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

Matthew M. Guzzo^{a,*} & Paul J. Blanchfield^{a,b}

^a Department of Biological Sciences, University of Manitoba, 50 Sifton Road, Winnipeg, Manitoba, Canada, R3T 2N2

^b Freshwater Institute, Fisheries and Oceans Canada, 501 University Crescent, Winnipeg, Manitoba, Canada, R3T 2N6

* Corresponding author email: mattguzzo12@gmail.com (M.M. Guzzo)

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 d. 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, moreso 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.

Keywords: cold-water fish, air temperature, precipitation, thermal stratification, global warming, temperate lake

Introduction

Cold water with high dissolved oxygen (DO) concentrations (i.e. oxythermal habitat) defines the habitat requirements of cold-water fish (Gibson and Fry 1953, 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 1953, 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, and vulnerable life-history, make lake trout a sentinel species for studying the effects of 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). But, with increases in air temperature expected to occur across seasons it is likely that changes in the thermal habitat phenology may be profound, and these may modulate changes in lake thermal structure. Here, we use long-term meteorological and limnological monitoring data collected over the past 44 years to quantify how variations in air temperature and precipitation have altered the lake trout habitat in four small Boreal Shield lakes. Our specific objectives were to (1) quantify how variations in air temperature and precipitation relate to the temporal changes in thermal habitat for lake trout, and (2) determine if long-term trends in oxythermal habitat have occurred, and how they relate to air temperature and precipitation.

Materials and Methods

Study site and datasets

This study used long-term monitoring data collected during 1970–2013 within the Experimental Lakes Area (ELA), located in the Boreal Shield of northwestern Ontario, Canada (49°40'N,

93°44W). The ELA is a set of 58 lakes and their watersheds closed to the public for conducting aquatic research (Blanchfield et al. 2009a). The forests of ELA are dominated by jackpine (*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 in excess of 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 Canada's Rawson Lake (Lake 239) meteorological station since 1969. Annual dates of winter ice-formation and break-up dates (hereafter 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 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, ON, 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, MA, USA). Sampling and laboratory methods were consistent over the entire study period. When changes in equipment or methods took place, vigorous calibrations were performed to ensure data were comparable (Stainton et al. 1977, Schindler et al. 1996a, Prairie 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 a given year, with air temperature calculated as a calendar year and precipitation calculated as a water year (November 1–October 31). 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 $<10\text{ }^{\circ}\text{C}$ and $\text{DO}>6\text{ mg}\cdot\text{L}^{-1}$, while usable habitat was bound between

temperatures $<15\text{ }^{\circ}\text{C}$ and $\text{DO}>4\text{ mg}\cdot\text{L}^{-1}$ (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 ($<15\text{ }^{\circ}\text{C}$) 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: (1) Winter – a period of cold temperatures ($1\text{--}4\text{ }^{\circ}\text{C}$), 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 ($4\text{--}15\text{ }^{\circ}\text{C}$) 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 $15\text{ }^{\circ}\text{C}$; (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 $\geq 15\text{ }^{\circ}\text{C}$; and, (4) Fall – the period occurring as lake temperatures cool to $<15\text{ }^{\circ}\text{C}$ 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 ($<10\text{ }^{\circ}\text{C}$) 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

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 ~30 y cycle (Prairie 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 had an effect on the phenology of thermal habitat, minimum volumes of oxythermal habitat, and lake surface water temperatures within each study lake. 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 dataset, we accepted a higher chance of type-1 error and considered $p < 0.1$ as statistically significant for all analyses. All data processing, analyses, and figures were completed in R (Version 3.2.1, R Development Core Team 2015).

Results

Air temperature and precipitation

Annual air temperatures at the ELA increased at a rate of $0.043\text{ }^{\circ}\text{C}\cdot\text{y}^{-1}$ from 1970 to 2013, representing a $1.84\text{ }^{\circ}\text{C}$ increase in mean temperature, from $1.77\text{ }^{\circ}\text{C}$ to $3.61\text{ }^{\circ}\text{C}$ (Fig. 2a). Annual temperatures were quite variable over the study period, ranging by $4.37\text{ }^{\circ}\text{C}$, with a minimum of $0.86\text{ }^{\circ}\text{C}$ and maximum of $5.23\text{ }^{\circ}\text{C}$, 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 $0.039\text{ }^{\circ}\text{C}\cdot\text{y}^{-1}$ and $0.078\text{ }^{\circ}\text{C}\cdot\text{y}^{-1}$, 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 (Prairie et al. 2009) indicating that ELA precipitation is part of a ~ 30 year cycle of wet and dry periods. During the study period, annual precipitation ranged by $1.45\text{ mm}\cdot\text{d}^{-1}$, from a minimum of $1.33\text{ mm}\cdot\text{d}^{-1}$ to a maximum of $2.78\text{ mm}\cdot\text{d}^{-1}$ (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 that summer precipitation rates were more variable in 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•d⁻¹.

