LAKE TROUT (*SALVELINUS NAMAYCUSH*) OTOLITHS AS INDICATORS OF PAST

CLIMATE PATTERNS AND GROWTH IN ARCTIC LAKES

By

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Abstract

The effects of climate change on freshwater ecosystems are amplified in high-latitude regions, however, Alaska climate data are limited due to the remote location of the Arctic. Predictions have indicated that warming temperatures owing to climate change could increase fish growth, but the magnitude and factors influencing these changes remain uncertain. Here I investigated the relationship between Lake Trout *Salvelinus namaycush* growth and physical and biological characteristics, fish community structure and climate patterns. I applied biochronology techniques to predict recent climate patterns from annual growth increments recorded on Lake Trout otoliths. Growth increments were also used to perform length-at-age back-calculations and to estimate the growth coefficient K, as described by a von Bertalanffy growth model. Lake Trout were captured from 13 climate-sensitive lakes in the Fish Creek watershed in Arctic Alaska during 2014 and 2015. Individual Lake Trout ($N = 53$) ranged from 471–903 mm fork length (FL; mean = 589.3 mm) and their readable annuli, representative of age, ranged from 9–55 annual growth increments. I constructed a growth chronology for the period 1977–2014 and used model selection to identify the best predictive model of relative Lake Trout growth (ring width index; RWI) as a function of climate descriptors. A single covariate model was the best predictor and indicated that RWI tracked mean August air temperature recorded at a local weather station from 1998–2013 ($P < 0.001$; $R^2_{adj} = 0.55$; $RMSE = 0.048$). Lake Trout growth (K) was subsequently modeled as a function of physical and biological characteristics, and fish community structure, using multiple linear regression. The highest ranked model included physical (i.e., depth, distance to river and coast, connectivity class, and number of stream intersections) and biological (sex) covariates. Model averaging indicated K was higher in deeper, well connected lakes, located further from the coast and was lower with increasing distance from

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a large river, though the relationship with depth was found to be the single significant covariate. This study demonstrated the utility of biochronology techniques to estimate past climate patterns in remote regions, and provided valuable knowledge regarding growth-environment relationships for Lake Trout. In turn, this information can be used to better understand the effects of a changing environment in sensitive Arctic lake ecosystems.

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General Introduction

High-latitude ecosystems, such as those found in Arctic Alaska, have shown increased effects of climate change relative to other regions across the Earth (Serreze et al. 2000). For example, climate records indicate that air temperatures in Arctic North America increased 0.6°C per decade from 1981–2013, approximately three times the global average increase of 0.2°C per decade during the same time period (Comiso and Hall 2014). These patterns are expected to continue across the Arctic into the near future (Serreze and Barry 2011). As temperatures increase, many physical and biological processes will be affected (Hinzman et al. 2005), such as declines in sea ice (Wendler et al. 2014), warming of permafrost (Osterkamp and Romanovsky 1999), increasing lake temperatures (O'Reilly et al. 2015), and changes in lake ice phenology (Arp et al. 2010). The direction of these changes is well documented, yet the rate, magnitude, and future implications for Arctic regions are uncertain.

Aquatic ecosystems, specifically lakes, dominate the landscape of Arctic Alaska, covering 20–40% of the region (Grosse et al. 2013). Climate change directly affects Arctic lake temperature through the aforementioned processes (Carpenter et al. 2011). For example, lake temperatures are known to be strongly related to air temperatures (Schneider and Hook 2010). Accordingly, increases in air temperatures are expected to result in increased lake temperatures across Arctic Alaska (Rouse et al. 1997). This is especially true for lakes on the Arctic Coastal Plain, which are often minimally stratified (termed polymictic; Lewis 1983) during the ice-free period due to relatively shallow depths, high winds, and a short ice-free period (Hinkel et al. 2012). This mixing causes these lakes to be more responsive to inter-annual variability in terms of air temperature and, therefore, more sensitive to climate warming in the region (Adrian et al. 2009).

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Water temperature is often a defining physical characteristic in aquatic ecosystem processes (Brett 1956). Lake temperature changes may have implications for aquatic biota because warmer lake temperatures lead to increased summer stratification and changes to primary productivity (Rouse et al. 1997; Hobbie et al. 2003; Prowse et al. 2006). Water temperatures and associated ecosystem changes play an important role in fish growth through metabolic processes (Clarke and Johnston 1999). In general, growth is expected to increase as temperature and productivity increase (McDonald et al. 1996; Reist et al. 2006; Carey and Zimmerman 2014). Growth in fishes is often used as a fundamental proxy for individual fitness, and growth rates have been shown to be influenced by physical and biological characteristics as well as fish community structure (Le Cren 1951; McDonald et al. 1996; Beauchamp 2009; Blair et al. 2013). These increases in growth may appear to be positive, but there are inherit problems associated with increased growth. Increased growth or abundance may cause a population to outgrow the available food source (Elliott 1990). For example, an individual-based bioenergetics model predicted that a 3°C increase in mean monthly water temperature during the ice-free months could alter Lake Trout *Salvelinus namaycush* growth and metabolism to the point where the increased demands for energy intake exceeded any corresponding increase in food availability (McDonald et al. 1996). As a top predator, Lake Trout hold an important place in aquatic food webs. Their diverse diet consists of forage fishes as well as invertebrates, allowing them to have impacts across a wide range of trophic levels (Hershey 1990). Changes to lake ecosystems are expected to have far reaching effects on growth; however, the specific effects of increasing lake temperatures on Lake Trout in Arctic Alaska lakes have yet to be quantified.

The science of dating annual growth layers in woody plants and the extrapolation of associated environmental information (dendrochronology) has provided a reliable proxy to

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reconstruct past environmental parameters in terrestrial ecosystems (Shroder 1980). These same techniques can be applied to aquatic ecosystems using annual growth increments recorded on fish otoliths. The method of using otoliths from long-lived fishes to measure growth and its relationship with environmental parameters has been tested and shown to be a reliable proxy for climate reconstruction (Smith et al. 2008; Black et al. 2013). Lake Trout otoliths provide an opportunity for this method due to this species' long life span and their distribution across Arctic Alaska and Canada (Wilson and Herbert 1998). Lake Trout are long-lived, known to exceed 50 years of age in Arctic ecosystems (Power 1978; Burr 1987). In other parts of their range, Lake Trout inhabit deep oligotrophic lakes that seasonally stratify. Because of minimal summer stratification and the short ice-free period, lakes on the Arctic Coastal Plain track seasonal variability in air temperature (Arp et at. 2010) and thus are quite variable in their temperature and productivity. Seasonal and inter-annual variability in air and lake temperatures should be reflected as measureable differences in Lake Trout growth which are recorded in the form of growth rings on otoliths. By combining growth data recorded from Lake Trout otoliths with biochronological techniques, recent historic patterns can be reconstructed, allowing for a better understanding of how climate change affects aquatic ecosystems in Arctic Alaska.

Due to the lack of comprehensive climate data available in this region and the opportunity provided by biochronological analysis of Lake Trout otoliths, the overall goal of chapter one was to examine the relationship between Lake Trout growth and climate to reconstruct past climate patterns in this Arctic region. Specifically, my objectives were to use annual increments recorded on Lake Trout otoliths to build a growth chronology, evaluate relationships among Lake Trout growth and climate descriptors, and use this relationship to hind-cast climate patterns based on Lake Trout growth patterns. I expected that the Lake Trout growth

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chronology would show a positive relationship with climate descriptors (e.g., air temperature), allowing me to hind-cast estimates of multi-decadal climate patterns.

Given impending changes to physical, biological, and fish community structure in Arctic lakes and the importance of Lake Trout as a top predator in these systems, the overall goal of chapter two was to better understand how individual Lake Trout growth varied among lakes with differing physical and biological characteristics, and fish community structure. Specifically, my objectives were to estimate individual growth rates (K; von Bertalanffy 1938) and examine relationships among K and physical and biological characteristics, and fish community structure measured for study lakes. A better understanding of how Lake Trout growth is influenced by environmental factors will provide critical information about this top predator in the warming Arctic.

Literature Cited

Adrian, R., C. M. O'Reilly, H. Zagarese, S. B. Baines, D. O. Hessen, W. Keller, D. M. Livingstone, R. Sommaruga, D. Straile, E. Van Donk, G. A. Weyhenmeyer, and M. Winder. 2009. Lakes as sentinels of climate change. Limnology and Oceanography 54:2283–2297.

Arp, C. D., B. M. Jones, M. Whitman, A. Larsen, and F. E. Urban. 2010. Lake temperature and ice cover regimes in the Alaskan Subarctic and Arctic: integrated monitoring, remote sensing, and modeling. Journal of the American Water Resources Association 46:777–791.

Beauchamp, D. A. 2009. Bioenergetic ontogeny: Linking climate and mass-specific feeding to
life-cycle growth and survival of salmon. Pages 53–72 *in* C. C. Krueger and C.
E. Zimmerman, editors. Pacific salmon: Ecology and management of western Alaska's
populations. American Fisheries Society, Symposium 70, Bethesda, Maryland.

Black, B. A., V. R. von Biela, C. E. Zimmerman, and R. J. Brown. 2013. Lake Trout otoliths
chronologies as mulitdecadal indicators of high-latitude freshwater ecosystems. Polar
Biology 36:147–153.

Blair, J. M., I. Ostrovsky, B. J. Hicks, R. J. Pitkethley, and P. Scholes. 2013. Growth of Rainbow
Trout *Oncorhynchus mykiss* in warm-temperate lakes: implications for environmental
change. Canadian Journal of Fisheries and Aquatic Sciences 70:815–823.

Brett, J. R. 1956. Some principles in the thermal requirements of fishes. Quarterly Review of
Biology 31:75–87.

Burr, J. M. 1987. Synopsis and bibliography of Lake Trout *Salvelinus namaycush* in Alaska.
Alaska Department of Fish and Game Fishery Manuscript No. 5, Juneau.

Carey, M. P., and C. E. Zimmerman. 2014. Physiological and ecological effects of increasing
temperature on fish production in lakes of Arctic Alaska. Ecology and Evolution 4:1981–
1993.

Carpenter, S. R., E. H. Stanley, and M. J. Vander Zanden. 2011. State of the world's freshwater
ecosystems: physical, chemical, and biological changes. Annual review of Environment
and Resources 36:75–99.

Clarke, A., and N. M. Johnston. 1999. Scaling of metabolic rate with body mass and temperature
in teleost fish. Journal of Animal Ecology 68:893–905.

Comiso, J. C., and D. K. Hall 2014. Climate trends in the Arctic as observed from space. Wiley
    Interdisciplinary Reviews: Climate Change 5:389–409.

Elliott, J. M. 1990. Mechanisms responsible for population regulation in young migratory trout,
    Salmo trutta. II. Fish growth and size variation. The Journal of Animal Ecology 59:71–
    185.

Grosse, G., B. M. Jones, and C. D. Arp. 2013. Thermokarst lakes, drainage, and drained basins.
    Pages 325–352 *in* J. Shroder, R. Giardino, and J. Harbor, editors. Treatise on
    geomorphology, vol. 8, glacial and periglacial geomorphology. Academic Press, San
    Diego, California.

Hershey, A. E. 1990. Snail populations in Arctic lakes: competition mediated by predation?
    Oecologia 82:26–32.

Hinkel, K. M., J. D., Lenters, Y., Sheng, E. A., Lyons, R. A., Beck, W.R., Eisner, E.F., Maurer,
    J., Wang, B. L., Potter. 2012. Thermokarst lakes on the Arctic Coastal Plain of Alaska:
    Spatial and temporal variability in summer water temperature. Permafrost and Periglacial
    Processes 23:207–217.

Hinzman, L.D., N. D. Bettez, R. W. Bolton, S. F. Chapin, M. B. Dyurgerov, C. L. Fastie, B.
    Griffith, R. D. Hollister, A. Hope, H. P. Huntington, A. M. Jensen, G. J. Jia, T.
    Jorgensen, D. L. Kane, D. R. Klein, G. Kofinas, A. H. Lynch, A. H. Lloyd, D. A.
    McGuire, F. E. Nelson, W. C. Oechel, T. E. Osterkamp, C. H. Racine, V. E.
    Romanovsky, R. S. Stone, D. A. Stow, M. Sturm, C. E. Tweedie, G. L. Vourlitis, M. D.
    Walker, D. A. Walker, P. J. Webber, J. M. Welker, K. S. Winker, and Yoshikawa, K.
    2005. Evidence and implications of recent climate change in northern Alaska and other
    Arctic regions. Climate Change 72:251–298.

Hobbie, J. E., N. Bettez, L. A. Deegan, J. A. Laundre, S. MacIntyre, S. Oberbauer, J. O'Brien G.

    Shaver, and K. Slavik. 2003. Climate forcing at the Arctic LTER site. Pages 74–91 *in* D.

    Greenland, D. G. Goodin, and R. C. Smith, editors. Climate variability and ecosystem

    response at long-term ecological research (LTER) sites. Oxford University Press, New

    York.

Le Cren, E. D. 1951. The length-weight relationship and seasonal cycle in gonad weight and

    condition in the perch *Perca fluviatilis*. The Journal of Animal Ecology 20:201–219.

Lewis, W. M., 1983. A revised classification of lakes based on mixing. Canadian Journal of

    Fisheries and Aquatic Sciences 40:1779–1787.

McDonald, M. E., A. E. Hershey, and M. C. Miller. 1996. Global warming impacts on Lake

    Trout in Arctic lakes. Limnology and Oceanography 41:1102–1108.

O'Reilly, C. M., S., Sharma, D. K. Gray, S. E. Hampton, J. S. Read, R. J. Rowley, P., Schneider,

    J. D. Lenters, P. B. McIntyre, B. M. Kraemer, and G. A. Weyhenmeyer. 2015. Rapid and

    highly variable warming of lake surface waters around the globe. Geophysical Research

    Letters 42:773–781.

Osterkamp, T. E. and V. E. Romanovsky. 1999. Evidence for warming and thawing of

    discontinuous permafrost in Alaska. Permafrost Periglacial Process 10:17–37.

Power, G. 1978. Fish population structure in Arctic lakes. Journal of the Fisheries Board of

    Canada 35:53–59.

Prowse, T. D., F. J. Wrona, J. D. Reist, J. J. Gibson, J. E. Hobbie, L. M. Lévesque and W. F.

    Vincent. 2006. Climate change effects on hydroecology of Arctic freshwater ecosystems.

    AMBIO: A Journal of the Human Environment 35:347–358.

Reist, J. D., F. J. Wrona, T. D. Prowse, M. Power, J. B. Dempson, R. J. Beamish, J. R. King, T. J. Carmichael and C. D. Sawatzky. 2006. General effects of climate change on Arctic fishes and fish populations. AMBIO: A Journal of the Human Environment 35:370–380.

Rouse, W. R., M. S. Douglas, R. E. Hecky, A. E. Hershey, G. W. Kling, L. Lesack, P. Marsh, M. McDonald, B. J. Nicholson, N. T. Roulet, and J. P. Smol. 1997. Effects of climate change on the freshwaters of arctic and subarctic North America. Hydrological Processes 11:873–902.

Schneider P., and S. J. Hook. 2010. Space observations of inland water bodies show rapid surface warming since 1985. Geophysical Research Letters 37:22405–22409.

Serreze, M. C., J. E. Walsh, F. S. Chapin III, T. Osterkamp, M. Dyurgerov, V. Romanovsky, W. C. Oechel, J. Morison, T. Zhang, and R. G. Barry. 2000. Observational evidence of recent change in the northern high-latitude environment. Climatic Change 46:159–207.

Serreze, M. C., and R. G. Barry. 2011. Processes and impacts of Arctic amplification: A research synthesis. Global and Planetary Change 77:85–96.

Shroder, J. F. 1980. Dendrogeomorphology review and new techniques of tree-ring dating. Progress in Physical Geography 4:161–188.

Smith, N. G., C. C. Krueger, and J. M. Casselman. 2008. Growth chronologies of White Sucker, *Castostomus commersoni*, and Lake Trout, *Salvelinus namaycush*: a comparison among lakes and between trophic levels. Environmental Biology of Fishes 81:375–386.

von Bertalanffy, L. 1938. A quantitative theory of organic growth (inquiries on growth laws II). Human Biology 10:181–213.

Wendler G., B., Moore, and K., Galloway. 2014. Strong temperature increase and shrinking sea ice in Arctic Alaska. Open Atmospheric Science Journal 8:7–15.

Wilson, C. C., and P. D. N. Hebert. 1998. Phylogeography and postglacial dispersal of Lake

Trout *Salvelinus namaycush* in North America. Canadian Journal of Fisheries and

Aquatic Sciences 55:1010–1024.

Chapter 1: Lake trout (*Salvelinus namaycush*) otoliths as biochronological indicators of recent climate patterns in Arctic Alaska[1]

Abstract

The effects of climate change are amplified in high-latitude ecosystems. Despite this, due to the remote nature of Arctic Alaska, long-term climate data are limited. To better understand these ecosystems, long-term, spatially comprehensive climate estimates are needed. Here we applied biochronology techniques to predict recent (~40 years) climate patterns from annual growth increments recorded on adult lake trout (*Salvelinus namaycush*) otoliths ($N = 53$). Lake trout were captured from 13 lakes in the Fish Creek watershed in Arctic Alaska. Individual lake trout ranged from 471–903-mm fork length (mean = 589.3 mm), their readable annuli, representative of age, ranged from 9–50 annual growth increments. Following correction for age-related growth decline, a growth chronology was constructed for the period 1977–2014 and model selection was used to identify the best predictive model of a standardized metric of relative lake trout growth (ring width index; RWI) as a function of climate descriptors. A single covariate model was the best predictor, indicating that RWI tracked mean August air temperature recorded at a local weather station for the period 1998–2013 ($P < 0.001$; $R^2_{adj} = 0.55$; RMSE = 0.048). Based on the RWI predicted mean August temperature, no clear warming trend was apparent for this period, which is consistent with station data. However, when RWI was predicted from modeled mean August temperatures, a clear trend was identified showing increasing RWI from 1950–2014. Using otoliths as an alternative data source provided an

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opportunity to reconstruct patterns in recent climate and subsequent ecological responses. Such

data are critical for understanding rapidly changing freshwater systems in data sparse regions.

Introduction

High-latitude ecosystems, such as those found in Arctic Alaska, show increased effects of climate change relative to other regions globally (Serreze et al., 2000). This is largely attributed to positive feedback effects termed Arctic Amplification (Serreze and Francis, 2006); for example, during the period 1979–2012, mean annual air temperature in Barrow, Alaska increased 2.7°C, approximately one order of magnitude higher than the global increase for the same time period (Wendler et al., 2014). These patterns are expected to continue as sea ice declines across the Arctic into the near future (Serreze and Barry, 2011). As air temperatures increase, many physical changes are expected, including, declining sea ice (Serreze et al., 2007), thawing permafrost (Osterkamp and Romanovsky, 1999), increasing lake temperatures (O'Reilly et al. 2015), and changing lake ice phenology (Arp et al., 2010). Although the direction of these changes is well documented, the rate, magnitude, and future implications for ecological processes in Arctic regions remain poorly constrained (Hinzman et al., 2005).

Long-term air temperature data are limited in northern Alaska, owing both to sparse population density, and to the costs and logistics associated with accessing this remote region (R. Vose, National Climatic Data Center, unpublished data). Available data often include only the past few decades and are incomplete due to the difficulties maintaining instruments in this harsh environment (Rasmussen et al., 2012). It is often difficult to detect significant air temperature increases over short time periods, and continuous data over periods of 30 years or more are needed (Hansen et al., 2010). Moreover, long-term weather stations are typically located in the few communities of the region (e.g., Barrow, Alaska), sparsely distributed, and situated near the Arctic coast. As a result, environments for which climate is monitored in Arctic Alaska are often

not representative of the region as a whole (e.g., inland or higher elevation locations; Cherry and Jacobs, 2012).

Research assessing past climate patterns has been at the forefront of climate change research in recent decades (Crowley, 2000; Comiso et al., 2008). A variety of paleoclimate methods have been developed, including analysis of lake and marine sediments, ice cores, and glacial movements (Overpeck et al., 1997). These methods, however reliable, often lack the temporal precision needed to assess shorter and more recent time periods (Barnekow et al., 2007). To properly study climate patterns and make informed management decisions in this remote environment, precise, multi-decadal estimates of past temperature patterns are needed.

