Polar Biol
DOI 10.1007/s00300-012-1245-9

ORIGINAL PAPER

Lake trout otolith chronologies as multidecadal indicators of high-latitude freshwater ecosystems

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Received: 18 June 2012 / Revised: 9 September 2012 / Accepted: 10 September 2012
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Abstract High-latitude ecosystems are among the most vulnerable to long-term climate change, yet continuous, multidecadal indicators by which to gauge effects on biology are scarce, especially in freshwater environments. To address this issue, dendrochronology (tree-ring analysis) techniques were applied to growth-increment widths in otoliths from lake trout (*Salvelinus namaycush*) from the Chandler Lake system, Alaska (68.23°N, 152.70°W). All otoliths were collected in 1987 and exhibited highly synchronous patterns in growth-increment width. Increments were dated, the widths were measured, and age-related growth declines were removed using standard dendrochronology techniques. The detrended time series were averaged to generate an annually resolved chronology, which continuously spanned 1964–1984. The chronology positively and linearly correlated with August air temperature over the 22-year interval ($p < 0.01$), indicating that warmer summers were beneficial for growth, perhaps by increasing fish metabolic rate or lake productivity. Given the broad distribution of lake trout within North America, this study suggests that otolith chronologies could be used to examine responses between freshwater ecosystems and environmental variability across a range of temporal and spatial scales.

Keywords Dendrochronology · Sclerochronology · Climate change · Gates of the Arctic National Park and Preserve · *Salvelinus namaycush*

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Introduction

Rates of climate change are among the most pronounced at high latitudes, with potentially severe consequences for the dynamics and function of arctic and subarctic freshwater ecosystems (Williamson et al. 2009). Increasing temperature is one of the first-order impacts, which in lakes could profoundly change the timing of stratification, freeze date, spring turnover, or other seasonal events closely linked to productivity and trophic structure (Anderson et al. 1996; Arhonditsis et al. 2004; Schneider et al. 2009). For example, a four-decade warming trend corresponded to declines in population density and a shift from one to two generations per year for a calanoid copepod species in Lake Washington, USA (Winder et al. 2009). Long-term sampling regimes are critically important for detecting such changes, yet in most cases such records do not exist, especially in aquatic ecosystems.

In the absence of direct observations, periodic growth increments have proven to be a useful and versatile proxy for describing past environmental variability. The archetypal example is tree-ring data, which have been extensively applied to reconstruct various aspects of climate, disturbance, and productivity in forested ecosystems. Indeed, the existing network of chronologies serves as one of the leading indicators of environmental variability and change at a global scale (Fritts 1976; D'Arrigo et al. 1999;

Published online: 23 September 2012

Sherriff and Berg 2009). Beyond trees, a wide array of long-lived freshwater and marine species including bony and cartilaginous fish, bivalves, and corals also form annual growth increments that occur in calcified or hardened structures such as otoliths, vertebrae, or shells. Increments in these organisms arise due to seasonal variation in growth rates and can be used to investigate dynamics of aquatic taxa and ecosystems analogous to those addressed by tree-ring data in terrestrial settings (Guyette and Rabeni 1995; Pereira et al. 1995; Black et al. 2008b; Smith et al. 2008).

A relatively recent advance is the application of the tree-ring technique of crossdating to ensure that every growth increment is assigned the correct calendar year of formation (Marchitto et al. 2000; Strom et al. 2004; Black et al. 2005). Crossdated chronologies have now been generated from otolith and shell growth-increment widths in a number of marine and freshwater fish and bivalve species, and final chronologies are of a quality comparable with those developed from tree-ring data (Guyette and Rabeni 1995; Black et al. 2008a, 2009; Rypel 2009). In the California Current Ecosystem of the northeast Pacific Ocean, Black et al. (2010) demonstrated that Pacific rockfish (*Sebastes* spp.) otolith chronologies strongly reflect interannual variability in primary productivity, as corroborated by records of seabird reproductive success. Farther north in the eastern Bering Sea, yellowfin sole (*Limanda aspera*) growth-increment chronologies very strongly relate to bottom temperatures ($r^2 = 0.81$), consistent with reports of increasing flatfish abundance and biomass following a regime shift to warm ocean conditions in the late 1970s (Matta et al. 2010). Thus, long-lived fish or historically collected otoliths can provide exactly dated, multidecadal histories of environmental variability in aquatic ecosystems.