Thermal habitat phenology

The average length of the winter ice-covered season decreased over time, becoming 19 d 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 d greater than in the first half of the study (Fig. 3). There was marginal, but non-significant evidence that spring ice-off dates became earlier over time ($slope=-0.21$ d•y⁻¹, $p=0.11$). Ice-off dates ranged by 42 d, with the earliest being on April 5, 2012 and latest on May 17, 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 d in the second half of the study. In contrast, there was strong evidence that fall ice-on dates became later over time ($slope=0.21$ d•y⁻¹, $p=0.002$), increasing by since 1970. Seven of the eight latest ice-on dates have occurred since 1999. Fall ice-on dates ranged by 31 d, with the earliest on November 4, 1991 and latest on December 1, 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 is in agreement 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 one 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 (Fig. 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 and fall ice-on dates were strongly related to air temperatures experienced during their respective seasons (Fig. 5a, d). Overall, Mar-May and Sep-Nov air temperatures accounted for 75 % and 61 % of the variation in ice-off and ice-on dates, respectively. Ice-off was 4.38 d earlier for every 1 °C increase in average Mar-May air temperature (Fig. 5a). In contrast, warmer Sep-Nov air temperatures meant later ice-on dates, where ice formed 3.64 d later for every 1 °C increase in average Sep-Nov air temperature (Fig. 5d). The slopes (Lake x 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 ($est=-2.51$, $se=0.33$, $r^2=0.30$, $p<0.001$; Fig. 5b) and began 2.51 d 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 ($est=1.82$, $se=0.40$, $r^2=0.13$, $p<0.001$) and the slopes (Lake x 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 d for every 1 °C increase in Mar-May air temperature (Fig. 5c). Interestingly, the length of spring only decreased by 0.59 d for each day that the ice retreated later into spring ($est=0.59$, $se=0.07$, $r^2=0.35$, $p<0.001$, 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 one week (5 d) to almost two months (59 d) (Fig. 5c). In the fall season, the slopes (Lake x 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 ($est=1.77$, $se=0.38$, $r^2=0.14$, $p<0.001$), where summer lasted 1.77 d 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 ($est=2.14$, $se=0.43$, $r^2=0.15$, $p<0.001$); the slopes (Lake x 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 d, and increased in length by 2.15 d 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 y), while those sampled for shorter time periods (the last 26–27 y) showed no trends (Fig. 6a). The surface water temperatures of all lakes were highly related to Jun-Aug air temperatures, which explained 78 % of the variation in summer surface water temperature (Fig. 6b). Because of the similarly strong relationships between Jun-Aug air temperature and summer surface water temperature, we expect that Lake 373 and Lake 442 would have shown similar increases in surface water temperature if 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 than 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 (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 (Fig. 4b, e).

Oxythermal habitat

We did not test for monotonic trends in the maximum extent of isotherm, oxyclines, or minimum habitat volumes because these measures are highly dependent on precipitation and watershed processes that were cyclic over the study period (Fig. 2c, d, Fig. 7). Qualitative observation of Figure 7, specifically the longest datasets from Lake 239 and Lake 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 (Fig. 2c, d). This was corroborated by the fact that annual maximum depths of the 10 °C 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 °C 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 not differ (Lake x 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 x 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 $6 \text{ mg}\cdot\text{L}^{-1}$ and $4 \text{ mg}\cdot\text{L}^{-1}$ oxyclines were relatively constant over the study period, except for the $4 \text{ mg}\cdot\text{L}^{-1}$ 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 (Fig. 2c, d, Fig. 7b). The maximum extent of the $6 \text{ mg}\cdot\text{L}^{-1}$ 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 $4 \text{ mg}\cdot\text{L}^{-1}$ 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: $\text{est}=0.07$, $\text{se}=0.03$, $z=2.22$, $p=0.03$), 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 one week up to 75 and 100 d, and in Lake 442, optimal habitat has been completely 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 occur 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 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, Prairie 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 the 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 are in agreement 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 (Schindler et al. 1990, Magnuson et al. 2000, Futter 2003, Keller 2007, Latifovic and Pouliot 2007, Benson et al. 2012, Sharma and Magnuson 2014, Sharma et al. 2016). Winter (i.e. period of ice-cover) is often recognized to be a period when cold water temperatures slow metabolic processes and limit growth (Kerr 1971); however, indication that lake trout feed almost exclusively 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 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 started both earlier during warmer springs), the slope of the relationship for the start date of summer was lower than 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 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 likely 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 as a result 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 to 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 °C 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 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 2–4 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 1953, 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, VanderZanden 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 four 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 ; m³), maximum depth (Z_{max} ; m), watershed area (A_w ; ha), watershed to surface area ratio (A_w/A_s), light attenuation coefficient ($mE_{inst} \cdot m^{-1} \cdot sec^{-1}$), 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	3.0×10^6	27.4	97.5	3.8	0.29	6.5
239	1970–2013	54.3	5.7×10^6	30.4	393.3	7.2	0.65	4.0
373	1986–2013	27.3	3.0×10^6	20.8	80.6	3.0	0.38	6.3
442	1987–2013 ²	16.0	1.4×10^6	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.