The science of dating annual growth layers in woody plants and the extrapolation of associated environmental information, *dendrochronology*, has provided a reliable proxy to reconstruct past environmental parameters in terrestrial ecosystems (Shroder, 1980). The subject *biochronology,* with respect to this study, refers to applying these same techniques to aquatic ecosystems using the annual growth increments recorded on the calcified or siliceous material of mollusk shells, corals, and fish otoliths. Growth increments recorded on otoliths from long-lived fish species indicate growth and their relationship with environmental parameters allow climate reconstruction (Smith et al., 2007; Black, 2009; Black et al., 2013). For example, a study conducted in the Pacific Northwest found that growth chronologies of three long-lived marine species, yelloweye rockfish (*Sebastes ruberrimus*), splitnose rockfish (*S. diploproa*), and the bivalve species geoduck (*Panopea generosa*), significantly correlated with the Pacific Decadal Oscillation, an index of sea surface temperatures in the North Pacific Ocean (Black, 2009). This example shows that biochronological methods can provide valuable estimates of past climate, particularly when empirical data are not available.

Regional climate, specifically air temperature, directly influences lake temperatures (Adrian et al., 2009). Accordingly, increases in air temperatures have resulted in increased lake temperatures throughout the globe (Schneider and Hook, 2010) and across the Arctic Alaska (Arp et al., 2016). Lake temperatures play an important role in fish growth both directly (e.g., metabolic processes; Kitchell et al., 1977; Magnuson et al., 1990) and indirectly through environmental and trophic processes (e.g., dissolved oxygen levels, lake ice dynamics, prey productivity; Stefan et al., 2001; Alexeev et al., 2016). In order to maximize growth potential lake trout, a cold-water species, inhabit a waters ranging over 6–13°C (Martin and Olver, 1980; Snucins and Gunn, 1995). As a result of warming water temperatures, and the expected increases in prey productivity, lake trout growth is expected to increase (McDonald et al., 1996).

Lake trout otoliths provide an opportunity to apply emerging biochronological methods to predict climate patterns (Black et al., 2013). First, the species is broadly distributed across Arctic Alaska and Canada, two remote regions that lack long-term climate data (Wilson and Herbert, 1998). Second, lake trout are a long-lived fish, known to exceed 50 years of age in Arctic ecosystems (Power, 1978), and thus their growth chronologies could provide valuable insight into climate patterns in the recent past. In many areas within their range, lake trout are characteristic of deep oligotrophic lakes that stratify seasonally (Ryder, 1972); as a result, their growth rates may be less sensitive to air temperature patterns. However, on the Arctic Coastal Plain (ACP), lake trout are found in relatively shallow, polymictic lakes (Lewis, 1983; L. Moulton, MJM Research, LLC, unpublished data) that experience minimal summer stratification and a short ice-free period. Thus, they closely track seasonal variability in air temperature (Arp et al., 2010; Hinkel et al., 2012). As a result, lake trout growth in this region is expected to be correlated with seasonal and inter-annual variability in air and lake temperatures. This hypothesis

is supported by previous biochronological research, which indicated that variability in air temperatures correlated with variability in lake trout growth (Black et al., 2013). For these reasons, and owing to the correlation among climate, lake thermal regimes, and growth, lake trout may be an ideal indicator of climate in the Arctic.

Due to the lack of comprehensive climate data available in this region and the opportunity provided by biochronological analysis of lake trout otoliths, our overall goal was to examine the relationship between lake trout growth and air temperature and sea ice conditions to reconstruct past climate patterns in this Arctic region. Specifically, our objectives were to: 1) use growth-increment analysis to measure lake trout growth; 2) use these measurements to build a growth chronology; 3) evaluate relationships among lake trout growth and climate; and 4) hind-cast climate patterns based on lake trout growth patterns. We expected that a lake trout growth chronology would show a positive relationship with climate descriptors (e.g., air temperature), ultimately allowing us to make inferences into multi-decadal climate patterns. To better constrain the unique Arctic ecosystem and provide informed recommendations for conservation and management, a long-term, spatially comprehensive knowledge of past temperature patterns is needed.

Materials and methods

Study area

This study focused on the central portion of the ACP in northern Alaska (Figure 1.1). The ACP is a lake-rich region where lakes may comprise >20% of the landscape (Sellmann et al., 1975; Hinkel et al., 2005; Arp and Jones 2009). Lakes in the central ACP formed through flooding of

natural depressions during the beginning of the Holocene period (Rawlinson, 1993). Lake size reflects the surrounding topography and lakes often have an elliptical shape perpendicular to the prevailing Northeast winds typical of this region (Sellmann et al., 1975; Hinkel, 2006). Lakes in this region are often shallow, and generally must exceed 1.6 m for floating ice to be present (Grunblatt and Atwood, 2014). Floating ice (i.e., liquid water remains present) during the winter months is essential for fish persistence; therefore this study focused on relatively deep (> 5 m) lakes.

Limnological and fish sampling occurred within the Fish Creek watershed (FCW). The FCW covers 4,900 km^2 of the ACP and encompasses 4,362 lakes < 1 ha (Jones et al., 2017) (Figure 1.1). At least 16 fishes, both resident and migratory species, use lakes, rivers, and streams within the FCW. The most common species in the FCW and surrounding region include ninespine stickleback (*Pungitius pungitius*), Alaska blackfish (*Dallia pectoralis*), and least cisco (*Coregonus sardinella*) (Whitman et al., 2011; Haynes et al., 2014). Lake trout are less common, but are known to occur in deep lakes throughout FCW (L. Moulton, MJM Research, LLC, unpublished data).

The FCW is located within the federally managed National Petroleum Reserve-Alaska, and is a focal watershed for monitoring effects of climate change and land use (Whitman et al., 2011). This project compliments two other freshwater ecological studies being conducted in the FWC, namely 1) a three year interdisciplinary study focused on freshwater habitat (Fish CAFE), and 2) a lake monitoring research project spanning 2012–2015, the Circum-Artic Lake Observation Network (CALON). Results of the Fish CAFE and CALON projects, as well as ongoing climate monitoring by the US Geological Survey (Urban and Clow, 2014) provided a

rich dataset that has proved valuable in site selection and other aspects of this project (see below).

Site selection

Over 4,300 lakes have been identified within the Fish Creek Watershed (Jones et al., 2017), but it is largely unknown which of these lakes contain lake trout. A subset of lakes was chosen using a lake classification scheme developed using hydrogeomorphic attributes to characterize lake types (Jones et al., 2017). This subset of lakes was selected for sampling using three criteria: depth, connectivity, and surface area. Lakes were designated as either deep or shallow by using Synthetic Aperture Radar (SAR) to determine whether each lake ice regime is considered bedfast (shallow) or floating (deep). This cutoff occurs in the FCW at a depth of approximately 1.6 m (Grunblatt and Atwood, 2014). Lakes containing deeper pools were manually identified using color infrared (CIR) orthophotography. Lakes without deep pools were not expected to contain lake trout and thus were not included in our sampling frame. Connectivity classes were assigned using the ArcGIS hydrology toolset with data collected from Interferometric Synthetic Aperture Radar (IfSAR). Lakes were then assigned one of four connectivity classes: isolated, seasonally connected, perennially connected, or flow through. Isolated lakes are not expected to contain lake trout and were subsequently not included. These same IfSAR data were used to estimate and classify lakes by surface area (i.e., large or small); for the purpose of this study, this cutoff was defined as greater or less than 200 ha. (Jones et al., 2017). Preliminary data from plankton tows and fish sampling conducted during the 2014 Fish CAFE field effort, as well as previous studies in nearby regions, predicted these three physical attributes to be representative of variation in primary and secondary productivity and fish community structure (Haynes et al., 2014; Laske et al., 2016).

Fish capture

Lake trout were captured during 2014 and 2015 using a combination of baited set lines (jug sets), angling, and sinking gill nets. Hook-less jug sets are a passive angling technique in which high visibility floating buoys are attached to a bottom weight using a heavy line, with bait attached to the weight on a lighter 1–2-m leader. These jug sets were checked every 24 hours at a minimum. When time and weather allowed, experimental gill nets were also deployed in the deepest areas of each lake. One experimental variable-mesh gill net measured 38 m x 1.8 m, with five panels ranging in bar mesh size from 1.3 to 6.5 cm. The other gill net measured 30 m x 1.8m, with three panels ranging in bar mesh size from 6 to 9 cm. To minimize bycatch, gill nets were checked every 2 to 3 hours. These passive collection techniques complimented the angling methods to target adult lake trout. Based on data from a pilot study conducted in 2014, only large adult lake trout (> 471-mm fork length) assumed to be long lived were collected to ensure sufficient annuli recorded on the otoliths to facilitate building a long-term growth chronology. Fish were euthanized via decapitation, morphological measurements of fork length (mm) and weight (kg) were taken, and sex was identified by opening the body cavity and observing gonads. Finally, both sagittal otoliths were removed using the guillotine method (Secor et al., 1991).

Otolith analysis

Once collected, otoliths were cleaned and stored dry in paper envelopes until embedded in epoxy. Otoliths were then sectioned on the transverse plane using a low-speed wafering saw (Buehler, Lake Bluff, Illinois) before being affixed to a microscope slide. Digital images of each

sectioned otolith were taken with a 5.0 megapixel digital camera (DFC425, Leica Camera, Inc., Allendale, New Jersey) affixed to a compound microscope (Leica DM 2000) using transmitted light.

Digital images were used to assign a calendar year to each readable annulus and allow visual crossdating techniques to ensure the correct year was assigned to the correct annulus. Crossdating is a technique employed by dendrochronologists under the assumption that that an environmental variable (e.g., temperature) limits growth. As a result, annuli width patterns will vary as a function of environmental variation. This environmental control on growth is expected to result in similar patterns of annuli width in individuals collected within a region (Stokes and Smiley, 1996; Black et al., 2005).

After visual crossdating, annuli widths were measured using Image Pro Plus 7.0 software (Media Cybernetics, Rockville, MD, USA) using the caliper tool, beginning at the otolith margin and proceeding on a continuous transect to as close to the focus as possible (Figure 1.3). Although care was taken to measure each annulus perpendicular to the axis of growth (von Biela et al., 2015), these methods require clear identifiable annuli thus owing to variation in otolith growth patterns the exact location and length of the measurement transect varied between individuals. Each annulus was defined by, and measured from, the outside margin of the translucent zone (a narrow dark band under transmitted light) to the outside margin of the next translucent zone (Beckman and Wilson, 1995) and resulted in annual raw ring width values (mm). During otolith formation, material is not deposited uniformly; thus, transverse sections are used to improve clarity. Despite this method, otolith clarity was still inconsistent (Chilton and Beamish, 1982) and annuli from early growth years were often unclear. Because of this

variability, and because juvenile lake trout ecology in the ACP region is poorly understood, we omitted early growth year increments from further analysis.

Biochronology analysis

The dendrochronolgy software COFECHA (Holmes, 1983) was used to statistically verify visual crossdating (Grissino-Mayer, 2001). Each individual series was fit to a cubic spline. Compared to many dendrochronology studies, which are conducted on trees where individual ages can exceed thousands of years, our lake trout series was relatively short. To account for the limited series length, we applied a flexible spline of 16 years (Brian Black, University of Texas at Austin, personal communication). To standardize the series the raw ring width values were divided by the values predicted by the spline, resulting in a series with a mean = 1.0. Each individual series was removed from the master series and correlation analysis performed, which resulted in a series inter-correlation (SIC) value and mean sensitivity index. The SIC value is the mean of each series correlation with the master series; the mean sensitivity index is a measure of inter-annual variability. In addition to calculating a SIC value for the entire sample, individual series were grouped SIC values were calculated by lake. Series with low (SIC < 0.10) or negative correlation values were visually inspected for potential dating errors. Final date assignments were never forced and always made through visual inspection.

Before the growth chronology could be constructed, each series was standardized individually using the dendrochronology program library (dplR; Bunn et al., 2013) in Program R (R Development Core Team, 2015) this was done because otoliths were not measured on standard axes. Each raw series was fit to a cubic spline and standardized by dividing the raw ring widths by the value predicted by the cubic spline, resulting in a ring width index (RWI, unitless) corrected for low-frequency variation (e.g., age-related growth decline). High frequency-

variation remained in the series, thereby isolating the climate signal. Finally, the mean of each standardized time series was used to build the final growth chronology (Black et al., 2005; 2013).

Climate and sea ice data

Climate and sea ice data were obtained from weather station records and satellite observations, respectively. Empirical temperature data from the weather station closest to our study area, located at Inigok, Alaska (70° 00.162 N 153° 05.302 W), were available for the period 1998–2014 (Urban and Clow, 2014). We summarized air temperature (May-October) measurements taken every two hours as daily means from which we calculated a suite of descriptors that included mean monthly and multi-month values (e.g., mean monthly, average air temperature July through September, etc.; Appendix 1). These descriptors were expected to have a high level of collinearity thus Pearson correlations were examined to reduce the number of descriptors to include in further analysis. In addition, weekly satellite observations were used to quantify Arctic Ocean sea ice extent to a 0.25° × 0.25° spatial resolution (Walsh et al., 2015).

Growth and climate relationship

Linear regression and model selection were used to identify the best set of climate descriptors that predicted lake trout growth (RWI). The variance inflation factor (VIF) was used to identify collinear descriptors. We retained variables with VIF < 10 for further analysis and to meet assumptions of linear models (Montgomery et al., 2015; Beatty et al., 2014). Because we were interested in identifying the best predictive model, we fit all subsets of RWI as a function of non-collinear climate descriptors using the "regsubsets" function of the R software package leaps (R Development Core Team 2015). The models were organized by length and those with the highest

adjusted R^2 (R^2_{adj}) values for each length were retained for further analysis. Based on this refined

subset, we used Akaike's information criterion (AIC) and Akaike weights (w_i) to rank the

models. The model with the lowest AIC and highest w_i was considered the top model.

Hind-casting climate and model comparisons

We used the results of the model selection to hind-cast climate patterns across the period covered

by the growth chronology by refitting the linear model to predict climate descriptors based on

observed RWI. In addition, we used modeled estimates of air temperature from the dynamical

downscaled Weather Research and Forecast model optimized for Arctic regions (Polar-WRF) to

predict RWI for the period 1950–2014. The Polar-WRF model predicts air temperature at three-

hour intervals using a biased-corrected approach. These data were used to calculate daily means

which were then summarized into descriptors identical to those calculated based on observed

data (e.g., mean monthly, average air temperature May through August, etc.) This model was run

using the National Centers for Environmental Prediction (NCEP) analysis dataset (Kalnay et al.,

1996). Regressions were performed between the growth chronology (RWI) and climate

descriptors determined from previous model selection analysis. Finally, we also compared

predictive performance between models based on observed and modeled climate descriptors

using the R^2_{adj} and root-mean-squared-error (RMSE) statistics.

Results

Fish capture

Otoliths were extracted from 53 adult lake trout captured from 13 lakes in the FCW during 2014

($N = 13$) and 2015 ($N = 40$). Fish were captured using angling ($N = 27$), jug sets ($N = 18$), and

gill nets ($N = 8$). Individuals ranged from 471–903 mm FL (mean = 589.3 mm FL; Figure 1.4).

The number of readable annuli per individual ranged from 9–50 (mean = 21.2), and the sex ratio

was skewed toward females ($N = 34$) over male ($N = 18$), with one individual of unknown sex. A

simple binomial test confirmed that the probability of a captured individual being female was

greater than 0.5 ($P = 0.018$; Table 1.1).

Crossdating analysis

Of the 53 lake trout captured, 49 had otoliths with sufficient clear, readable annuli. Although the

oldest individual had clear readable annuli measuring back to 1965, in accordance with existing

literature that suggested a minimum sample depth of five individuals, we limited our chronology

to the period 1977–2014 (Figure 1.5). During crossdating, several years were identified to have

consistently wide ring widths: 2007, 2004, and 1989 (Figure 1.3). Conversely, 2003, 1985, and

1983 were identified as years with consistently narrow growth rings. Based on results of the

COFECHA analysis, this series was found to have a mean series inter-correlation (SIC) of 0.327

(SD = 0.15). Individual series correlation coefficients had a large amount of variation, and

ranged from 0.054–0.697 (SD = 0.15). When grouped by lake, mean SIC values showed less

variation and ranged from 0.251–0.466 (SD = 0.07). Within-lake variation differed among lakes

when SIC values were grouped by lake; standard deviations were 0.009–0.214. Inter-annual ring-

width variability (mean sensitivity index) was 0.231.

Growth and climate relationship

Evaluation of the full correlation matrix showed a high degree of collinearity between observed

and modeled data. Therefore, 10 descriptors calculated from air temperature measured at the

Inigok weather station were selected for further analysis (Table 1.2). The VIF analysis resulted in further reduction to six climate descriptors. These remaining climate descriptors were used in final model selection. The single variable model with mean August temperature,

$$RWI = 0.77 + 0.03(Ag),\qquad\qquad(1.1)$$

performed best (R^2_{adj} = 0.55, P < .001, AICc = -43.46, w_i = 0.76, Table 1.3) and indicated that RWI increased with mean August temperature (Figure 1.6). This model was used for all further predictions.

Hind-casting climate

We refit the best model of RWI as a function of mean August temperature to hind-cast climate based on lake trout growth as follows:

$$\textit{Mean August Temperature (°C)} = -11.70 + 18.96\ (RWI).\qquad\qquad(1.2)$$

The mean August temperatures hind-casted by the growth chronology using Eqn 1.2 correlated closely with observed mean August temperatures over where those data were available (1998–2014), (Pearson's r = 0.76) (Figure 1.6, Appendix 1.A.). Predicted August temperatures revealed some distinct patterns, such as a warming trend from 1978–1982 followed by cooler years over 1983–1988. Conversely, 1998–2003 exhibited a cooling trend followed by a warm and variable period over 2004–2014. After removing 1977 from the time series, a year that significantly influenced the series (Bonferroni P = < 0.001), the predicted August temperatures suggest a

warming trend for the period 1978 – 2014, although this relationship was not statistically significant ($P = 0.45$) (Figure 1.7).

Comparisons with existing climate models

We examined the predictive performance of models with observed and Polar-WRF modeled mean August temperature as independent variables to predict lake trout growth (RWI). The model using Polar-WRF modeled mean August temperature,

$$RWI = 0.0849 + 0.019(Ag), \tag{1.3}$$

explained about one half of the variation in RWI relative to the model with observed data ($R^2_{adj} = 0.224$ vs. 0.55) and was less precise (RMSE = 0.049 vs. 0.080). Although the model that included observed mean August temperature (Eqn 1.1) performed better relative to modeled mean August temperature, the Polar-WRF predicted mean August temperature relationship with the growth chronology was significant ($P = 0.002$). Based on Eqn 1.3, RWI was predicted to have increased over time ($R^2 = 0.102$, $F = 7.17$, $P = .009$) across the period for which climate data were available (1950–2015; Figure 1.8).

Discussion

Biochronology is a useful tool to reconstruct past environmental conditions, yet it has been applied almost exclusively to marine ecosystems (Strom et al., 2004; Black, 2009). Our research is one of few studies that apply these techniques to freshwater systems (Guyette and Rabeni, 1995; Ostazeski and Spangler, 2001; Morrongiello et al., 2011; Black et al., 2013). We found

that inter-annual variation in lake trout growth was correlated with variation in mean August air temperatures. This relationship allowed us to construct an accurate growth chronology that provides multi-decadal air temperature and fish growth estimates for this data-sparse region. Although these estimates provide valuable information to regional resource managers in this sensitive ecosystem, our methods and results include assumptions worth further discussion.