In this study, we develop a new environmental proxy for high-latitude lakes in North America from the otolith growth-increment widths of lake trout (*Salvelinus namaycush*), a long-lived species ubiquitous in deep arctic and subarctic lakes of Alaska and Canada (Wilson and Hebert 1998). Lake trout are typically the apex predator, feeding on a wide range of prey items from invertebrates to fish, and as such, are likely to integrate the impacts of climate variability across multiple tropic levels (McDonald et al. 1996; Hobbie et al. 1999). Moreover, some long-term forecasts predict lake trout extirpation in high-latitude lakes due to increased metabolic rates and decreased oxygen availability associated with warming temperatures, and growth-increment chronologies may provide a means by which to document such declines (McDonald et al. 1996; Hobbie et al. 1999). To preliminarily address these issues, we construct a growth-increment chronology using otoliths from lake trout collected from the Chandler Lake system, a network of deep oligotrophic lakes north of the Brooks Range of northern Alaska. Our objectives are to (1) evaluate the potential to develop a crossdated growth-increment chronology for lake trout otoliths and (2) identify the relationship between climate and growth. Although tree-ring chronologies have been widely used as an annually resolved indicator of climate history in Alaska, lake trout will represent a new environmental archive specific to high-latitude aquatic ecosystems. In addition, lake trout such as those at Chandler Lake occur north of tree line, and as such may be of particularly high value given the rarity of other sources of growth-increment data in arctic environments.

Materials and methods

The Chandler Lake system (68.23°N, 152.70°W) is located in the Gates of the Arctic National Park and Preserve and contains six lakes: Round, Little Chandler, Chandler, Amiloyak, and two unnamed lakes (Fig. 1). Formed by glacial scouring and moraine damming, Chandler Lake lies in the Chandler River valley at an elevation of 888 m, has a surface area of 1,300 ha, and a maximum depth of 22 m (Livingstone 1955; Burr 1993; Troyer and Johnson 1994). The ice-free period varies from year-to-year with ice-off occurring in mid or late June and freeze-up in early to mid-October (Troyer and Johnson 1994). In addition to lake trout, Chandler Lake contains arctic char (*Salvelinus alpinus*), burbot (*Lota lota*), arctic grayling (*Thymallus arcticus*), round whitefish (*Prosopium cylindraceum*), and slimy sculpin (*Cottus cognatus*) (Burr 1993). Lake trout from Chandler Lake are primarily piscivorous, feeding heavily on arctic grayling (Troyer and Johnson 1994), and are a subsistence resource for residents of nearby Anaktuvuk Pass. Harvest levels are low and there was little concern of overexploitation during and prior to the collection period (Troyer and Johnson 1994; Burr 2006).

Lake trout were collected by the US Fish and Wildlife Service in 1987 using gill nets or hook and line angling (Troyer and Johnson 1994). A total of 26 intact otoliths representing lake trout from Chandler, Little Chandler, Amiloyak, and Round lakes remained in archives for use in this study. Samples were combined given that Troyer and Johnson (1994) documented some movement of lake trout and arctic char among lakes in the system. The annual periodicity of lake trout otoliths growth increments has previously been validated using bomb radiocarbon (Campana et al. 2008).

In the laboratory, otoliths were embedded in epoxy, sectioned on the transverse plane using a low-speed wafering saw, and affixed to a microscope slide. After drying, otoliths were ground with 1,200 grit wet-dry sandpaper followed by polishing with 10 μm lapping film to improve clarity of the macrostructure. Digital images of each otolith were captured at a magnification of 60× on a black background using reflected light and a digital camera