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718 **Table 2.** Results of linear regressions testing for relationships between the annual estimates of the maximum depth of the thermal
719 barrier for lake trout and mean annual precipitation. Individual regressions were performed because significant differences because,
720 significant differences in slopes or intercepts were found for both isotherm measures (see Results for ANCOVA statistics).

Lake	Measure	<i>Estimate</i>	<i>Standard error</i>	<i>df</i>	<i>t-value</i>	<i>p-value</i>	<i>r</i> ²
224	15 °C isotherm	-1.92	0.37	28	-5.16	<0.001	0.47
	10°C isotherm	-1.95	0.67	28	-1.50	0.007	0.20
239	15 °C isotherm	-0.54	0.36	37	-3.93	0.14	0.03
	10 °C isotherm	-0.54	0.53	37	-4.85	0.32	0.00
373	15 °C isotherm	-1.35	0.34	21	-2.90	<0.001	0.40
	10 °C isotherm	-1.56	0.95	21	-1.02	0.08	0.10
442	15 °C isotherm	-1.29	0.27	16	-1.79	<0.001	0.57
	10 °C isotherm	-1.16	0.53	16	-2.17	0.04	0.18

721 **Bold** values are significant at $p<0.1$.

Figure captions

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 ~30 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 $p < 0.1$.

748

749 **Figure 4.** Long-term variations in the phenology of lake trout thermal habitat constraint in four
750 small boreal shield lakes within the Experimental Lakes Area, including (a) start date of summer
751 (i.e. date that the 15 °C isotherm develops), (b) the end date of summer (i.e. date that the 15 °C
752 isotherm breaks down),, and (c) length of summer (i.e. number of days with a 15 °C isotherm). A
753 trend line and corresponding Sen's slope estimate are present in plots where a Mann-Kendall
754 test indicated a significant monotonic trend at $p < 0.1$. The label on the left of each plot indicates
755 the individual study lake. The y-axes of among lakes are scaled the same so that differences in
756 magnitude can be compared.

757

758 **Figure 5.** Relationships between spring and fall air temperature and timing of important
759 limnological events in four small Boreal Shield lakes located within the Experimental Lakes Area
760 during 1970–2013. Panels a–c are relationships between spring air temperature and (a) end
761 date of winter (i.e. spring ice-off date), (b) start date of summer (i.e. date that the 15 °C isotherm
762 develops), (c) length of spring (i.e. number of days between end of winter and start of summer).
763 Panels d–e are relationships between fall air temperature and (d) start date of winter (i.e. fall
764 ice-on date), (e) end date of summer (i.e. date that the 15 °C isotherm breaks down), (f) length
765 of fall (i.e. number of days between end of summer and start of winter).

766

767 **Figure 6.** Long-term variations in (a) surface (1 m depth) water temperature and relationships
768 between summer air temperature and (b) surface water temperature and (c) summer length, in
769 four small boreal shield lakes within the Experimental Lakes Area. A trend line and
770 corresponding statistics are present in plots where a Mann-Kendall test or regression indicated
771 a significant relationship at $p < 0.1$.

772

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 - 15 °C isotherm) and dissolved oxygen (panel b - 4 mg•L⁻¹ oxycline) boundaries and corresponding habitat volumes (panel c). Dashed lines and hollow points refer to theoretical optimal lake trout thermal habitat (panel a - 10 °C isotherm) and dissolved oxygen (panel b - 6 mg•L⁻¹ oxycline) boundaries and corresponding habitat volumes (panel c). Horizontal dot-and-dash lines on panel “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.

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789 Figure 1.

790 Figure 2

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792 Figure 3

Figure 4

Figure 5

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