While the mean sensitivity (0.231) was similar to results from other otolith-based biochronologies (0.256; Black et al., 2013), the mean series inter-correlation (SIC = 0.327) was lower than expected compared to other studies. For example, biochronologies using otoliths from Pacific rockfishes found higher SIC values (0.54–0.65; Black, 2009). The SIC value represents the degree to which growth is synchronous between an individual and the composite growth chronology. Low SIC is possibly due to the lack of fish movement caused by seasonally limited connectivity among lakes. Due to the extreme seasonality of this region, fish passage through shallow-water connections is limited to the short summer season (Heim et al., 2015). Moreover, lakes within our study area have different physical characteristics (e.g., depth, connectivity), which subsequently work to mediate (i.e., filter) the effects of increased air temperature differently (Robertson and Ragotzkie, 1990). As a result of the lack of habitat connectivity and environmental heterogeneity among lakes, lake trout in one lake type (i.e., small, shallower, seasonally connected) experience different water temperature conditions than in another lake type (i.e., large, deeper, well connected). This difference, in concert with other ecological factors, leads to variation in growth rates, which was evaluated by calculating mean SIC values for each lake and making comparisons to the mean SIC value of the entire sample. These results showed less variation, with mean SIC values grouped by lake ranging from 0.251–0.466 (SD = 0.07); in contrast, individual SIC values ranged from 0.054–0.697 (SD = 0.15). For example,

mean SIC values for two lakes that shared a strong connection were higher (0.466 and 0.407) but the mean SIC value for a seasonally connected lake was lower (0.257). This difference suggests that individuals isolated in this seasonally connected lake showed less growth synchrony with the entire sample, corroborating the SIC value (0.327) for our chronology. Regardless, when evaluating the sample as a whole, 60% of the individual series had SIC values ≥ 0.3, a criterion that indicates strong synchrony among series when crossdating otolith-based biochronologies (B. Black, personal communication, June 4, 2016).

Our model (Eqn 1.3) predicted increased lake trout growth with higher modeled mean August temperatures for Alaskan Arctic lakes (Figure 1.8), which is consistent with findings elsewhere that increased water temperatures result in higher metabolic rates and higher growth rates in lake trout (Brett and Groves, 1979; McDonald et al., 1996). However, our results are potentially complicated by a number of ecological factors. First, available prey species differ among Arctic lakes (Haynes et al., 2014); as a result, lake trout growth may be affected by productivity of lower trophic levels in addition to direct temperature effects. Generally, increases in water temperatures are associated with increased productivity of prey species (Carey and Zimmerman, 2014), but different prey species may react differently to temperature. Another second complicating factor was due to the disproportionate number of females in our samples. Female lake trout invest more energy into reproductive growth than males (Le Cren, 1951), and have less energy available for somatic growth which is associated with ring-width variation (Campana 1984). This is further complicated because female lake trout exhibit skip spawning in years with low resource availability, allowing more disproportionately more energy to be allocated to somatic growth in those years (Martin and Olver, 1980). Adoption of this tactic by individuals in this study could introduce variation in ring widths such as wide growth rings in

years of skip spawning despite cold temperature conditions or vice versa. Unfortunately, little is known about lake trout spawning behavior in this region.

We found that over half of the variation in lake trout growth was explained by mean August temperature. August was the warmest month with respect to water temperatures and dependably ice-free; across the region lakes were well mixed during this period (Figure 1.2; Arp et al., 2013). Higher temperatures are expected to be associated with increased growth (McDonald et al., 1996). Because our study lakes minimally stratify, water conditions are isothermal and respond closely to air temperatures, thus lake trout are subject to variation in air temperatures. August temperatures also show a high degree of collinearity with mean summer temperatures, which typically represent the primary growing period for fishes on the ACP (Carey and Zimmerman, 2014). There are several ecological explanations for the importance of August temperatures to lake trout. Although little is known about lake trout spawning behavior in this region, in other Arctic lakes lake trout have been documented spawning during the first week of September (Burr 1987). August could be a time of heavy pre-spawn feeding and movement to spawning areas, this may be indicative of fish capture results, with August being our most productive month of capture ($N = 26$).

Another caveat of our research is that removal of age-related growth to maximize the climate signal downplays the importance of ecological and genetic variability, both major factors in growth. While the intent is to simply isolate the climate signal, these standardization techniques may inflate the influence of climate as a driver of growth (Morrongiello et al., 2012). We believe that this inherent problem is less prevalent in this study due to the likelihood that seasonal growth is limited to the short summer season (Reist et al., 2006). This unique

seasonality is represented in the high contrast between the opaque and translucent zone typical of otoliths collected at high latitudes (Beckman and Wilson, 1995).

Despite high sampling effort, our sample size was relatively small due to the remoteness of our study area and compounded by our limited knowledge of the regional distribution of lake trout. Many biochronology studies have a large sample size, usually as a result of sampling from archives, or capture of commercially harvested species. Such studies often have the luxury of removing non-compliant or short-lived individuals. The life span of lake trout and our lower sample size resulted in a mean series length of 20.4 years, which is short relative to sample sizes in similar studies (Black et al., 2005). As a result, the well documented warming trend detected from long term (>100 years; van Wijngaarden, 2015) air temperature records available in other Arctic regions was not detected in lake trout growth measurements within our sampling time period. Although the mean August temperature warming trend we detected was positive, we were unable to confirm a significant relationship. It is expected that a larger number of older individuals would have allowed for a chronology spanning a longer time period, crucial in detecting this warming trend.

Lake trout in the ACP are at the northernmost edge of their range (Mecklenburg et al., 2002). Populations living at the edge of their distribution are more likely to experience physiological stress, be locally adapted, and have a higher risk of local extinction (Hoffman and Parsons, 1997, Gotelli and Taylor, 1999). Our results indicated that lake trout growth has increased since the 1950s with warming summer air temperatures. A continued increase in temperatures is likely to impact lake trout populations indirectly through a longer ice-free period, changes to deep-water dissolved oxygen, and changes to primary productivity (Clilverd et al., 2009; Arp et al., 2010). For ectothermic organisms such as lake trout, higher temperatures

directly affect growth and metabolism (Brett and Groves, 1979). The positive relationship between growth and temperature has limits however, and for lake trout, water temperatures higher than approximately 13°C are thought to be unfavorable (Martin and Olver, 1980). Increased growth or population size could result in resource limitation or negative density effects. For example, it has been estimated that juvenile lake trout in Toolik Lake would need to consume more than eight times as much food given a 3°C increase in July water temperatures (McDonald et al., 1996). Moreover productivity of least cisco, an important lake trout prey species, is expected to increase as climate warms across the Arctic (Carey and Zimmerman, 2014). This potential increased productivity may affect lake trout by increasing adult food availability, or may increase forage competition with juvenile lake trout. Thus, temperature changes can lead to changes in aquatic food webs that can reach across trophic levels.

Future research opportunities could build on the techniques used in this study to learn more about this poorly understood region. Our study primarily used observed and modeled air temperatures as our climate descriptors. Ongoing lake monitoring efforts are providing new water temperature data, which could prove valuable for further aquatic studies instead of relying on air temperature as a proxy for water temperature. Air temperature and water temperature have a strong relationship but there are many confounding factors (i.e., depth, wind, etc.; Livingstone and Lotter, 1998). Recent research has shown that sea ice decline has measureable effects on lake ice phenology in Arctic lakes (Alexeev et al., 2016). Although sea ice was not a significant climate descriptor in this study, populations of lake trout are present in the Teshekpuk Lake watershed, a coastal watershed that is affected significantly by sea ice decline. Applying our methods to this and other similar watersheds could prove insightful toward a better understanding of the role of sea ice decline Arctic fish population dynamics.

Lake trout are ecologically important in Arctic lakes. We have found that lake trout growth has increased since the 1950s in response to a warming Arctic. Future climate change is likely to impact these populations both directly and indirectly through ecosystem changes. As a top predator, impacts to lake trout populations would reach across trophic levels. This study has demonstrated the utility of biochronology techniques, as well as provided valuable knowledge on how a large bodied, long lived fish may react to climate change.

Acknowledgements

References

Adrian R, O'Reilly CM, Zagarese H et al. (2009) Lakes as sentinels of climate change. Limnology and Oceanography, 54, 2283–2297.

Alexeev VA, Arp CD, Jones BM, Cai L (2016) Arctic sea ice decline contributes to thinning lake ice trend in northern Alaska. Environmental Research Letters, 11, 074022.

Arp CD, Jones BM (2009) Geography of Alaska lake districts: identification, description, and analysis of lake-rich regions of a diverse and dynamic state. U.S. Geological Survey Scientific Investigations Report 2008-5215, 40 pp.

Arp CD, Jones BM, Whitman M, Larsen A, Urban FE (2010) Lake temperature and ice cover regimes in the Alaskan subarctic and Arctic: integrated monitoring, remote sensing, and modeling. Journal of the American Water Resources Association, 46, 777–791.

Arp, CD., Jones BM, Grosse G (2013). Recent lake ice-out phenology within and among lake districts of Alaska, USA. Limnology and Oceanography, 58, 2013–2028.

Arp CD, Jones BM, Grosse G, Bondurant AC, Romanovsky VE, Hinkel KM, Parsekian AD (2016) Threshold sensitivity of shallow Arctic lakes and sublake permafrost to changing winter climate. Geophysical Research Letters, 43, 6358–6365.

Barnekow L, Loader NJ, Hicks S, Froyd CA, Goslar T (2007) Strong correlation between summer temperature and pollen accumulation rates for *Pinus sylvestris*, *Picea abies* and *Betula* spp. in a high-resolution record from northern Sweden. Journal of Quaternary Science, 22, 653–658.

Beatty, SJ, Morgan, DL, Lymbery, AJ (2014). Implications of climate change for potamodromous fishes. Global Change Biology, 20, 1794–1807.

Beckman, DW, Wilson, CA (1995) Seasonal timing of opaque zone formation in fish otoliths. In: Recent developments in fish otolith research (eds Secor, DH, Dean JM, Campana, SE, Belle W), pp. 27–44. Baruch institute for marine biology and coastal research, University of South Carolina Press, South Carolina.

Black BA, Boehlert GW, Yoklavich MM (2005) Using tree-ring crossdating techniques to validate annual growth increments in long-lived fishes. Canadian Journal of Fisheries and Aquatic Sciences, 62, 2277–2284.

Black BA (2009) Climate-driven synchrony across tree, bivalve, and rockfish growth-increment chronologies of the northeast Pacific. Marine Ecology Progress Series, 378, 37–46.

Black BA, von Biela VR, Zimmerman CE, Brown RJ (2013) Lake trout otolith chronologies as multidecadal indicators of high-latitude freshwater ecosystems. Polar Biology, 36, 147–153.

Brett JR, Groves TDD (1979) 6 – Physiological energetics. In: Fish Physiology (eds Hoar WS, Randall DJ, Brett JR), pp. 279–352. Academic Press, New York.

Bunn AG, Korpela M, Biondi F, Campelo F, Mérian P, Qeadan F, Zang C (2013) dplR: dendrochronology program library in R. R package version 1.5.6.

Burr, JM (1987) Synopsis and bibliography of Lake Trout (*Salvelinus namaycush)* in Alaska. Alaska Department of Fish and Game, Fishery Manuscript No. 5, Juneau.

Campana SE (1984) Lunar cycles of otolith growth in the juvenile starry flounder (*Platichthys stellatus)* Marine Biology, 80, 23–246.

Carey MP, Zimmerman CE (2014) Physiological and ecological effects of increasing temperature on fish production in lakes of Arctic Alaska. Ecology and Evolution, 4, 1981–1993.

Cherry JE, Jacobs AS (2012) Hydroclimate observations in Arctic Alaska: analysis of past networks and recommendations for the future. Report to the Arctic Landscape Conservation Cooperative, 143pp.

Chilton DE, Beamish RJ (1982) Age determination methods for fishes studied by the Groundfish Program at the Pacific Biological Station. Canadian Special Publication of Fisheries and Aquatic Sciences, 60.

Clilverd H, White D, Lilly M (2009) Chemical and physical controls on the oxygen regime of ice-covered Arctic lakes and reservoirs. JAWRA Journal of the American Water Resources Association, 45, 500–511.

Comiso JC, Parkinson CL, Gersten R, Stock L (2008) Accelerated decline in the Arctic sea ice cover. Geophysical Research Letters, 35, L01703.

Crowley TJ (2000) Causes of climate change over the past 1000 years. Science, 289, 270–277.

Gotelli NJ, Taylor CM (1999) Testing metapopulation models with stream-fish assemblages. Evolutionary Ecology Research, 1, 835–845.

Grissino-Mayer HD (2001) Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. Tree-Ring Research, 57, 205–221.

Grunblatt J, Atwood D (2014) Mapping lakes for winter liquid water availability using SAR on the North Slope of Alaska. International Journal of Applied Earth Observation and Geoinformation, 27, 63–69.

Guyette RP, Rabeni CF (1995) Climate response among growth increments of fish and trees. Oecologia, 104, 272–279.

Hansen J, Ruedy R, Sato M, Lo K (2010) Global surface temperature change. Reviews of Geophysics, 48, RG4004.

Haynes TB, Rosenberger AE, Lindberg MS, Whitman M, Schmutz JA (2014) Patterns of lake occupancy by fish indicate different adaptations to life in a harsh Arctic environment. Freshwater Biology, 59, 1884–1896.

Heim KC, Wipfli MS, Whitman MS, Arp CD, Adams J, Falke JA (2015) Seasonal cues of Arctic grayling movement in a small Arctic stream: the importance of surface water connectivity. Environmental Biology of Fishes, 99, 49–65.

Hinkel KM, Frohn RC, Nelson FE, Eisner WR, Beck RA (2005) Morphometric and spatial analysis of thaw lakes and drained thaw lake basins in the western Arctic Coastal Plain, Alaska. Permafrost and Periglacial Processes, 16, 327–341.

Hinkel, K (2006) Comment on "Formation of oriented thaw lakes by thaw slumping" by Jon D. Pelletier. Journal of Geophysical Research 111, F01021.

Hinkel, KM, JD, Lenters, Y, Sheng, EA Lyons, RA, Beck, WR, Eisner, EF, Maurer, J, Wang, BL, Potter (2012) Thermokarst lakes on the Arctic Coastal Plain of Alaska: Spatial and temporal variability in summer water temperature. Permafrost and Periglacial Processes, 23, 207–217.

Hinzman, LD, Bettiez, ND, Bolton RE et al. (2005) Evidence and implications of recent climate change in northern Alaska and other Arctic regions. Climate Change, 72, 251–298.

Hoffmann AA, Parsons PA. (1997) Extreme Environmental Change and Evolution. Cambridge University Press, Cambridge.

Holmes RL (1983) Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bulletin, 43, 69–78.

Kalnay E, Kanamitsu M, Kistler R et al. (1996) The NCEP/NCAR 40-year reanalysis project. Bulletin of the American Meteorological Society, 77, 437–471.

Kitchell JF, Stewart DJ, Weininger D (1977) Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). Journal of the Fisheries Research Board of Canada, 34, 1922–1935.

Laske SM, Haynes TB, Rosenberger AE, Koch JC, Wipfli MS, Whitman M, Zimmerman CE (2016) Surface water connectivity drives richness and composition of Arctic lake fish assemblages. Freshwater Biology, 61, 1090–1104.

Le Cren, ED (1951) The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). The Journal of Animal Ecology, 20, 201–219.

Lewis, WM (1983) A revised classification of lakes based on mixing. Canadian Journal of Fisheries and Aquatic Sciences, 40, 1779–1787.

Livingstone DM, Lotter AF (1998) The relationship between air and water temperatures in lakes of the Swiss Plateau: a case study with palaeolimnological implications. Journal of Paleolimnology, 19, 181–198.

Magnuson JJ, Meisner JD, Hill DK (1990) Potential changes in the thermal habitat of Great Lakes fish after global climate warming. Transactions of the American Fisheries Society, 119, 254–264.

Martin NV, Olver CH (1980) The lake charr, (*Salvelinus namaycush*). In: Charrs: salmonid fishes of the genus *Salvelinus* (eds Balon EK, Junk W), pp. 205–277, The Hague, The Netherlands.

McDonald ME, Hershey AE, Miller MC (1996) Global warming impacts on lake trout in Arctic lakes. Limnology and Oceanography, 41, 1102–1108.

Mecklenburg CW, Mecklenburg TA, Thorsteinson LK (2002) Fishes of Alaska. American Fisheries Society, Bethesda, Maryland.

Montgomery, DC, Peck EA, Vining GG (2015) Introduction to linear regression analysis, 2nd edition. John Wiley and Sons, New York, New York.

Morrongiello JR, Crook DA, King AJ, Ramsey DSL, Brown P (2011) Impacts of drought and predicted effects of climate change on fish growth in temperate Australian lakes. Global Change Biology, 17, 745–755.

Morrongiello, JR, RE, Thresher, DC, Smith (2012) Aquatic biochronologies and climate change. Nature Climate Change, 2, 849–857.

O'Reilly, CM, Sharma S, Gray DK et al (2015) Rapid and highly variable warming of lake surface waters around the globe. Geophysical Research Letters, 42, 773–781.

Ostazeski JJ, Spangler GR (2001) Use of biochronology to examine interactions of freshwater drum, walleye and yellow perch in the Red Lakes of Minnesota. Environmental Biology of Fishes, 61, 381–393.

Osterkamp TE, Romanovsky VE (1999) Evidence for warming and thawing of discontinuous permafrost in Alaska. Permafrost Periglacial Process, 10, 17–37.

Overpeck J, Hughen K, Hardy D et al. (1997) Arctic environmental change of the last four centuries. Science, 278, 1251–1256.

Power G (1978) Fish population structure in Arctic lakes. Journal of Fisheries Research Board of Canada, 35, 53–59.

R Development Core Team (2015) R: A Language and Environment for Statistical Computing. R

    Foundation for Statistical Computing, Vienna, Austria.

Rasmussen R, Baker B, Kochendorfer J et al. (2012) How well are we measuring snow: The

    NOAA/FAA/NCAR winter precipitation test bed. Bulletin of the American

    Meteorological Society, 93, 811–829.

Rawlinson, SE (1993) Surficial geology and morphology of the Alaskan central Arctic coastal

    Plain: Alaska Division of Geological & Geophysical Surveys Report of Investigation 93.

Reist JD, Wrona FJ, Prowse TD et al. (2006) General effects of climate change on Arctic fishes

    and fish populations. AMBIO: A Journal of the Human Environment, 35, 370–380.

Robertson DM, Ragotzkie RA (1990) Changes in the thermal structure of moderate to large sized

    lakes in response to changes in air temperature. Aquatic Sciences, 52, 360–380.

Rouse WR, Douglas MSV, Hecky RE et al. (1997) Effects of climate change on the freshwaters

    of Arctic and subarctic North America. Hydrological Processes, 11, 873–902.

Ryder, RA, (1972) The limnology and fishes of oligotrophic glacial lakes in North America

    (about 1800 A.D.). Journal of Fisheries Research Board of Canada, 29, 617–628.

Schneider P, Hook SJ (2010) Space observations of inland water bodies show rapid surface

    warming since 1985. Geophysical Research Letters, 37, 22405–22409.

Secor, DH, Dean JH, Laban EH (1991). Manual for otolith removal and preparation for

    microstructural examination. Electric Power Research Institute and Belle W. Baruch

    Institute for Marine Biology and Coastal Research, Columbia, South Carolina

Sellmann PV, Brown J, Lewellen RI, McKim H, Merry C (1975) The classification and

    geomorphic implications of thaw lakes on the Arctic Coastal Plain, Alaska. CRREL

Research Report 334, Army Cold Regions Research and Engineering Laboratory, Hanover, NH, USA.

Serreze MC, Walsh JE, Chapin FS et al. (2000) Observational evidence of recent change in the northern high-latitude environment. Climatic Change, 46, 159–207.

Serreze MC, Francis JA (2006) The Arctic amplification debate. Climatic Change, 76, 241–264.

Serreze MC, Holland MM, Stroeve J (2007) Perspectives on the Arctic's shrinking sea ice cover. Science, 315, 1533–1536.

Serreze MC, Barry RG (2011) Processes and impacts of Arctic amplification: A research synthesis. Global and Planetary Change, 77, 85–96.

Shroder JF (1980) Dendrogeomorphology: review and new techniques of tree-ring dating. Progress in Physical Geography, 4, 161–188.

Smith NG, Krueger CC, Casselman JM (2007) Growth chronologies of white sucker, *Catostomus commersoni*, and lake trout, *Salvelinus namaycush*: a comparison among lakes and between trophic levels. Environmental Biology of Fishes, 81, 375–386.

Snucins, EJ, Gunn JM. (1995) Coping with a warm environment: behavioral thermoregulation by lake trout. Transactions of the American Fisheries Society, 124, 118–123.

Stefan HG, Fang X, Eaton JG (2001) Simulated fish habitat changes in North American lakes in response to projected climate warming. Transactions of the American Fisheries Society, 130, 459–477.

Stokes MA, Smiley TL (1996) An Introduction to Tree-Ring Dating. University of Chicago Press, Chicago.

Strom A, Francis RC, Mantua NJ, Miles EL, Peterson DL (2004) North Pacific climate recorded in growth rings of geoduck clams: A new tool for paleoenvironmental reconstruction. Geophysical Research Letters, 31, L06206.

