults, the decline in body size could only be achieved when age of maturity was reduced from 6 to 4

years old, as found in empirical data. In fact, when age of maturity was held constant, the size and

consumption of adult fish actually increased over time, in contrast to the observed trends. Together

these results suggest that early growth and development increases with warming, likely due to shorter

winters and in turn longer periods when optimal temperatures for growth existed each year (i.e.

growing seasons). This finding of plastic maturity with warming is supported by studies that have found

that maturation is linked to temperature and growth rate (Alm 1959, Policansky 1982, 1983). When

these results are linked back to findings of Chapter 2, it suggests that reductions in maximum adult body

size could be a result of three factors. First, advanced maturation results in investment of energy into

reproductive organs at an earlier age, thereby slowing growth. Second, reductions in life span prevent

lake trout from reaching larger sizes. Third, longer summers reduce the ability of adult fish to make up

growth lost to reproduction in the previous years.

Chapter 4 of my thesis applied knowledge gained from Chapters 1-3 to analyze a comparable

two year dataset from a larger northern lake that contained pelagic prey fish and two other predatory

fish. The Canadian North is expected to warm at a rate nearly double that than the rest of country (IPCC

2014, Warren and Lemmen 2014) and may have implications alter the ecology and growth of lake trout, but little information exists on the seasonal ecology of lake trout in this region. Chapter 4 found that similar to the southern ELA lakes studied in Chapters 1-3, the behaviour and in turn diet of lake trout were governed in part by a combination of ice-cover and the existence of water temperatures > 15 ˚C. The consistent finding that temperatures of 15 ˚C direct the behaviour of lake trout suggests this may provide the best criteria to measure changes in thermal habitat for this species, especially since aerobic scope declines rapidly above this temperature (Evans 2007, Kelly et al. 2014). Another interesting finding in Chapter 4 was lake trout's reduced use of the littoral zone in the northern lake, particularly in spring, relative to the small southern lakes. This lower use of the littoral zone may have been a result of the predation threat of large northern pike, availability of pelagic prey fish, or due to the lack of prey fish species in this region, as stickleback were found off deep drop-offs rather than close to shore, where cyprinids are found in southern lakes (Guzzo et al. 2014). Bioenergetics simulations informed by empirical data on temperature occupancy, daily activity, and seasonal diet indicated that the annual growth, consumption, and growth efficiency of both immature and mature lake trout would all increase under a 2 ˚C warming scenario relative to current conditions observed during this study. These results are comparable to bioenergetics results of Chapter 3, which found that immature lake trout and adult lake trout (assuming a constant age of maturity) would have greater growth and consumption over a period of warming in the small southern lakes.

Based on the research completed in this thesis, I suggest that the most immediate impacts of warming to north-temperate lake trout populations are as follows:

1. Changes in phenology of seasonal water temperature, particularly longer summers, will reduce lake trout's access to important littoral resources, leading to lower annual growth and condition, and this impact will be magnified in lakes without pelagic prey fish.

2. Longer open-water seasons (i.e. reduced ice-cover) increase the length of the growing season, which allows immature fish to grow and mature faster, but will have a shorter lifespan, which will lead to reduced maximum adult body sizes.

3. Later cooling in fall will delay fall spawning.

4. The main difference between the impacts of warming between southern (ELA) and northern lake is that the impact of warming on the growth of lake trout in the northern lake appears beneficial, at least in the short-term, but not so for ELA lakes. However, if shifts in maturity occur in the northern lakes, then similar changes in size-structure as found in the ELA lakes may arise over time.

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