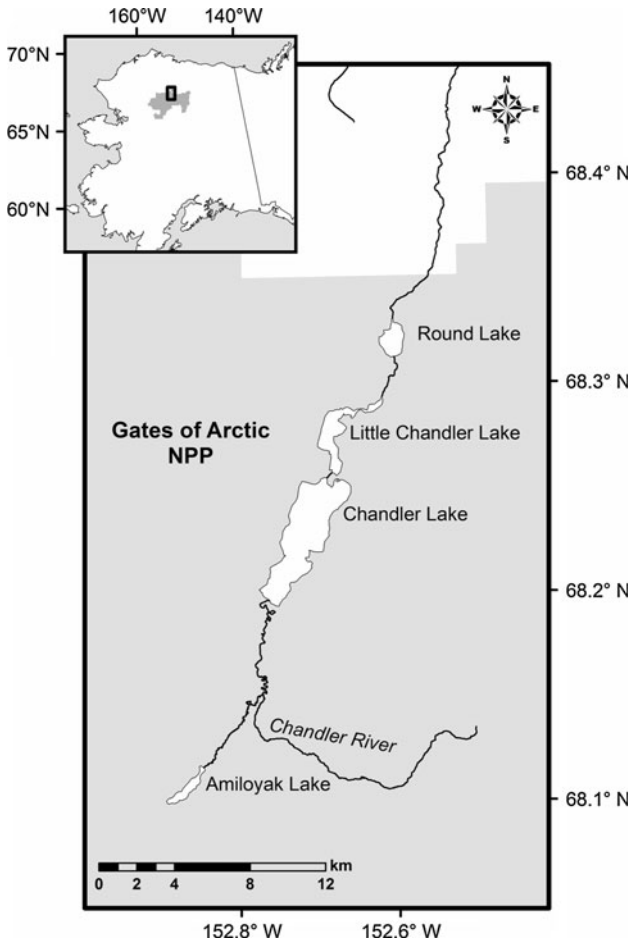

Fig. 1 Map of the lakes from which otoliths were collected, all within the boundaries of the Gates of the Arctic National Park and Preserve (*shaded areas*). *Inset*: Location of the study area (*box*) and Gates of the Arctic NPP (*shaded*) in northern Alaska

(Leica DCF295 3.0 megapixel) attached to a dissection microscope (Leica MZ9.5) (Fig. 2).

Once photographed, otoliths were visually crossdated to ensure that the correct calendar year was assigned to each growth increment. A fundamental technique of dendrochronology, crossdating is based on the assumption that

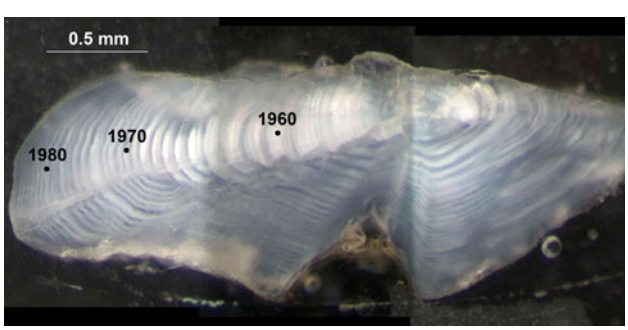

Fig. 2 A transverse cross-section of a sagittal otolith from a lake trout collected in April, 1989, from Chandler, Lake, Alaska, USA. Decadal growth increments (1980, 1970, and 1960) are *dotted*

some aspect of climate limits growth, and as climate varies over time, it induces a synchronous growth pattern in all individuals from a given species and region (Fritts 1976; Yamaguchi 1991). Crossdating is the process of matching synchronous growth patterns among individuals, beginning at the marginal increment formed during the known year of capture and proceeding toward the core. If a growth increment has been missed or falsely added, the growth pattern for that individual will be offset by a year relative to that in the other specimens, thereby identifying the mistake (see Black et al. 2005; Black et al. 2008b; Rypel 2009 for crossdating procedures in aquatic organisms).