Urban, FE, Clow CD (2014) DOI/GTN-P climate and active-layer data acquired in the National Petroleum Reserve–Alaska and the Arctic National Wildlife Refuge, 1998–2013, Rep. 892, U.S. Geological Survey, Reston, Virginia.

van Wijngaarden WA (2015) Arctic temperature trends from the early nineteenth century to the present. Theoretical and Applied Climatology, 122, 567–580.

von Biela VR, Kruse GH, Mueter FJ, Black BA, Douglas DC, Helser TE, Zimmerman CE (2015) Evidence of bottom-up limitations in nearshore marine systems based on otolith proxies of fish growth. Marine Biology, 162, 1019–1031.

Walsh, JE, Chapman WL, Fetterer F (2015) Gridded monthly sea ice extent and concentration, 1850 onwards, Version 1.1. Boulder, Colorado USA: National Snow and Ice Data Center.

Wendler G, Moore B, Galloway K (2014) Strong temperature increase and shrinking sea ice in Arctic Alaska. Open Atmospheric Science Journal, 8, 7–15

Whitman, MS, Arp CD, Jones B, Morris W, Grosse G, Urban F, Kemnitz R (2011) Developing a long-term aquatic monitoring network in a complex watershed of the Alaskan Arctic Coastal Plain. In: Proceedings of the Fourth Interagency Conference on Research in Watersheds: Observing, Studying, and Managing for Change. (eds Medley CN, Patterson G, Parker MJ), pp 15–20, Reston, Virginia: U.S. Geological Survey

Wilson CC, Hebert PDN (1998) Phylogeography and postglacial dispersal of lake trout (*Salvelinus namaycush*) in North America. Canadian Journal of Fisheries and Aquatic Sciences, 55, 1010–1024.
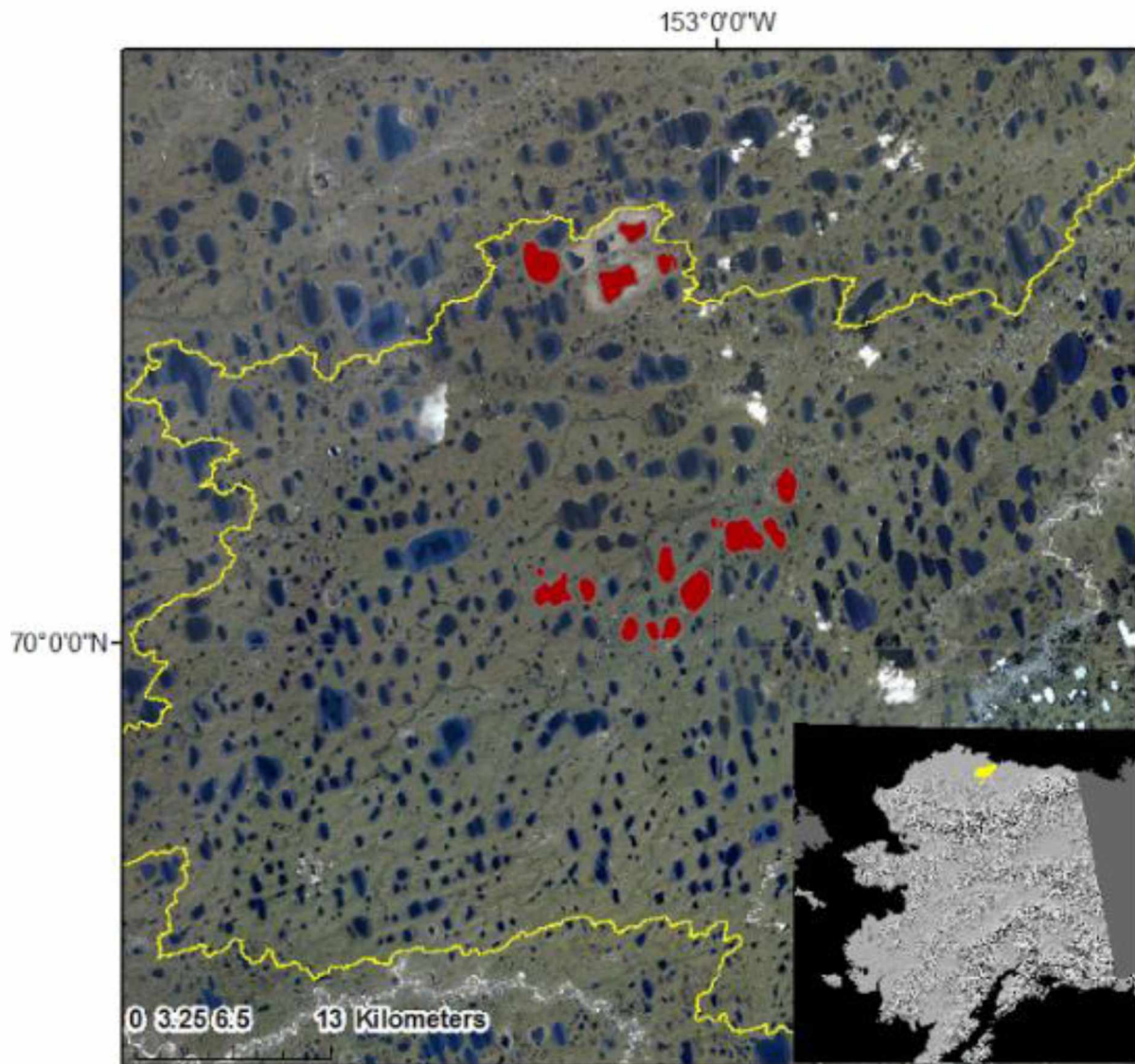
Figure 1.1. Location of the study area in Fish Creek watershed, Alaska, (inset: highlighted in yellow), lakes where lake trout were captured (red highlights).
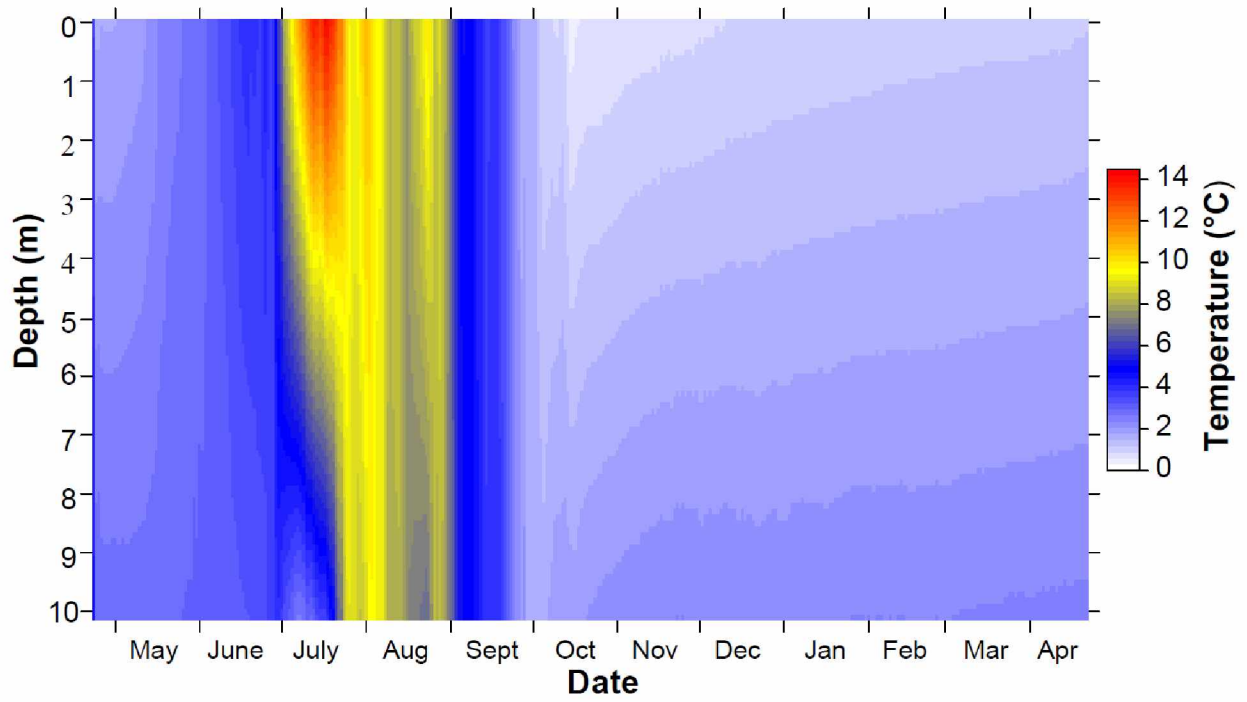
Figure 1.2. Example lake temperature profile for a deep, polymictic lake, located in the Fish Creek watershed, Alaska. Lake profile depicts water temperature (°C), indicated by color, and shows lake mixing patterns by depth, y-axis, and date, x-axis.
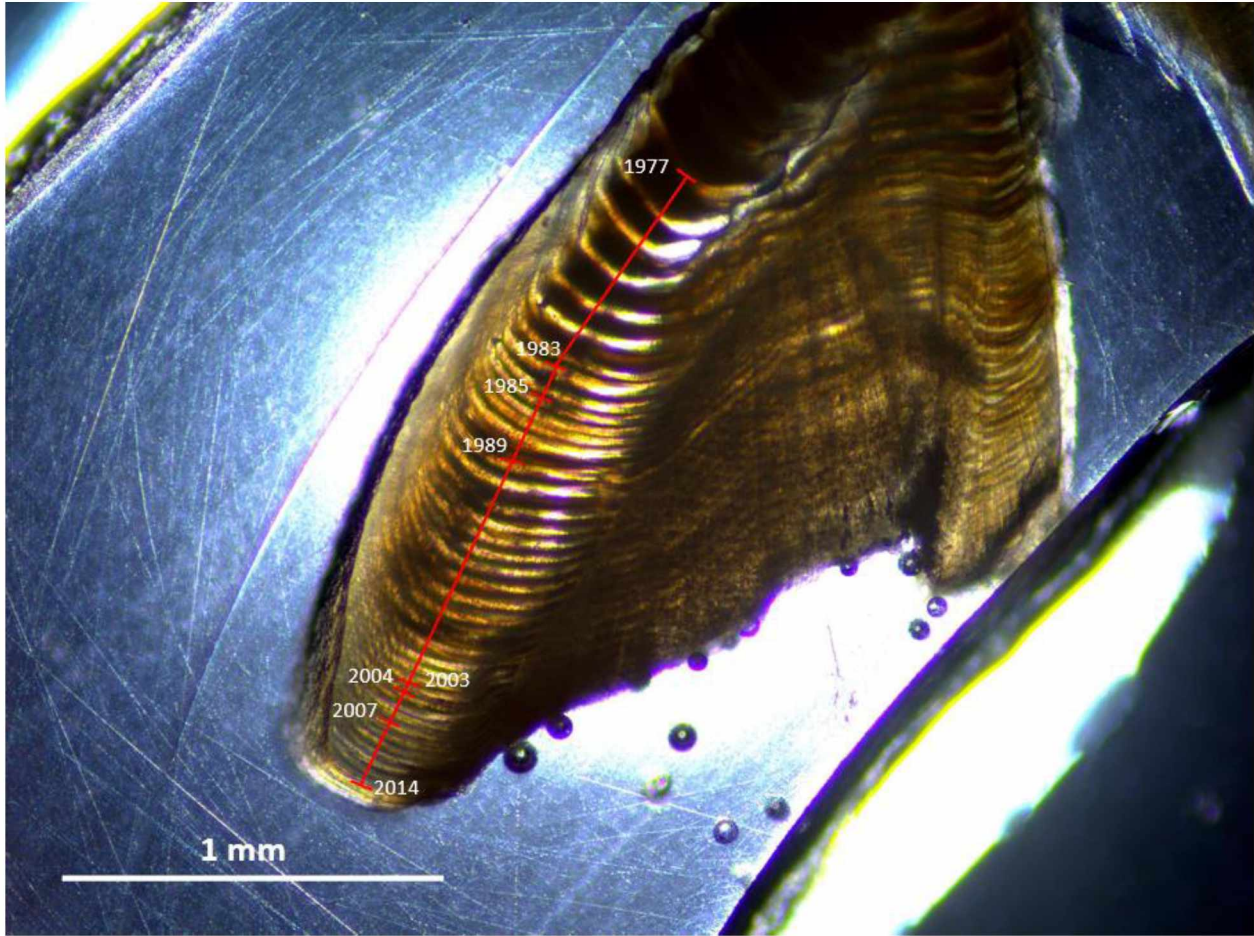
Figure 1.3. Example otolith image with measurement transect from 2014-1977. Regions with presumed higher (2007, 2004, 1989) and lower (2003, 1985, 1983) growth years are indicated.
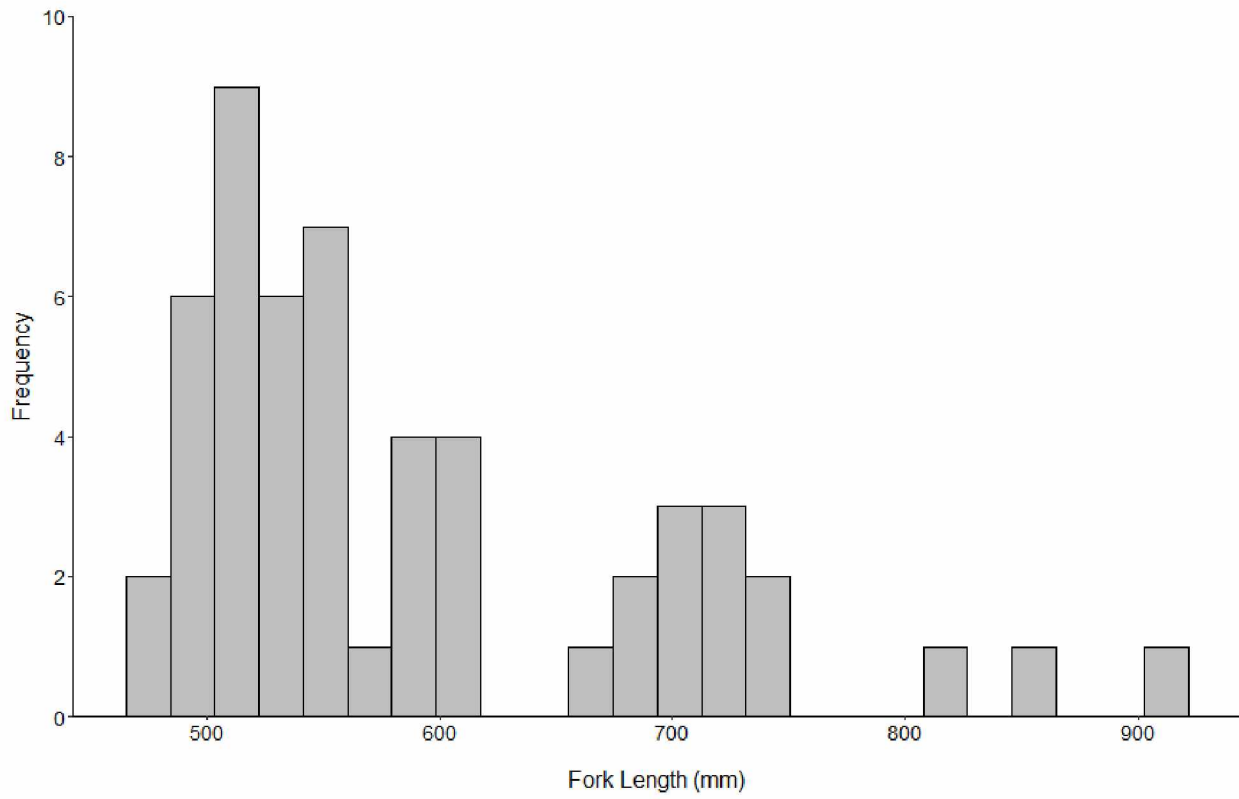
Figure 1.4. Fork length (mm) frequency of adult lake trout collected from lakes in the Fish Creek watershed, Alaska, during 2014 and 2015.
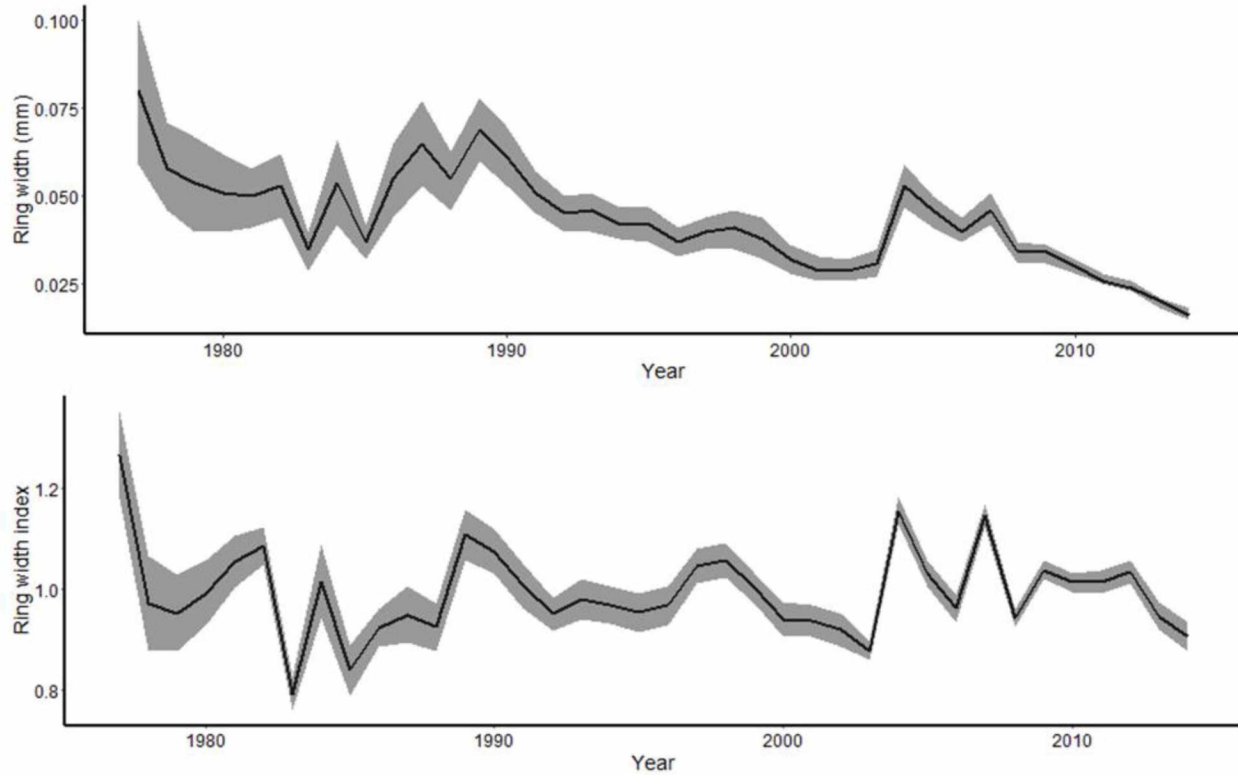
Figure 1.5. Mean raw ring width (mm; x-axis; upper panel) and ring width index corrected for age related growth decline (unitless; x-axis; lower panel) for 49 lake trout from 1977–2014. Grey shaded area is the standard error.
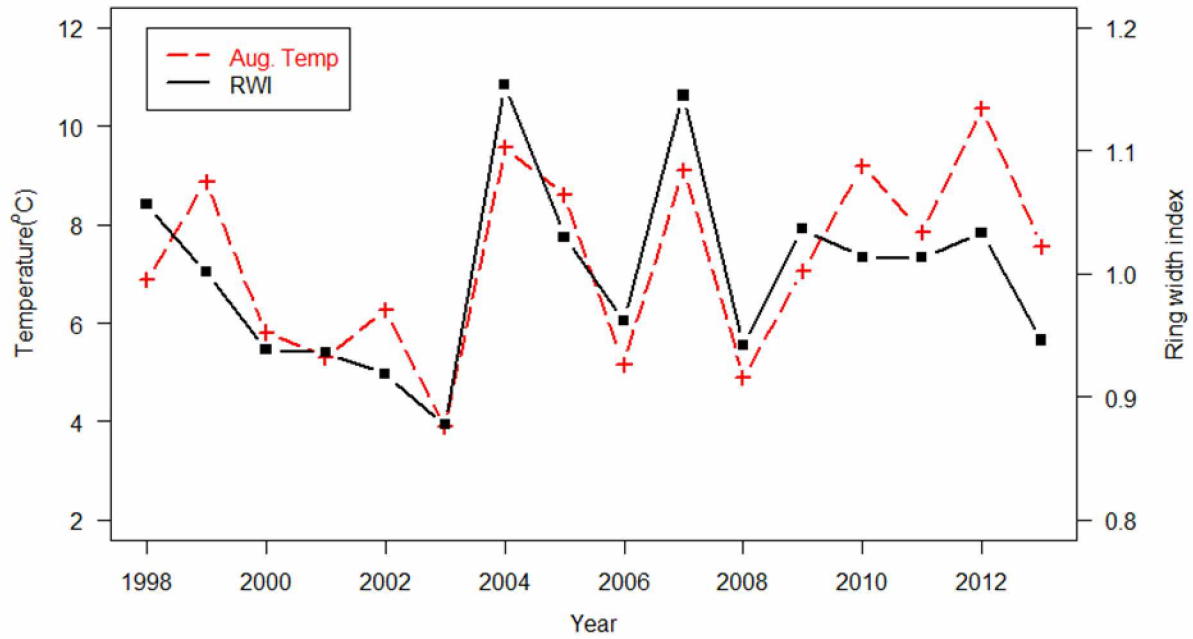
Figure 1.6. Mean August temperature (°C; dashed red line, left y-axis) observed at the Inigok weather station from 1998 to 2013, and growth chronology corrected for age related growth decline (RWI; solid black line, right y-axis, unitless) for the same period.
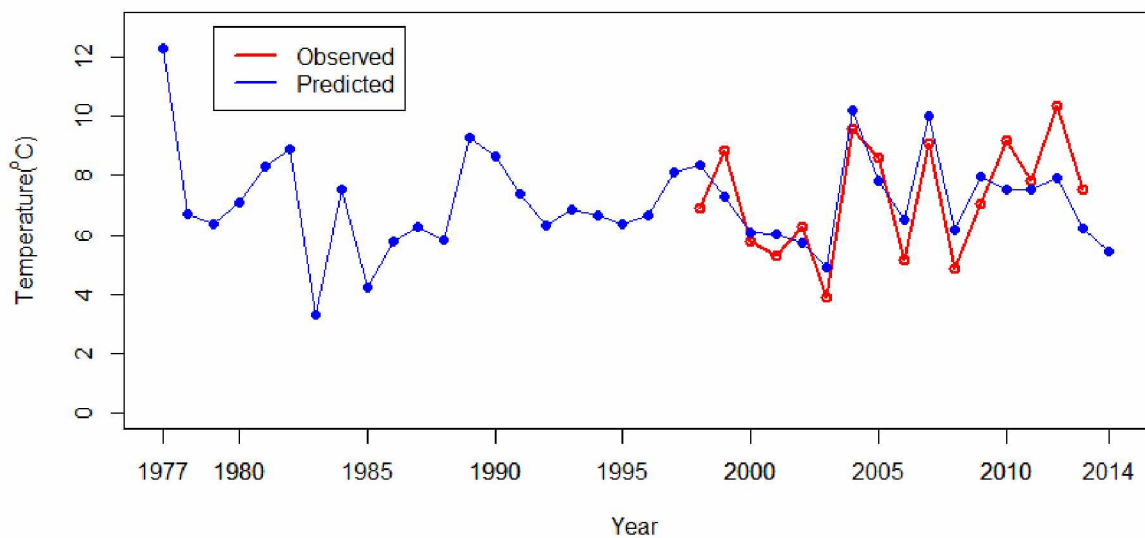
Figure 1.7. Mean August temperature (°C; y-axis) observed at the Inigok weather station through

time (x-axis; red line) and predicted by a lake trout growth chronology (y-axis; blue line) over

1977–2014.
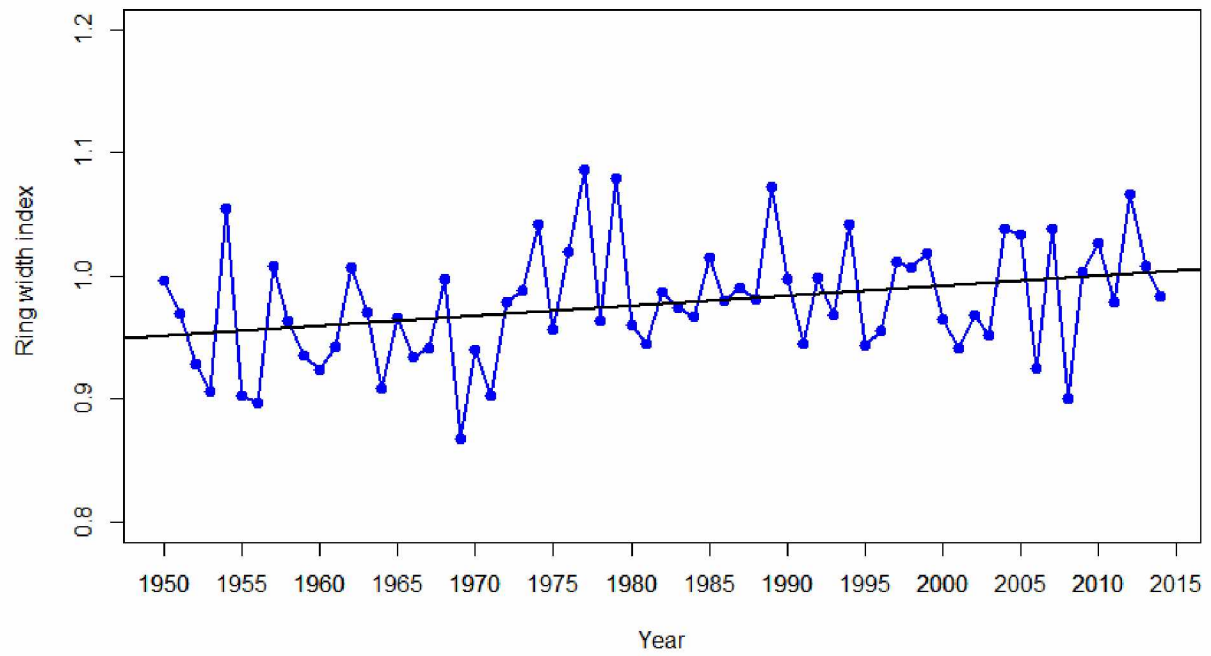
Figure 1.8. Ring width index (RWI, unitless) representing lake trout growth predicted from

modeled mean August temperature estimated by the Polar-WRF model over 1950–2014.

Table 1.1. Summary statistics of lake trout captured in the Fish Creek watershed, Alaska, in 2014 and 2015 by lake. Lakes are categorized by surface area: Small (Sml) = < 200 ha, Large (Lrg) = > 200 ha; and connectivity class: seasonally connected, perennially connected or flow through. Depth is maximum depth (m). The number of fish captured, sex, mean, minimum, maximum, and standard deviation of fork length (mm) are shown.

Lake	Category	Depth (m)	N	Male	Female	Fork length (mm)			
						Mean	Min	Max	SD
621	Sml-seasonal	9.8	3	1	1	662.3	546	737	102.1
750	Lrg-flow through	9.5	3	0	3	857.6	824	903	40.8
756	Lrg-seasonal	9.8	5	1	4	700.8	683	726	21.6
757	Sml-seasonal	10.1	5	1	4	505.2	471	548	30.0
1822	Lrg-perennial	12.5	5	1	4	555.4	507	601	33.6
2208	Lrg-perennial	12.2	5	2	3	535.2	506	546	16.5
2361	Lrg-flow through	6.7	4	1	3	503.8	482	536	23.3
2367	Sml-perennial	12.2	4	2	2	536.5	494	545	47.5
2373	Lrg-perennial	14.5	2	1	1	557.5	520	595	53.0
2385	Lrg-flow through	-	3	1	2	517.5	514	523	5.1
2204	Lrg-flow through	4.0	1	0	1	589	-	-	-
Inigok	Lrg-flow through	13.7	6	3	3	531.0	491	602	41.9
Ini-004	Sml-perennial	12.5	6	3	3	667.1	588	732	62.8

Table 1.2. Summary statistics for climate descriptors used in models predicting lake trout growth in the Fish Creek Watershed, Alaska, by month. All descriptors except sea ice are based on means of bi-hourly air temperature observations at Inigok, Alaska. Months are May (My), June (Jn), July (Jy). August (Ag), September (S), and October (O).

Climate Descriptor	Mean	Min.	Max.	Std. Error	Std. Deviation
Annual	-10.5	-15.6	-6.0	0.4	1.9
Jn, Jy, Ag	7.9	5.3	10.2	0.3	1.3
My, Jn, Jy, Ag	4.6	-3.3	6.9	0.6	2.3
My, Jn, Jy, Ag, S	4.0	-1.7	5.5	0.4	1.7
My	5.3	-12.0	-1.8	0.7	2.7
Jn	6.6	4.2	9.0	0.4	1.6
Jy	10.6	7.3	13.0	0.4	1.4
Ag	7.3	3.9	10.4	0.5	1.9
O	-7.2	-13.5	-3.5	0.6	2.5
Sea ice	0.6	0.1	1.0	0.1	0.3

Table 1.3. Summary of model selection statistics for models predicting lake trout growth from climate descriptors ranked by AICc. Abbreviations are as follows: K = the number of parameters, including the intercept and residual variance; (AICc) = value for a particular model compared with the top-ranked model; ΔAICc= the difference in the corrected Akaike information criterion. w_i = Akaike weights; L-L = the log-likelihood; RMSE = the root mean squared error; R^2_{adj} = describes the relationship between a particular model and the growth chronology. Months are May (My), June (Jn), July (Jy). August (Ag), September (S), and October (O).

Model	K	AICc	ΔAICc	w_i	LL	RMSE	R^2_{adj}
Ag	3	-43.46	0.00	0.76	25.73	0.048	0.55
Ag + Jn	4	-40.93	2.53	0.21	26.29	0.047	0.55
Ag + Jn + Jy	5	-36.86	6.60	0.03	26.42	0.046	0.52
Ag + Jy + My + O	6	-30.45	13.01	0.00	25.89	0.048	0.44
Ag + Jn + Jy+ O + Sea ice	7	-25.25	18.21	0.00	26.63	0.046	0.43
Ag + My + Jn + Jy + O + Sea ice	8	-16.77	26.69	0.00	26.67	0.046	0.37

APPENDIX

APPENDIX 1.A. Ring width index (RWI), mean August air temperature (°C) recorded at Inigok,

Alaska, weather station, and mean August temperature (°C) predicted by regression using RWI.

Year	RWI	Inigok temp.	RWI temp.
1977	1.26	NA	12.28
1978	0.97	NA	6.71
1979	0.95	NA	6.36
1980	0.99	NA	7.10
1981	1.05	NA	8.29
1982	1.08	NA	8.88
1983	0.79	NA	3.33
1984	1.01	NA	7.53
1985	0.83	NA	4.21
1986	0.92	NA	5.79
1987	0.94	NA	6.29
1988	0.92	NA	5.82
1989	1.10	NA	9.29
1990	1.07	NA	8.66
1991	1.00	NA	7.39
1992	0.95	NA	6.32
1993	0.97	NA	6.86
1994	0.96	NA	6.65
1995	0.95	NA	6.38
1996	0.96	NA	6.65
1997	1.04	NA	8.13
1998	1.05	6.88	8.34
1999	1.00	8.86	7.29
2000	0.93	5.81	6.10
2001	0.93	5.29	6.05
2002	0.91	6.25	5.72
2003	0.87	3.89	4.94
2004	1.15	9.57	10.18
2005	1.03	8.60	7.83
2006	0.96	5.16	6.54
2007	1.14	9.10	10.01
2008	0.94	4.89	6.16
2009	1.03	7.06	7.96
2010	1.01	9.18	7.51
2011	1.01	7.84	7.52
2012	1.03	10.3	7.90
2013	0.94	7.56	6.24
2014	0.90	NA	5.47

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Chapter 2: Variation in Lake Trout Growth Rates across Arctic Lakes[1]

Abstract

Freshwater habitats in the Arctic are experiencing increased effects of climate change. Despite ongoing research in the region, the implications for climate-sensitive, polymictic lake ecosystems are largely unknown. Predictions have indicated that warming water temperatures will increase fish growth, but the magnitude and specific factors influencing these changes are uncertain. Here, we investigated the relationship between physical and biological characteristics, as well as fish community structure, and Lake Trout *Salvelinus namaycush* growth. Lake Trout ($N = 53$) were captured from 13 lakes in the Fish Creek watershed in Northern Alaska. Individuals ranged from 471–903 mm fork length (mean = 589.3 ± 102.5 SD), and ranged in age from 12–55 years (mean = 24.9 ± 11.6 SD). Otolith increment analysis and the biological-intercept method were used to back-calculate length-at-age and these estimates were used to construct Walford plots from which the growth coefficient K was calculated; K ranged from 0.757–0.990 (mean = 0.901 ± 0.05 SD). Lake Trout K was modeled as a function of physical and biological characteristics and fish community structure using multiple linear regression, and seven candidate models were evaluated and ranked using Akaike's information criterion. The highest ranked model included physical (depth, distance to river and coast, connectivity class, and number of stream intersections) and biological (sex) covariates. Model averaging indicated K was higher in deeper, well connected lakes that were located farther from the coast and was lower for poorly connected lakes with increasing distance from a large river. An improved

understanding of the role of the environment on Lake Trout growth is important for conservation and management of this top predator in changing Arctic lake ecosystems.

Introduction

Across the Arctic, freshwater systems are experiencing increased effects of climate change relative to other regions (Prowse et al. 2006). For example, sediment cores collected from lakes on Baffin Island, Canada, show increased primary productivity that correlates with warming temperatures associated with anthropogenic activities (Michelutti et al. 2005). Despite these changes, the overall scope and magnitude of a warming climate and the effects on sensitive Arctic ecosystems remains largely unknown. It has been predicted that fish growth will increase with warming temperatures, but as aquatic ecosystems and food availability changes, the magnitude of these changes is uncertain (Carey and Zimmerman 2014). Growth in fishes is often used as a fundamental proxy for individual fitness, and growth rates have been shown to be influenced by physical and biological factors, and fish community structure (Le Cren 1951; McDonald et al. 1996; Blair et al. 2013), which are directly linked to environmental change. Lakes are a dominant feature across the Arctic landscape (Hinkel et al. 2005), but due to the remote nature of Arctic regions, limnological data are sparse relative to other regions globally. However, recent Arctic lake monitoring and lake classification efforts (Whitman et al. 2011; Jones and Zuck 2016) have provided new information which we can use to investigate the influence of environmental variation on fish growth in the Arctic.

Fish species experience indeterminate growth, meaning they grow throughout their life span (Weatherley and Gill 1987). However, indeterminate growth is rarely linear; in general, growth rate declines with increasing size and age (Sebens 1987; Mommsen 2001) and with habitat limitations, density-dependent competition, or genetics (McKay et al. 1986; Lorenzen and Enberg 2001). Biological factors, including sex, have also been shown to influence variation in fish growth. Reproductive energy requirements are much higher for females; thus, females may

have less energy available for somatic growth (Le Cren 1951; Saillant et al. 2001). This is further evident in variation of age and size at sexual maturation, with males often reaching maturity at an earlier age and at a smaller size (Burr 1987). For these reasons, variation in growth may be intrinsically different between sexes; as a result, it is imperative to differentiate between sexes when making inferences on patterns of fish growth.

The physical environment influences habitat quality and plays a pivotal role in fish growth in lakes (Blair et al. 2013). For example, lake characteristics such as depth and connectivity may influence growth through a number of mechanisms (e.g., temperature, lake ice phenology; King et al. 1999; Arp et al. 2015). Depth influences growth by providing thermal refuge and, through behavioral thermoregulation, controls species distribution within the water column (Beitinger and Fitzpatrick 1979; Olson et al. 1988; Snucins and Gunn 1995). Because fishes are ectotherms, they often inhabit an optimum thermal range where, if food availability is unlimited, maximum growth can be achieved (Magnuson et al. 1979; Weatherley and Gill 1987). For example, Lake Trout *Salvelinus namaycush*, a characteristic top predator in Arctic lakes, has an optimal temperature range of 6–13°C and must move to cold, deep waters to thermoregulate and reach maximum growth potential (Martin and Olver 1980). Another strategy that fish employ is to move between water bodies to seek suitable environmental conditions; however, the ability to do so is often limited if habitats are poorly connected (Kennedy 1941; Gowan and Fausch 1996) and in Arctic lake systems, dispersal can be hindered by low stream flow in connecting streams, ice, or human development (Fagan 2002; Heim et al. 2015). Connectivity among lakes allows fish to select optimum habitat as environmental conditions change seasonally, allowing for maximum growth to be achieved. In Arctic lake systems, connectivity

has been shown to be an important predictor of fish species richness, a metric of food web structure and prey availability (Haynes et al. 2014; Laske et al. 2016).

Lake Trout undergo ontogenic diet shifts throughout their life span. Juvenile Lake Trout are functionally planktivorous; as individuals get older and increase in size, swimming ability, and gape size, larger prey items can be consumed (Mittelbach and Persson 1998). However, the ability to make these diet shifts is dependent on prey availability and food web structure (Sherwood et al. 2002). A recent study of Arctic fishes found that connectivity was a driver of fish species assemblage, and a permanent channel connection was necessary for large-bodied fish species (e.g., Lake Trout, Arctic Grayling *Thymallus arcticus*, Broad Whitefish *Coregonus nasus*) to be present (Laske et al. 2016). Top predators such as Lake Trout benefit from the presence of large-bodied prey items because, where available, foraging on larger prey items generally have lower forage energy costs than feeding on smaller prey items (Pazzia et al. 2002). Empirical studies have shown that growth rates increase as prey size increases. For example, when planktivorous Lake Trout with stunted growth were transferred to a lake with a fish prey base, individuals shifted to piscivory and growth rates increased (Konkle and Sprules 1986), highlighting the influence of prey availability on diets and Lake Trout growth.

Arctic lakes are unique in that they minimally stratify (Welch et al. 1987) and have cold temperatures, a short ice-free season (Brewer 1958), and low productivity (Michelutti et al. 2005); all of these elements are expected to be affected by climate change. High-latitude studies have indicated that water temperatures are warming (O'Reilly et al. 2015); thus, as prey productivity increases under warmer conditions, growth of Arctic fishes may also increase (McDonald et al. 1996; Carey and Zimmerman 2014; E. Torvinen, University of Alaska Fairbanks, unpublished data). Because of the oligotrophic nature and simple food webs of these

lakes, top predators such as Lake Trout, could be food stressed in situations where increased prey productivity may increase growth (McDonald and Hershey 1989; McDonald et al. 1996). Any changes to growth rates of Lake Trout would likely affect lower trophic levels and the aquatic ecosystem as a whole (Carpenter et al. 1985; Hershey et al. 1990).

Given impending changes to physical and biological processes and fish community structures in Arctic lakes, and the importance of Lake Trout as a top predator in these systems, our overall goal was to better understand how individual Lake Trout growth varied across lakes with differing environmental characteristics. Specifically, our objectives were to 1) back-calculate length-at-age using otolith growth-increment analysis; 2) estimate individual growth rates (K; von Bertalanffy 1938); and 3) examine relationships among K and physical and biological factors, and fish community structure measured for study lakes. A better understanding of the influence of environmental factors on Lake Trout growth will provide critical data to assess changes to freshwater systems in the warming Arctic.

Methods

Study area. — This study focused on patterns of growth in Lake Trout collected from lakes in the Fish Creek watershed (FCW), located in the central portion of the Arctic Coastal Plain (ACP) in northern Alaska (Figure 2.1). This area is dominated by topographic depression lakes (Carter 1981; Jorgenson and Shur 2007), which comprise >20% of the surface landscape (Hinkel et al. 2005; Arp and Jones 2009). The FCW covers 4,900 km^2 and includes 4,362 lakes > 1 ha (Jones et al. 2017). Lake surface area reflects the surrounding topography (Sellmann et al. 1975; Hinkel 2006), and most lakes in this region are smaller than 20 ha surface area (Jones et al. 2017). Lakes in the region exhibit a short ice-free season with ice-out usually occurring in

late June and freeze-up by late September. At least 16 resident and migratory fish species inhabit the FCW and surrounding region; Arctic Grayling, Broad Whitefish, Least Cisco *Coregonus sardinella*, and Ninespine Stickleback *Pungitiuspungitius* are the most prevalent (Whitman et al. 2011; Laske et al. 2016).

Site selection. — Over 4,300 lakes have been identified within the FCW (Figure 2.1), and study lakes were selected using a lake classification scheme developed to characterize lake types based on remotely-sensed hydrogeomorphic attributes (Jones et al. 2017). Based on previous work in the region (Haynes et al. 2014; Laske et al. 2016), we expected that lake depth, connectivity, and surface area would represent major gradients in primary and secondary productivity and fish community structure; thus we categorized lakes for sampling based on the aforementioned three criteria. Lakes were classified as shallow or deep based on their ice regime as determined by Synthetic Aperture Radar Digital Surface Model (SAR); lakes with bedfast ice were classified as shallow, and those with floating ice deep. In the FCW, the cutoff between bedfast and floating ice regimes occurs at a depth of approximately 1.6 m (Grunblatt and Atwood 2014). Shallow lakes were not expected to contain Lake Trout and thus, were not included in the sampling frame. Connectivity classes were estimated using the ArcGIS hydrology toolset (ESRI 2011) based on Interferometric Synthetic Aperture Radar (IfSAR) data using stream contributing area criteria and low-flow field surveys. Lakes were assigned one of four connectivity classes: isolated, seasonally connected, perennially connected, or flow through. Seasonally and perennially connected were defined as having an intersection with at least one stream with contributing area of 15 and 25 km^2, respectively. Flow through lakes had a contributing area stream of >25 km^2 (Jones et al., in review). Because lake connectivity has been shown to influence fish species richness in nearby regions (Laske et al. 2016), it was not

expected that isolated lakes support Lake Trout and we subsequently excluded them from further analysis. IfSAR data were also used to classify lakes by surface area (ha; small < 200 ha, large ≥ 200 ha). Based on this rationale and owing to logistical constraints associated with accessing this remote region, nine flow-thorough (six large, three small), five seasonally connected (two large, three small), and 13 perennially connected (six large, seven small) were selected for sampling.

Lake Trout capture. — Lake trout were captured during the 2014 and 2015 field effort using a combination of baited set lines (jug sets), angling, and sinking gill nets. Hook-less jug sets are a passive angling technique in which high visibility floating buoys are attached to a bottom weight using a heavy line and baits are attached to the weight on a lighter 1–2 m leader. These jug sets were checked at least once every 24-hour period. When time and weather allowed, two types of experimental gill nets were also deployed in the deepest areas of each lake. One experimental variable-mesh gill net measured 38 m x 1.8 m, with five panels ranging in bar mesh size from 1.3 to 6.5 cm. The other gill net measured 33 m x 1.8 m, with three panels ranging in bar mesh size from 6 to 9 cm. To minimize bycatch, gill nets were checked every 2 to 3 hours. These passive collection techniques complimented angling methods to target adult Lake Trout. Angling methods consisted of casting heavy spoons (>15 g) or spinners either from shore or large inflatable kayaks. Only large adult Lake Trout greater than 471-mm fork length (FL) were collected. Fish were euthanized via decapitation, morphological measurements of FL (mm), and weight (kg) were taken, and sex was identified by opening the body cavity and observing gonads. Finally, both sagittal otoliths were removed using the guillotine method (Secor et al. 1991).

Limnological data.—Physical limnological attributes of study lakes were measured using a combination of field-based and remotely-sensed methods. Maximum depth (m) was measured

using a weighted transect tape in the field along two perpendicular linear transects. Remotely-sensed attributes included distance to coast (km), connectivity class, number of stream intersections, and distance to river (km). Distance to coast was measured using color infrared orthophotography as the straight line distance from the focal lake to the mouth of the Fish Creek delta (Figure 2.1). Connectivity was the connectivity class (see *Site selection*), and streams was the number of second-order streams (Strahler 1957) flowing into or out of lake as determined using IfSAR DSM data. Distance to river was the straight line distance from a focal lake to the nearest fifth-order or higher stream, also derived from IfSAR DSM data.

Fish community structure. — Fish species richness was surveyed to establish prey availability and trophic structure using the multimethod occupancy approach for Arctic lakes described by Haynes et al. (2013). This approach recommends sampling using multiple gear types: minnow traps, fyke nets, gill nets, jug sets, and beach seines. Sixteen minnow traps were used in sampling; eight traps were affixed to shore and eight traps were sunk in a deep hole within a lake and these were checked and removed after a 12-hour period. Two hoop net constructed Fyke nets, with 0.3-cm mesh and a frame opening of 1.1 x 1.1 m, were set perpendicular from shore near a lake outlet where available. Two 15.2 x 1.2 m wings and a 30.5-m centerline with 0.6-cm mesh were attached to each fyke net. Fyke nets were checked twice during a 24-hour period. Shorelines were sampled using a 15-m x 1.2-m beach seine with 3-mm mesh, and two replicates were conducted at three different locations (Haynes et al. 2013).

Otolith analysis. — Otoliths were stored dry in paper envelopes until embedded in epoxy, then sectioned on the transverse plane using a low-speed wafering saw (Buehler, Lake Bluff, Illinois) before being affixed to a microscope slide. Digital images of each sectioned otolith were

taken with a 5.0 megapixel digital camera (DFC425, Leica Camera, Inc., Allendale, New Jersey) affixed to a compound microscope (Leica DM 2000) using transmitted light.

Once clear images were acquired, annuli were counted and widths were measured using Image Pro plus 7.0 software (Media Cybernetics, Rockville, Maryland, USA) using the caliper tool, beginning at the otolith margin and proceeding on a continuous transect to the focus. Each annuli was defined by, and measured from, the outside margin of the translucent zone (a narrow dark band under transmitted light) to the outside margin of the next translucent zone (Beckman and Wilson 1995) and resulted in annual ring width values (mm). Although care was taken to measure each annuli perpendicular to the axis of growth (von Biela et al. 2015), the exact location and length of the measurement transect varied between individuals. Because these methods require clear identifiable annuli to assess variation in otolith growth patterns, inconsistencies between sequences were accounted for by multiplying by a standardization factor to maintain relative increment width differences while correcting for between-otolith inconsistencies (Campana 1984).

Crossdating techniques were used to validate age estimations using the software COFECHA (Holmes 1983, Torvinen 2017). Crossdating is a technique pioneered by dendrochronogists under the assumption that that an environmental variable (e.g., temperature) limits growth. As a result, annuli widths will vary as a function of environmental variation. This environmental control on growth is expected to result in similar patterns of annuli width in individuals collected within a region (Stokes and Smiley 1996; Black et al. 2005).

Length back-calculations and growth. — Once a standardized increment sequence was created, length was back-calculated using the biological intercept method (Campana 1990). This method is based on the relationship between length and age, but also includes the otolith width

of an age-0 Lake Trout. In this case, otolith width of an age-0 individual was assigned 0.137 mm, where fish length = 21.7 mm (Bronte et al. 1995; Hansen et al. 2012). These values were used in the biological intercept model (Campana 1990), a modified Fraser-Lee equation (Ricker 1975):

$$L_i = L_c + [(S_i - S_c)(L_c - L_o)]/(S_c - S_o),$$

where L_i = back-calculated length at the ith increment; L_c = length at capture; S_i = otolith radius at the ith increment; S_c = otolith radius at capture; L_o = length of fish at age-0; S_o = otolith width at age-0. It was found that back-calculated length-at-age estimates for early years were often poor quality and highly influenced individual growth curves. Material is not deposited uniformly during otolith formation, thus transverse sections are used to improve clarity. Despite this, otolith clarity is still inconsistent (Chilton and Beamish, 1982) and annuli from early growth years (first 1-5 annuli) are often unclear (Hansen et al. 2012). As a result, length estimations for the first five growth increments were omitted from further analysis.

We estimated fish growth coefficient (K), which describes how quickly an individual reaches maximum theoretical length (L_∞; Quist et al. 2012), based on length-at-age estimates using Walford plots (L_t vs. L_{t+1}) constructed for individual fish. The slope of the resulting line is equal to K, which is identical to K as described in the von Bertalanffy model (von Bertalanffy 1938).

Model selection.— Individual Lake Trout K was modeled as a function of biological and physical factors, as well as fish community structure of study lakes (Table 2.3) using multiple linear regression. Biological descriptors included sex, fish community structure included fish species richness, Least Cisco abundance, and Ninespine Stickleback abundance. Physical covariates were maximum depth, distance to coast, distance to river, connectivity class, and

number of stream intersections. It was expected that these covariates would have a high degree of multi-collinearity thus all continuous predictors were examined using the variance inflation factor (VIF). Covariates with a VIF > 10 were not considered in further analysis (Montgomery et al. 2015; Beatty et al. 2014). Based on the reduced subset of predictors, a set of seven candidate models were constructed that contained sets of explanatory variables hypothesized to best predict K (Burnham and Anderson 2002). Candidate models were compared simultaneously using Akaike's information criterion (AIC) adjusted for bias due to small sample size (AIC_c), and we considered the best model, given the data, that with the lowest AIC_c and highest Akaike weight (w_i). To account for model uncertainty, model averaging was used to calculate parameter estimates and variances from models in the confidence model set ($w_i > 0.05$) and we made inferences based upon these estimates. All analyses were conducted in Program R (R Development Core Team 2015) using the *glm* package.

Results

Lake Trout capture. — A total of 53 adult Lake Trout were captured from 13 lakes, ten lakes of which were large ($\geq$ 200 ha) lakes and three lakes which were small (< 200 ha). Four flow through, three seasonally, and six perennially connected lakes were sampled. Lake Trout were captured using angling ($N = 27$), jug sets ($N = 18$), and gill nets ($N = 8$). Individuals ranged from 471–903-mm FL (mean = 589.34 $\pm$ 102.5 SD), and the sex ratio was skewed to females (n = 34) over males (n = 18) with one individual of unknown sex (Table 2.1). A simple binomial test confirmed that the probability of a captured individual being female was greater than 0.5 (P = 0.018).

Physical data and fish community structure. — Of the thirteen lakes sampled, nine were systematically sampled to determine fish species richness and abundance. Species richness ranged from 4–8, with Ninespine Stickleback and Least Cisco being most abundant.

Maximum depth was measured in 12 lakes, and ranged from 3.96–14.48 m (mean = 10.6 ± 3.0 SD). Distance to coast ranged from 68.2–78.5 km (mean = 69.5 ± 5.9 SD), and distance to river from 0.08–4.97 km (mean = 1.5 ± 1.3 SD). Second order stream intersections ranged from one to eight for the 13 lakes (mean = 3.4 ± 2.1 SD).

Length back-calculations and growth. — Of the 53 Lake Trout collected, 47 fish had clear annuli representing the entire lifespan, allowing them to be aged; these individuals ranged in age from 12–55 years (mean = 24.9 ± 11.6 SD; Figure 2.2). Ages were verified via statistical crossdating which identified several years to have consistently wide ring widths: 2007, 2004, and 1989. Adversely, 2003, 1985, and 1983 resulted in consistently narrow growth rings (Figure 1.2). Based on results of the COFECHA analysis, this series was found to have a mean series inter-correlation (SIC) of 0.327. Individual series correlation coefficients ranged from 0.054 to 0.697, and inter-annual ring-width variability (mean sensitivity index) was 0.231. Individual growth coefficients (K) ranged from 0.757–0.990 (mean = 0.901 ± 0.05; Figure 2.2).

Model selection. — The highest ranked model included only physical covariates (depth, distance to river, distance to coast, connectivity class, and number of stream intersections) and accounted for 79% of the weight of candidate models. However, a model with the biological covariate, sex, was also included in the confidence model set and accounted for an additional 18% of model weights (Table 2.2). Model averaging indicated that K was higher in deeper, well connected lakes, located further from the coast (Figure 2.3), and decreased with distance from a large river. However, confidence intervals for all covariates, with the exception of maximum

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depth, overlapped zero, indicating uncertainty in the direction of effects for those factors (Table 2.3).

Discussion

Our research showed that Lake Trout growth coefficients were strongly influenced by physical characteristics such as depth in Arctic lakes and varied by sex. Because environmental change has direct effects on Arctic lake hydrology and geomorphology, knowledge of the relationships among these factors and fish growth will be key to understanding Arctic fishes in a changing environment. Here, we synthesize information from this research and related studies to describe how physical and biological characteristics and fish community structure, may influence Lake Trout growth, as well as discuss assumptions and implications associated with this study.

We found that Lake Trout growth responded strongest to maximum lake depth; growth rates were higher in deeper lakes. Lake temperature and dissolved oxygen, key factors in fish growth and energetics, vary with depth, and in deep lakes are expected to provide thermal refuge, favorable for Lake Trout growth (Martin and Olver 1980). Lake depth has been found to influence fish community structure, increasing fish species richness, by providing adequate habitat, especially oxygenated water for overwintering populations (Hershey et al. 2006; Leppi et al. 2016). A species rich ecosystem, likely to be found in a deeper lake, may provide a higher quality, and more diverse and stable prey base for Lake Trout (Magnuson et al. 1998). Lake depth is likely to be of increasing importance as lake temperatures warm and ice-free period increases. These effects could cause an increased level of stratification in typically polymictic Arctic lakes (Lewis 1983). As mentioned above, warmer lake temperatures are likely to increase Lake Trout growth, but only if productivity increases provide sufficient resources to support such

growth (McDonald et al. 1996; Carey and Zimmerman 2014). Deeper lakes, associated with a higher quality prey base may become increasingly important for Lake Trout to reach maximum growth potential in a warming Arctic.

The top model of Lake Trout growth rates included only physical covariates and indicated that Lake Trout growth rate increased with the number of connecting streams, although considerable uncertainty surrounded this estimate. The number of stream intersections can be used as a metric of among-lake connectivity a factor which has been demonstrated to provide important foraging opportunities and be a driver of species richness for Arctic fish species (Haynes et al. 2014; Heim et al. 2015; Laske et al. 2016). Stream inlets into lakes are ecotones where terrestrial, lotic, and lentic ecosystems interact. Allochthonous material (e.g., particulate organic matter) and terrestrial invertebrates are deposited into streams, which in turn enter lake systems at stream mouths (Vannote et al. 1980; Cole et al. 2006). This energy input influences fish distribution within lakes and may result in prey aggregations near stream mouths (L. Moulton, MJM Research, LLC, unpublished data) and could be particularly important in the Arctic during spring snowmelt and corresponding peak river discharge (Bowling et al. 2003). Such periods of high flows allow fish to travel between water bodies (Heim et al. 2015), leading to a period of high foraging activity and also occur within the period Arctic lake temperatures are likely within the optimal thermal range of Lake Trout. Overall, a higher number of streams feeding into Arctic lakes likely provide increased feeding opportunities for Lake Trout, thus increasing growth in lakes with multiple connecting streams.

We found that Lake Trout growth increased with distance from the Arctic Coast, likely as a result of warmer air temperatures further from the coast which lead to warmer lake temperatures and increased Lake Trout growth in this region (Hinkel et al. 2012; Black et al.

2013; E. Torvinen, University of Alaska Fairbanks, unpublished data). The Arctic Ocean and Beaufort Sea play a significant role in climate patterns across the Arctic Coastal Plain where this study was conducted, and marine-related climate effects decrease as distance from the coast increases (Alexeev et al. 2016). For example, variability in lake ice thickness and phenology is associated with sea ice conditions, where years with large amounts of nearshore sea ice result in colder temperatures, less snow, and thicker lake ice (Zhang and Jeffries 2000). In the Beaufort Sea, sea ice loss from climate change has led to more nearshore, open-water areas (Wendler et al. 2014) and increased snow cover, which has resulted in thinner lake ice, a pattern which declines as distance from the coast increases (Alexeev et al. 2016). Other climate descriptors, such as cloud cover, wind, and air temperature, also vary as distance from the coast increases and have direct effects on lake water temperature and mixing (Schindler et al. 1990; Fee et al. 1996) which may play a role in Lake Trout growth.

Model selection indicated the model consisting of physical covariates and the single biological covariate sex out-ranked models containing fish community structure covariates (fish species richness and prey species abundance). These ecosystem characteristics have a higher degree of variability than physical characteristics (Ball et al. 2007). Because fish community structure sampling only occurred during a single season, this snapshot of the aquatic ecosystem affecting long-lived Lake Trout may not have captured among-lake variation in processes that influence growth throughout the species long life span. For example, prey quality varies among species, including Ninespine Stickleback and Least Cisco, and abundance of these fishes varies among years (Ball et al. 2007). Such temporal variation in prey availability patterns likely plays a role in Lake Trout growth that is difficult to isolate given the long life span of this species.

Studies in remote regions, such as the Arctic, allow researchers the unique opportunity to study fish ecology in populations largely unexploited by humans. For example, in populated areas, growth trends in long-lived individuals are often influenced by fishing-induced mortality. In the case of this current study, ecological inferences based on patterns of Lake Trout growth in remote Arctic lakes could be extended beyond these populations to the species as a whole. Moreover, excluding depth and sex, covariates used in the highest ranking model were measured using remote-sensing techniques, highlighting the versatility of using such data to predict ecological responses. The ability to map Lake Trout growth across the Arctic based on remotely-sensed lake attributes would be extremely useful for future studies of this ecologically important species because such data are often the only available in remote Arctic regions. Through this study, valuable ecological knowledge with regards to Lake Trout, a top predator, has been gained, this is vital to the understanding of changing Arctic aquatic ecosystems.

Acknowledgements

Literature Cited

Alexeev, V. A., C. D. Arp, B. M. Jones, and L. Cai. 2016. Arctic sea ice decline contributes to thinning lake ice trend in northern Alaska. Environmental Research Letters 11:074022.

Arp, C. D., and B.M. Jones. 2009. Geography of Alaska lake districts: Identification, description, and analysis of lake-rich regions of a diverse and dynamic state. Scientific Investigations Report 2008-5215. US Geological Survey, Anchorage, Alaska.

Arp, C. D., B. M. Jones, A. K. Liljedahl, K. M. Hinkel, and J. A. Welker. 2015. Depth, ice thickness, and ice-out timing cause divergent hydrologic responses among Arctic lakes. Water Resources Research 51:9379–9401.

Ball, J. R., D. Esler, and J. A. Schmutz. 2007. Proximate composition, energetic value, and relative abundance of prey fish from the inshore eastern Bering Sea: implications for piscivorous predators. Polar Biology 30:699–708.

Beatty, S. J., D. L. Morgan, and A. J. Lymbery. 2014. Implications of climate change for potamodromous fishes. Global Change Biology 20:794–807.

Beckman, D. W., and C. A. Wilson. 1995. Seasonal timing of opaque zone formation in fish otoliths. Pages 27–44 *in* D. H. Secor, J. M. Dean, S. E. Campana, and W. Belle, editors. Recent developments in fish otolith research. Baruch institute for marine biology and coastal research, University of South Carolina Press. Columbia, South Carolina.

Beitinger, T. L., and L. C. Fitzpatrick. 1979. Physiological and ecological correlates of preferred temperature in fish. American Zoologist 19:319–329.

Black, B. A., G. W. Boehlert, and M. M. Yoklavich. 2005. Using tree-ring crossdating techniques to validate annual growth increments in long-lived fishes. Canadian Journal of Fisheries and Aquatic Sciences 62:2277–2284.

Black, B. A., V. R. von Biela, C. E. Zimmerman, and R. J. Brown. 2013. Lake Trout otolith chronologies as multidecadal indicators of high-latitude freshwater ecosystems. Polar Biology 36:147–153.

Blair, J. M., I. Ostrovsky, B. J. Hicks, R. J. Pitkethley, and P. Scholes. 2013. Growth of Rainbow Trout *Oncorhynchus mykiss* in warm-temperate lakes: implications for environmental change. Canadian Journal of Fisheries and Aquatic Sciences 70:815–823.

Bowling, L. C., D. L. Kane, R. E. Gieck, L. D. Hinzman, and D. P. Lettenmaier. 2003. The role of surface storage in a low-gradient Arctic watershed. Water Resources Research 39:1087.

Brewer, M. C. 1958. The thermal regime of an Arctic lake. Transactions American Geophysical Union 39:278–284.

Bronte, C. R., J. H. Selgeby, J.H. Saylor, G. S. Miller, and N. R. Foster. 1995. Hatching, dispersal, and bathymetric distribution of age-0 wild Lake Trout at the Gull Island Shoal complex, Lake Superior. Journal of Great Lakes Research 21:233–245.

Burnham KP, Anderson DR. 2002. Chapter 2. Information and likelihood theory: a basis for model selection and inference. Pages 49–97 *in* Model Selection and Multimodel Inference: A Practical Information - Theoretic Approach, 2nd edition. Springer: New York.

Burr, J. M. 1987. Synopsis and bibliography of Lake Trout *Salvelinus namaycush* in Alaska. Alaska Department of Fish and Game, Fishery Manuscript No. 5, Juneau.

Campana, S. E. 1984. Lunar cycles of otolith growth in the juvenile Starry Flounder *Platichthys stellatus*. Marine Biology 80:239–246.

Campana, S. E. 1990. How reliable are growth back-calculations based on otoliths? Canadian Journal of Fisheries and Aquatic Sciences 47:2219–2227.

Carey, M. P., and C. E. Zimmerman. 2014. Physiological and ecological effects of increasing temperature on fish production in lakes of Arctic Alaska. Ecology and Evolution 4:1981–1993.

Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. BioScience 35:634–639.

Carter, L. D. 1981. A Pleistocene sand sea on the Alaskan Arctic coastal plain. Science 211:381–383.

Chilton, D. E., and R. J. Beamish. 1982. Age determination methods for fishes studied by the Groundfish Program at the Pacific Biological Station. Canadian Special Publication of Fisheries and Aquatic Sciences 60. Ottawa, Canada.

Cole, J. J., S. R. Carpenter, M. L. Pace, M. C. Van de Bogert, J. L. Kitchell, and J. R. Hodgson. 2006. Differential support of lake food webs by three types of terrestrial organic carbon. Ecology Letters 9:558–568.

ESRI 2011. ArcGIS Desktop: Release 10.2.1. Environmental Systems Research Institute. Redlands, California.

Fagan, W.F. 2002. Connectivity, fragmentation, and extinction risk in dendritic metapopulations. Ecology 83:3243–3249.

Fee, E. J., R. E. Hecky, S. E. M. Kasian, and D. R. Cruikshank. 1996. Effects of size, water

> clarity and climatic variability on mixing depths in Canadian Shield lakes. Limnology

> and Oceanography 41:912–920.

Gowan, C., and K. D. Fausch. 1996. Mobile Brook Trout in two high-elevation Colorado

> streams: re-evaluating the concept of restricted movement. Canadian Journal of Fisheries

> and Aquatic Sciences 53:1370–1381.

Grunblatt, J., and D. Atwood. 2014. Mapping lakes for winter liquid water availability using

> SAR on the North Slope of Alaska. International Journal of Applied Earth Observation

> and Geoinformation 27:63–69.

Hansen, M. J., N. A. Nate, C. C. Kruegerand, and M. S. Zimmerman. 2012. Age, growth,

> survival, and maturity of Lake Trout morphotypes in Lake Mistassini, Quebec.

> Transactions of the American Fisheries Society 141:1492–1503.

Haynes, T. B., A. E. Rosenberger, M. S. Lindberg, M. S. Whitman, and J. A. Schmutz. 2013.

> Method- and species-specific detection probabilities of fish occupancy in Arctic lakes:

> implications for design and management. Canadian Journal of Fisheries and Aquatic

> Sciences 70:1055–1062.

Haynes, T. B., A. E. Rosenberger, M. S. Lindberg, M. Whitman, and J. A. Schmutz. 2014.

> Patterns of lake occupancy by fish indicate different adaptations to life in a harsh Arctic

> environment. Freshwater Biology 59:1884–1896.

Heim, K. C., M. S. Wipfli, M. S. Whitman, C. D. Arp, J. Adams, and J. A. Falke. 2015. Seasonal

> cues of Arctic grayling movement in a small Arctic stream: the importance of surface

> water connectivity. Environmental Biology of Fishes 99:49–65.

Hershey, A. E. 1990. Snail populations in arctic lakes: competition mediated by predation? Oecologia 82:26–32.

Hershey, A. E., S. Beaty, K. Fortino, M. Keyse, P. P. Mou, W. J. O'Brian, and M. E. McDonald. 2006. Effect of landscape factors on fish distribution in Arctic Alaskan lakes. Freshwater Biology 51:39–55.

Hinkel, K. M., R. C. Frohn, F. E. Nelson, W. R. Eisner, and R. A. Beck. 2005. Morphometric and spatial analysis of thaw lakes and drained thaw lake basins in the western Arctic Coastal Plain, Alaska. Permafrost and Periglacial Processes 16:327–341.

Hinkel, K. 2006. Comment on "Formation of oriented thaw lakes by thaw slumping" by Jon D. Pelletier. Journal of Geophysical Research 111:F01021.

Hinkel, K. M., J. D., Lenters, Y., Sheng, E. A., Lyons, R. A., Beck, W.R., Eisner, E.F., Maurer, J., Wang, B. L., Potter. 2012. Thermokarst lakes on the Arctic Coastal Plain of Alaska: Spatial and temporal variability in summer water temperature. Permafrost and Periglacial Processes 23:207–217.

Holmes R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bulletin 43:69–78.

Jones, B. M. and C. Zuck. 2016. Fish Creek Watershed Lake Classification; NPRA, Alaska: U.S. Geological Survey data release available, https://dx.doi.org/10.5066/F7H70CXB.

Jorgenson, M. T., and Y. Shur. 2007. Evolution of lakes and basins in northern Alaska and discussion of the thaw lake cycle. Journal of Geophysical Research 112:F2S17.

Kennedy, W. A. 1941. The migration of fish from a shallow to a deep lake in spring and early summer. Transactions of the American Fisheries Society 70:391–396.

King, J. R., B. J. Shuter, and A. P. Zimmerman. 1999. Empirical Links between thermal Habitat, fish growth, and climate change. Transactions of the American Fisheries Society 128:656–665.

Konkle, B. R., and W. G. Sprules. 1986. Planktivory by stunted Lake Trout in an Ontario Lake. Transactions of the American Fisheries Society 115:515–521.

Laske, S. M., T. B. Haynes, A. E. Rosenberger, J. C. Koch, M. S. Wipfli, M. Whitman, and C. E. Zimmerman. 2016. Surface water connectivity drives richness and composition of Arctic lake fish assemblages. Freshwater Biology 61:1090–1104.

Le Cren, E. D. 1951. The length-weight relationship and seasonal cycle in gonad weight and condition in the perch *Perca fluviatilis*. The Journal of Animal Ecology 20:201–219.

Leppi, J. C., C. D. Arp, and M. S. Whitman. 2016. Predicting late winter dissolved oxygen levels in Arctic lakes using morphology and landscape metrics. Environmental management 57:463–473.

Lewis, W. M., (1983) A revised classification of lakes based on mixing. Canadian Journal of Fisheries and Aquatic Sciences 40:1779-1787.

Lorenzen, K., and K. Enberg. 2001. Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons. Proceedings of the Royal Society of London B: Biological Sciences 269:49–54.

Magnuson, J. J., L. B. Crowder, and P. A. Medvick. 1979. Temperature as an ecological resource. American Zoologist 19:331–343.

Magnuson, J. J., W. M. Tonn, A. Banerjee, J. Toivonen, O. Sanchez, and M. Rask. 1998. Isolation vs. extinction in the assembly of fishes in small northern lakes. Ecology 79: 2941–2956.

Martin N. V., and C. H. Olver. 1980 The Lake Charr, *Salvelinus namaycush*. Pages 205–277 *in*

    K. Balon, and W. Junk, editors. Charrs: salmonid fishes of the genus *Salvelinus*. The

    Hague, The Netherlands.

McDonald, M. E., and A. E. Hershey. 1989. Size structure of a Lake Trout *Salvelinus namaycush*

    population an Arctic lake: influence of angling and implications for fish community

    structure. Canadian Journal of Fisheries and Aquatic Sciences 46:2153–2156.

McDonald, M. E., A. E. Hershey, and M. C. Miller. 1996. Global warming impacts on Lake

    Trout in Arctic lakes. Limnology and Oceanography 41:1102–1108.

McKay, L. R., P. E. Ihssen, and G. W. Friars. 1986. Genetic parameters of growth in Rainbow

    Trout, *Salmo gairdneri*, as a function of age and maturity. Aquaculture 58:241–254.

Michelutti, N., A. P. Wolfe, R. D. Vinebrooke, B. Rivard, and J. P. Briner. 2005. Recent primary

    production increases in Arctic lakes. Geophysical Research Letters 32:L19715.

Mittelbach, G. G., and L. Persson. 1998. The ontogeny of piscivory and its ecological

    consequences. Canadian Journal of Fisheries and Aquatic Sciences 55:1454–1465.

Mommsen, T. P. 2001. Paradigms of growth in fish. Comparative Biochemistry and Physiology

    129:207– 219.

Montgomery, D. C., E. A. Peck, and G. G. Vining. 2015. Introduction to linear regression

    analysis (Volume. 821). John Wiley & Sons, New York.

O'Reilly, C. M., S., Sharma, D. K. Gray, S. E. Hampton, J. S. Read, R. J. Rowley, P., Schneider,

    J. D. Lenters, P. B. McIntyre, B. M. Kraemer, and G. A. Weyhenmeyer. 2015. Rapid and

    highly variable warming of lake surface waters around the globe. Geophysical Research

    Letters 42:773–781.

Olson, R. A., J. D. Winter, D. C. Nettles, and J. M. Haynes. 1988. Resource partitioning in summer by salmonids in South-Central Lake Ontario. Transactions of the American Fisheries Society 117:552–559.

Pazzia, I., M. Trudel, M. Ridgway, and J. B. Rasmussen. 2002. Influence of food web structure on the growth and bioenergetics of Lake Trout *Salvelinus namaycush*. Canadian Journal of Fisheries and Aquatic Sciences 59:1593–1605.

Prowse, T. D., F. J. Wrona, J. D. Reist, J. E. Hobbie, L. M. Lévesque, and W. F. Vincent. 2006. General features of the Arctic relevant to climate change in freshwater ecosystems. AMBIO: A Journal of the Human Environment 35:330–338.

Quist, M. C., M. A. Pegg, and D. R. DeVries. 2012. Age and growth. Pages 677–732 *in* A. V. Zale, D. L. Parrish, and T. M. Sutton, editors. Fisheries techniques, 3rd edition. American Fisheries Society, Bethesda, Maryland.

R Development Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada Bulletin 191, Ottawa, Canada.

Saillant, E., A. Fostier, B. Menu, P. Haffray, and B. Chatain. 2001. Sexual growth dimorphism in Sea Bass *Dicentrarchus labrax*. Aquaculture 202:371–387.

Schindler, D. W., K. G. Beaty, E. J. Fee, D. R. Cruikshank, E. D. DeBruyn, D. L. Findlay, G. A. Linsey, J. A. Shearer, M. P. Stainton, and M. A. Turner. 1990. Effects of climate warming on lakes of the central boreal forest. Science 250:967–970.

Sebens, K. P. 1987. The ecology of intermediate growth in animals. Annual Review of Ecology and Systematics 18:371–407.

Secor, D. H., J. H. Dean, and E. H. Laban. 1991. Manual for otolith removal and preparation for microstructural examination. Electric Power Research Institute and Belle W. Baruch Institute for Marine Biology and Coastal Research, Columbia, South Carolina

Sellmann, P. V., J. Brown, R. I. Lewellen, H. McKim, and C. Merry. 1975. The Classification and Geomorphic Implications of Thaw Lakes on the Arctic Coastal Plain. U.S. Army Cold Regions Research and Engineering Laboratory, Research Report 344:21.

Sherwood, G. D., I. Pazzia, A. Moeser, A. Hontela, and J. B. Rasmussen. 2002. Shifting gears: enzymatic evidence for the energetic advantage of switching diet in wild-living fish. Canadian Journal of Fisheries and Aquatic Sciences 59:229–241.

Snucins, E. J., and J. M. Gunn. 1995. Coping with a warm environment: behavioral thermoregulation by Lake Trout. Transactions of the American Fisheries Society 124:118–123.

Stokes M. A., and T. L. Smiley 1996. An introduction to tree-ring dating. University of Chicago Press, Chicago, Illinois.

Strahler, A. N. 1957. Quantitative analysis of watershed geomorphology. American Geophysical Union Transactions 38:913–920.

Torvinen, E. T. 2017. Lake Trout Otoliths as Indicators of Past Climate Patterns and Growth in Arctic Lakes. Master's Thesis. University of Alaska Fairbanks, Fairbanks, Alaska.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130–137.

von Bertalanffy, L. 1938. A quantitative theory of organic growth (inquiries on growth laws II). Human Biology 10:181–213.

von Biela, V. R., G. H. Kruse, F. J. Mueter, B. A. Black, D. C. Douglas, T. E. Helser, and C. E. Zimmerman. 2015. Evidence of bottom-up limitations in nearshore marine systems based on otolith proxies of fish growth. Marine Biology 162:1019–1031.

Weatherley, A. H., and H. S. Gill. 1987. The biology of fish growth. Academic Press, Orlando, Florida.

Welch, H. E., J. A. Legault, and M. A. Bergmann. 1987. Effects of snow and ice on the annual cycles of heat and light in Saqvaqjuac lakes. Canadian Journal of Fisheries and Aquatic Sciences 44:1451–1461.

Wendler G., B. Moore, and K. Galloway. 2014. Strong temperature increase and shrinking sea ice in Arctic Alaska. Open Atmospheric Science Journal 8:7–15.

Whitman, M. S., C. D. Arp, B. Jones, W. Morris, G. Grosse, F. Urban, and R. Kemnitz. 2011. Developing a long-term aquatic monitoring network in a complex watershed of the Alaskan Arctic Coastal Plain. Pages 15–20 *in* C. N. Medley, G. Patterson, and M. J. Parker, editors. Proceedings of the Fourth Interagency Conference on Research in Watersheds: Observing, Studying, and Managing for Change. Reston, Virginia.

Zhang, T., and M. O. Jeffries. 2000. Modeling interdecadal variations of lake ice thickness and sensitivity to climatic change in northernmost Alaska. Annals of Glaciology 31:339–47.
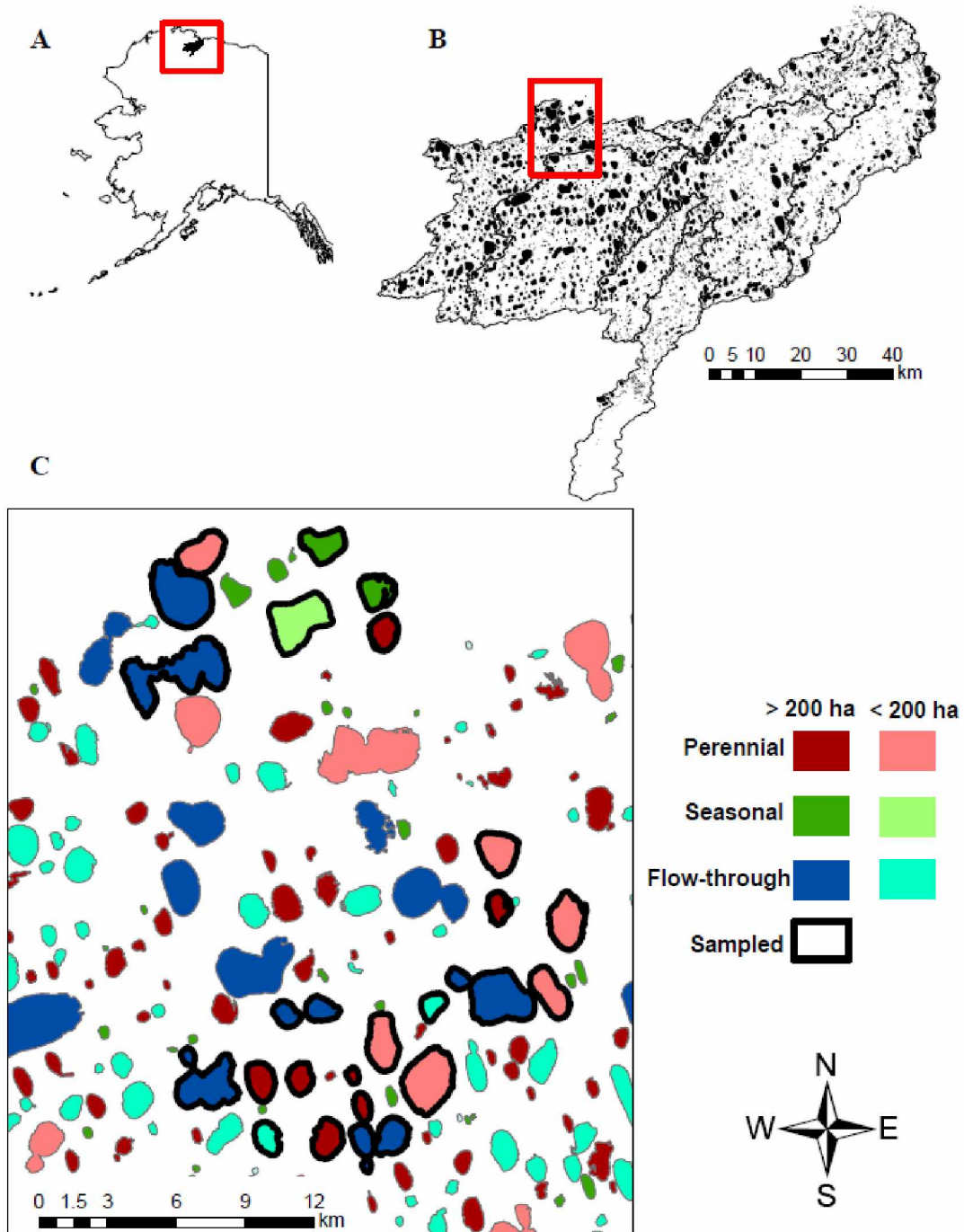
Figure 2.1. Location of Fish Creek Watershed (FCW), Alaska (A); study area within the FCW

(B); study lakes highlighted by size and connectivity class (C).
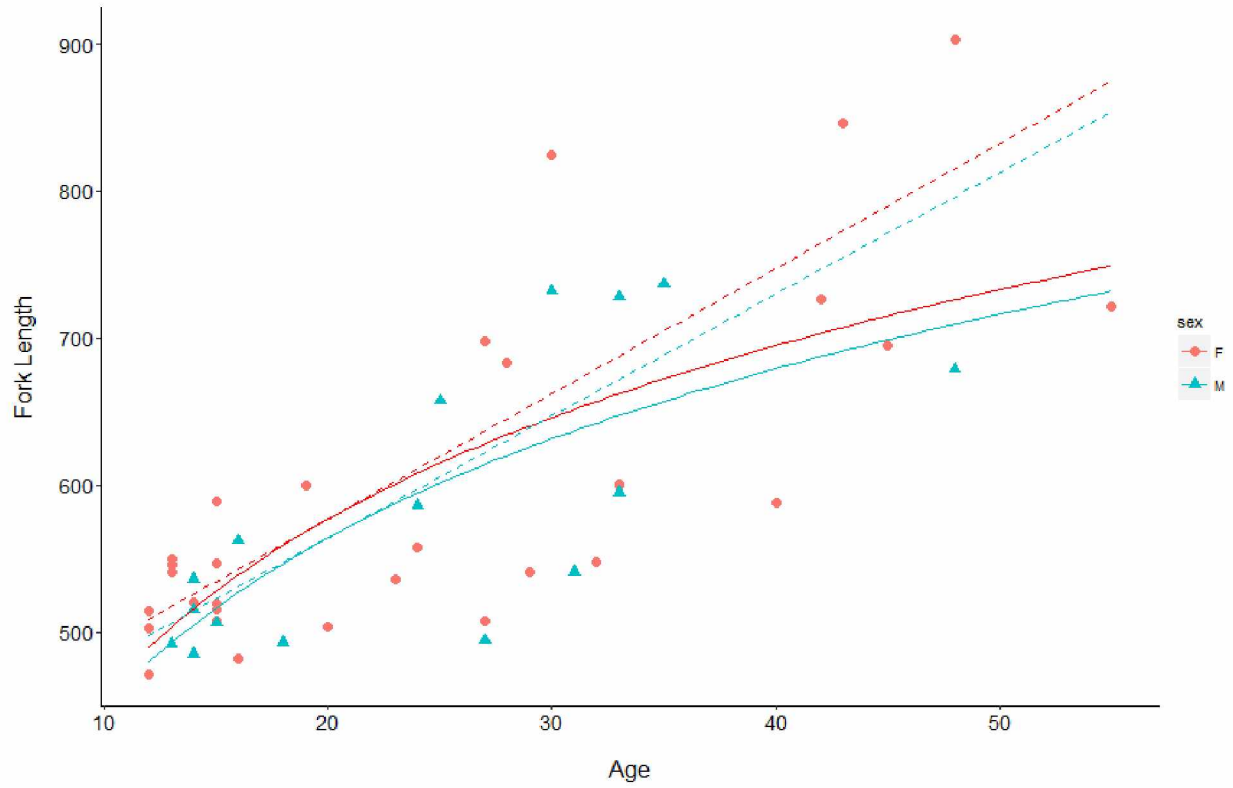
Figure 2.2. Observed (points) and modeled (solid lines) length-at-age of 16 male (blue) and 31 female (red) Lake Trout from the Fish Creek watershed, Alaska. Dashed lines are the tangent of each growth curve representative of growth coeffiecient *K*.
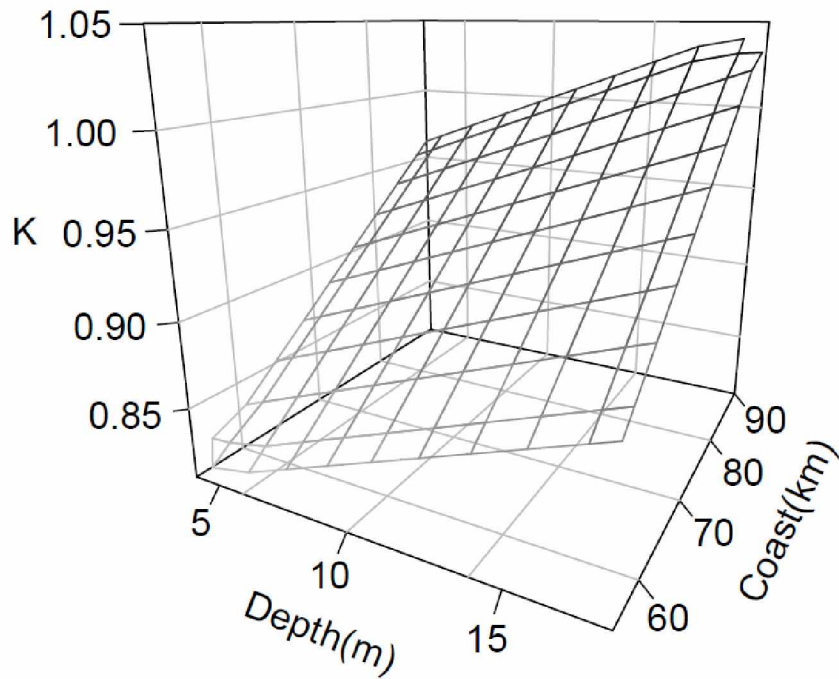
Figure 2.3. Estimated Lake Trout growth (*K;* y-axis) as a function of distance from the coast (km; x-axis) and maximum depth (m; z-axis) in 13 Arctic lakes. Parameters (Table 2.3) were estimated using multiple linear regression and average from the top two models ranked according to AIC$_c$.

Table 2.1. Summary of Lake Trout captured in the Fish Creek watershed, Alaska in 2014 and 2015 by lake. Lakes are categorized by surface area, S = < 200 ha, L = > 200 ha, and connectivity class: seasonally connected, perennially connected or flow through. Depth is maximum depth (m). The number of fish captured, sex, mean, minimum, maximum, and standard deviation of fork length (mm) are shown.

Lake	Category	Depth(m)	N	Male	Female	Fork length (mm) Mean	Min	Max	SD
621	S-seasonal	9.8	3	1	1	662.3	546	737	102.1
750	L-flow through	9.5	3	0	3	857.6	824	903	40.8
756	L-seasonal	9.8	5	1	4	700.8	683	726	21.6
757	S-seasonal	10.1	5	1	4	505.2	471	548	30.0
1822	L-perennial	12.5	5	1	4	555.4	507	601	33.6
2208	L-perennial	12.2	5	2	3	535.2	506	546	16.5
2361	L-flow through	6.7	4	1	3	503.8	482	536	23.3
2367	S-perennial	12.2	4	2	2	536.5	494	545	47.5
2373	L-perennial	14.5	2	1	1	557.5	520	595	53.0
2385	L-flow through	-	3	1	2	517.5	514	523	5.1
2204	L-flow through	4.0	1	0	1	589	-	-	-
Inigok	L-flow through	13.7	6	3	3	531.0	491	602	41.9
Ini-004	S-perennial	12.5	6	3	3	667.1	588	732	62.8

Table 2.2. Summary of model selection statistics for models predicting Lake Trout growth from physical and biological characteristics and fish community structure of Arctic lakes, ranked by AICc. Abbreviations are as follows: K = the number of parameters, including the intercept and residual variance; AICc = Akaike's information criteria corrected for small sample sizes; ΔAICc= the difference in AICc from the top model; w_i = Akaike weight; L-L = the log-likelihood. Depth = maximum depth (m), river = distance to river (km), coast = distance to coast (km), connect = connectivity class, streams = number of stream intersections, fish = fish species richness, STBK = Ninespine Stickleback abundance, and LESC = Least Cisco abundance.

Model	K	AICc	ΔAICc	w_i	LL
depth, river, coast, connect, streams	8	-138.25	0.00	0.79	79.12
sex	3	-135.24	3.00	0.18	70.91
depth, river, coast, connect, streams, sex	9	-131.72	6.53	0.03	77.51
fish, STBK, LESC	5	-117.71	20.54.	0.00	64.89
depth, river, coast, connect, streams, fish, STBK, LESC	10	-115.82	22.43	0.00	72.49
sex, fish, STBK, LESC	6	-110.40	27.84	0.00	62.76
depth, river, coast, connect, streams, fish, STBK, LESC, sex	11	-108.61	29.64	0.00	71.30

Table 2.3. Model-averaged parameter estimates (standard error), relative variable importance, and unconditional 95% confidence limits for covariates predicting Lake Trout growth (K) from Arctic lakes. Estimates are derived from the confidence set of models with $w_i > 0.05$ (Table 2.2).

Covariate	Parameter estimate	Relative importance	Lower 95% CL	Upper 95% CL	P-value
Intercept	0.89 ± 0.08	0.93	0.75	1.04	< .001
Depth	0.05 ± 0.03	0.93	0.02	0.09	0.01
River	-0.02 ± 0.01	0.93	-0.04	0.001	0.13
Coast	0.03 ± 0.02	0.93	-0.002	0.06	0.13
ConnectB	$< 0.01 \pm 0.06$	0.93	-0.11	0.11	0.98
ConnectC	-0.06 ± 0.08	0.93	-0.21	0.07	0.44
Streams	0.02 ± 0.01	0.93	-0.0002	0.03	0.11
Sex (M)	$< 0.01 \pm 0.01$	0.07	-0.03	0.04	0.80

General Conclusions

I demonstrated the utility of applying biochronology techniques to fish otoliths collected from Arctic lakes in Alaska, and investigated the relationship between growth of Lake Trout and physical and biological characteristics, and fish community structure, in addition to climate patterns. The main findings of this work were as follows:

- Forty-nine Lake Trout had otoliths with sufficient readable annuli, and series correlation coefficients ranged from 0.054 to 0.697. The mean series inter-correlation (SIC) was 0.327, and the inter-annual ring-width variability (mean sensitivity index) was 0.231.

- Growth, measured by the ring width index (RWI; unitless) for 49 Lake Trout from 13 Arctic lakes increased with mean August air temperature for the period 1977–2014 ($P < 0.001$; $R^2_{adj} = 0.55$; $RMSE = 0.048$).

- Predicted August temperatures for the period 1977-2014 correlated with observed values (Pearson's $r = 0.76$) and indicated a warming trend from 1978–1982 followed by cooler years during 1983-1988. Conversely, 1998–2003 exhibited a cooling trend followed by a warm and variable period from 2004–2014.

- The mean August temperature descriptor generated from the Polar-WRF climate model also predicted RWI for the period 1977–2014 ($P = 0.002$), and based on this relationship I observed a trend in increasing RWI ($R^2 = 0.102$, $P = .009$) for the period that modeled climate data were available (1950-2014).

- Forty-seven adult Lake Trout were able to be correctly aged and ranged in age from 12–55 years (mean = 24.9 ± 11.6 SD). Individual growth coefficients (K),

based on length-at-age back-calculations, ranged from 0.757–0.990 (mean = 0.901 ± 0.05 SD).

- The highest ranked model of K as a function of environmental characteristics of my study lakes included only physical covariates (depth, distance to river, distance to coast, connectivity class, and number of stream intersections) and accounted for 79% of the model weights. A model including the biological covariate, sex, was also included in the confidence model set and accounted for 18% of model weights.

- Model averaging indicated K was higher in deeper, well connected lakes, that were located further from the coast and was lower as distance from large rivers increased.

Based on patterns of growth from Lake Trout collected in Arctic lakes, results from chapter one indicated a significant relationship between growth and observed mean August temperature. Observed air temperature data for this region, measured at Inigok, Alaska, were only available from 1998-present, thus using Lake Trout otoliths provided me with a proxy to estimate temperature patterns beyond the observed period over the period for which Lake Trout growth data were available (1977–2014). Modeled air temperature estimates for this region were available from the down-scaled Polar-WRF climate model for the period 1950–2014 (Kalnay et al. 1996). A significant relationship between modeled mean August air temperature and the Lake Trout growth chronology was detected. Using this relationship, I was able to estimate Lake Trout growth, which increased significantly over this period (1950–2014). These results are important as they further enforce predictions that, if food availability is not a limiting factor, increasing

temperatures in the Artic will result in increased fish growth (McDonald et al. 1996; Carey and Zimmerman 2014).

This study has shown August temperature to be an important correlate with growth of Lake Trout in the Arctic for which there are several potential ecological and climate-related explanations. Increased water temperatures are associated with increased growth (Reist et al. 2006). In this region, August was the warmest month with respect to water temperatures and lakes were well mixed during this period. Moreover, August is the only month that is consistently ice-free, during which lake water temperatures are likely most responsive to variability in air temperatures (Arp et al. 2013). Although little is known about Lake Trout spawning behavior within my study area, Lake Trout have been documented spawning during the first week of September in other Arctic lakes (Burr 1987). As a result, August could be a time of heavy pre-spawn feeding, growth, and movement to spawning areas. With respect to Lake Trout growth, August is an important month during the short Arctic summer which can be detected through growth chronologies of this long-lived fish species.

This study highlights the utility of applied biochronology techniques to make inferences regarding past climate patterns and the influence of a changing climate on aquatic organisms. Despite Lake Trout being caught in lakes with varying physical characteristics, series inter-correlation values suggest an acceptable degree of growth synchrony among individuals across different lakes, a requirement for the use of crossdating techniques (Black 2005). As a result of this synchrony, I was able to construct an environmentally sensitive Lake Trout growth chronology. This method proved capable of tracking trends in mean August temperature, across the three decade growth chronology period. The resulting predictions of mean August temperature for this period indicated a slight increase in the overall warming trend; however, it

was not significant and coincides with observed climate patterns. This study demonstrated the utility of biochronology techniques, as well as provided valuable knowledge on how Lake Trout may react to a warming Arctic.

I found that Lake Trout growth rates responded most strongly to maximum lake depth, with growth rates increased in deeper lakes. Environmental conditions (e.g., water temperature and dissolved oxygen) associated with deep lakes are expected to be favorable for Lake Trout, a cold-water species (Martin and Olver 1980). Lake Trout, like many fish species, prefer habitat within a thermal range (6–13°C) optimal for metabolic processes (Gibson and Fry 1954). Deeper lakes are more likely to provide adequate thermal refuge, a factor likely to be of increasing importance as lake temperatures warm and ice-free period increases.

Warmer lake temperatures are likely to increase Lake Trout growth, if productivity increases correspondingly and food supply is unlimited (McDonald et al. 1996; Carey and Zimmerman 2014). Connectivity has been found to be a driving factor in fish species richness which is representative of prey diversity (Haynes et al. 2014; Laske et al. 2016). A species-rich ecosystem such as that found in a well-connected lake may provide a higher quality prey base for Lake Trout (Magnuson et al. 1998). With increased temperature and growth, energetic requirements also increase thus well-connected lakes are more likely to provide adequate prey for Lake Trout to achieve maximum growth (McDonald et al. 1996). A warming climate may also affect the hydrology of Arctic waters. Surface water levels may be reduced, thus reducing among-lake connectivity. As a result, migratory species (e.g., Broad Whitefish *Coregonus nasus*, Arctic Grayling *Thymallus arcticus*) may have inhibited movements (Craig 1984; Prowse et al. 2006; Heim et al. 2015) and reduce the abundance of large bodied, energetically beneficial, prey items for Lake Trout (Pazzia et al. 2002).

I found that Lake Trout growth increased with distance from the Arctic Coast. The Arctic Ocean and Beaufort Sea play a significant role in climate patterns across the Arctic Coastal Plain, and marine-related climate effects decrease as distance from the coast increases (Alexeev et al. 2016). For example, variability in lake ice thickness and phenology is associated with sea ice conditions, where years with large amounts of near shore sea ice result in colder temperatures, less snow, and thicker lake ice (Zhang and Jeffries 2000). As sea ice continues to decline I expect local air temperature to increase (Vihma 2014) potentially leading to increased Lake Trout growth.

Future research opportunities could build on the techniques used in this study to learn more about this poorly understood region. My study primarily used observed and modeled air temperatures as climate descriptors. Ongoing lake monitoring efforts are providing new water temperature data, which could prove valuable for further aquatic studies instead of relying on air temperature as a proxy for water temperature. These techniques could be expanded spatially in order to detect the sea ice signal and climate descriptors associated with sea ice loss. The Teshekpuk Lake watershed located in the Arctic Coastal Plain is situated near the coast and is known to contain long-lived Lake Trout, and applying these methods to this watershed may strengthen statistical relationships between climate descriptors and Lake Trout growth. My Lake Trout chronology was constructed for the period (1977–2014), but could be expanded in the future by constructing a new chronology and linking overlapping years. This could further strengthen relationships with climate descriptors as well as expand the chronology over a longer period, crucial in predicting longer-term temperature trends.

Other future research should aim to collect improved data representing fish community structure in Arctic lakes. Such studies could complement existing data by monitoring a subset of

lakes over time to quantify inter-annual variability in Arctic lake fish community components. Although my growth chronology could serve as a proxy of prey availability, without an empirically measured times series of these data only qualitative differences could be determined. This was evident in my chapter two where the relationship between fish community structure and Lake Trout growth was likely confounded owing to the different time scales of these metrics. A solution to this issue could be made by comparing growth increments that correspond to years when fish sampling occurred. Clearly, increased monitoring efforts and improved spatiotemporal specificity in Arctic lake ecosystem studies will improve our understanding of the role of climate warming in this sensitive environment.

In summary, this research contributes to a better understanding of Lake Trout ecology in the Arctic, as well as recent temperature patterns in this region and highlights the utility of applying biochronology techniques to long-lived fish species. Lake Trout are a top predator and changes to their growth and population dynamics will have impacts on lower trophic levels and the aquatic ecosystem as a whole. Further monitoring of this unique population warrants consideration in this rapidly changing ecosystem.

Literature Cited

Arp, C. D., B. M. Jones, and G. Grosse. 2013. Recent lake ice-out phenology within and among lake districts of Alaska, USA. Limnology and Oceanography 58:2013–2028.

Alexeev, V. A., C. D. Arp, B. M. Jones, and L. Cai. 2016. Arctic sea ice decline contributes to thinning lake ice trend in northern Alaska. Environmental Research Letters 11:074022.

Burr, J. M. 1987. Synopsis and bibliography of Lake Trout *Salvelinus namaycush* in Alaska. Alaska Department of Fish and Game Fishery Manuscript No. 5, Juneau.

Carey, M. P., and C. E. Zimmerman. 2014. Physiological and ecological effects of increasing

    temperature on fish production in lakes of Arctic Alaska. Ecology and Evolution 4:1981–

    93.

Craig P. C. 1984. Fish use of coastal waters of the Alaskan Beaufort Sea: a review. Transactions

    of the American Fisheries Society 132:265–282.

Gibson, E. S., and F. E. J. Fry. 1954. The performance of the Lake Trout, *Salvelinus namaycush*,

    at various levels of temperature and oxygen pressure. Canadian Journal of Zoology

    32:252–260.

Haynes, T. B., A. E. Rosenberger, M. S. Lindberg, M. Whitman, and J. A. Schmutz. 2014.

    Patterns of lake occupancy by fish indicate different adaptations to life in a harsh Arctic

    environment. Freshwater Biology 59:1884–1896.

Heim, K. C., M. S. Wipfli, M. S. Whitman, C. D. Arp, J. Adams, and J. A. Falke. 2015. Seasonal

    cues of Arctic Grayling movement in a small Arctic stream: the importance of surface

    water connectivity. Environmental Biology of Fishes 99:49–65.

Kalnay E, M. Kanamitsu, R. Kistler, W. Collins, D. Deaven, L. Gandin, M. Iredell, S. Saha, G.

    White, J. Woillen, and Y. Zhu. 1996. The NCEP/NCAR 40-year reanalysis project.

    Bulletin of the American Meteorological Society 77:437–471.

Laske, S. M., T. B. Haynes, A. E. Rosenberger, J. C. Koch, M. S. Wipfli, M. Whitman, and C. E.

    Zimmerman. 2016. Surface water connectivity drives richness and composition of Arctic

    lake fish assemblages. Freshwater Biology 61:1090–1104.

Magnuson, J. J., W. M. Tonn, A. Banerjee, J. Toivonen, O. Sanchez, and M. Rask. 1998.

    Isolation vs. extinction in the assembly of fishes in small northern lakes. Ecology 79:

    2941–2956.

Martin N. V., and C. H. Olver. 1980 The Lake Charr, *Salvelinus namaycush*. Pages 205–277 *In*

    K. Balon and W. Junk, editors. Charrs: salmonid fishes of the genus *Salvelinus*. The

    Hague, The Netherlands.

McDonald, M. E., A. E. Hershey, and M. C. Miller. 1996. Global warming impacts on lake trout

    in arctic lakes. Limnology and Oceanography 41:1102–1108.

Pazzia, I., M. Trudel, M. Ridgway, and J. B. Rasmussen. 2002. Influence of food web structure

    on the growth and bioenergetics of Lake Trout *Salvelinus namaycush*. Canadian Journal

    of Fisheries and Aquatic Sciences 59:1593–1605.

Prowse, T. D., F. J. Wrona, J. D. Reist, J. E. Hobbie, L. M. Lévesque, and W. F. Vincent. 2006.

    General features of the Arctic relevant to climate change in freshwater ecosystems.

    AMBIO: A Journal of the Human Environment 35:330–338.

Reist, J.D., F. J. Wrona, T. D. Prowse, M. Power, J. B. Dempson, R. J. Beamish, J. R. King, T. J.

    Carmichael, and C. D. Sawatzky. 2006. General effects of climate change on Arctic

    fishes and fish populations. AMBIO: A Journal of the Human Environment 35:370–380.

Vihma, T. 2014. Effects of Arctic sea ice decline on weather and climate: a review. Surveys in

    Geophysics 35:1175–1214.

Zhang, T., and M. O. Jeffries. 2000. Modeling interdecadal variations of lake ice thickness and

    sensitivity to climatic change in northernmost Alaska. Annals of Glaciology 31:339 –47.

Appendix

Appendix A. 2015 IACUC approval

Institutional Animal Care and Use Committee

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April 17, 2015

To: Jeffrey Falke, Phd
                 Principal Investigator

From: University of Alaska Fairbanks IACUC

Re: [722194-2] Lake Trout Otolith Project

The IACUC reviewed and approved the Revision referenced above by Designated Member Review.

Received:	April 14, 2015
Approval Date:	April 17, 2015
Initial Approval Date:	April 17, 2015
Expiration Date:	April 17, 2016

This action is included on the May 7, 2015 IACUC Agenda.

PI responsibilities:

• *Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.*

• *Ensure the protocol is up-to-date and submit modifications to the IACUC when necessary (see form 006 "Significant changes requiring IACUC review" in the IRBNet Forms and Templates)*

• *Inform research personnel that only activities described in the approved IACUC protocol can be performed. Ensure personnel have been appropriately trained to perform their duties.*

• *Be aware of status of other packages in IRBNet; this approval only applies to this package and the documents it contains; it does not imply approval for other revisions or renewals you may have submitted to the IACUC previously.*

• *Ensure animal research personnel are aware of the reporting procedures on the following page.*