After visual crossdating, the annual increment widths were measured continuously from the margin to as close to the focus as possible using the program ImagePro Plus v. 6.0. An annual increment was defined as the distance from the outer edge of one translucent zone (appears as the narrow dark zone under reflected light) to the outer edge of the next translucent zone, following the axis of growth along the longest possible radius between the nucleus and the dorsal edge of the transverse section. Next, crossdating was statistically verified with the Dendrochronology Program COFECHA (Holmes 1983; Grissino-Mayer 2001). In COFECHA, each otolith measurement time series was fit with a cubic spline with a 50 % frequency cutoff set at 15 years. Measurements were divided by the values predicted by the spline, thereby removing long-term trends and standardizing each time series to a mean of 1. Any remaining autocorrelation was removed via autoregressive modeling, which further enhanced high-frequency (year-to-year) growth patterns. Each standardized time series was then correlated with the average of all other standardized time series, the average of which was reported as the series intercorrelation (SIC). Time series with non-significant values were visually inspected for errors. COFECHA was also used to calculate the mean sensitivity, an index of high-frequency (year-to-year) variability among pairs of successive increments that ranges from a minimum of 0 (a pair of increments of the same width) to a maximum of 2 (a pair in which one width is 0) (Fritts 1976). Overall, cross-correlating high-frequency growth patterns among individuals statistically mimicked the visual crossdating process and provided an extra level of dating verification. COFECHA was used to screen the data for potential mistakes, but all decisions about crossdating were ultimately made by visually inspecting each individual. At no time did we "force" crossdating on an otolith; corrections were only made when the accidentally missed or falsely added increment was obviously visible upon re-inspection of the specimen.

To develop master chronologies for climate analysis, each set of the original growth-increment measurement time series was fit with a negative exponential function and divided by the values predicted. This detrending process contrasted with detrending for the purpose of statistical crossdating in

COFECHA, in which highly flexible cubic splines were employed to extract only high-frequency growth patterns. By using much more rigid negative exponential functions, age-related growth declines were removed while preserving as much environmentally induced variability as possible. Measurement time series detrended with negative exponential functions were averaged to calculate a final master chronology. Only those portions of the master chronology with at least five individuals contributing were retained to ensure adequate signal-to-noise ratios.

The lake trout chronology was compared with average monthly temperature, average monthly precipitation, and monthly accumulated degree days using climate data from Bettles Airport, Alaska, located approximately 150 km south of Chandler Lake. Bettles records were obtained through the NOAA National Climate Data Center (http://www.ncdc.noaa.gov). Monthly accumulated degree days were defined as the sum of daily means above 0 °C and were calculated from April through October, given that temperatures were persistently below freezing throughout the remaining months of the year. Monthly temperatures, precipitation, and accumulated monthly degree days were related to the lake trout master chronology via Spearman's rank correlation. Finally, the lake trout chronology was correlated with Hadley CRUT3 gridded (0.5° steps) land surface temperatures through the KNMI Climate Explorer (climexp.knmi.nl/).

Results

Otoliths that had at least ten consecutive increments with clearly identifiable boundaries were considered for use in chronology development. Of the 26 intact otoliths evaluated in this study, 17 met these criteria. Ten fish were captured in Chandler Lake, one was captured in Little Chandler Lake, one was captured in Amiloyak Lake, and five were captured in Round Lake. Although these samples were collected across multiple lakes, growth was highly synchronous among all individuals (Fig. 3). For example, 1981, 1978, and 1970 were consistently narrow while 1982, 1979, and 1974 were consistently wide, a pattern that was particularly evident after age-related growth declines had been removed (Fig. 3). In statistical verification of crossdating using COFECHA, each individual correlated with the mean of all others with an average coefficient (i.e., SIC) of 0.57. As a result of so few degrees of freedom in many samples, correlation coefficients ranged from 0.42 to 0.97, though all were significant at least at the $p < 0.10$ level while 12 were significant at $p < 0.05$. Given the clarity of growth increments, strong visual crossdating (Fig. 2), positive correlations in COFECHA, and that they were all live-collected, no samples were discarded. Mean sensitivity, an index of high-frequency variability in growth-increment width, was 0.256. Although the oldest individual provided measurements back to 1946, a minimum sample depth of five limited the chronology to 1964 through 1985 (Fig. 3). The chronology did not contain significant ($p < 0.05$) autocorrelation (first-order autocorrelation $r = -0.082$).

Among the variables considered in this study, the lake trout chronology did not significantly correlate with monthly averaged precipitation records (data not shown). There were, however, significant ($p < 0.01$) positive correlations with August air temperature and degree days, indicating that warm summertime conditions were favorable for growth (Fig. 4). When compared with gridded temperature data, peak correlations with the lake trout chronology occurred in the regions surrounding the Chandler Lake system (Fig. 5).

Discussion

Lake trout SIC and mean sensitivities (MS) were comparable with those observed in other fish, bivalves, or tree species in western North America, including flatfish from the Bering

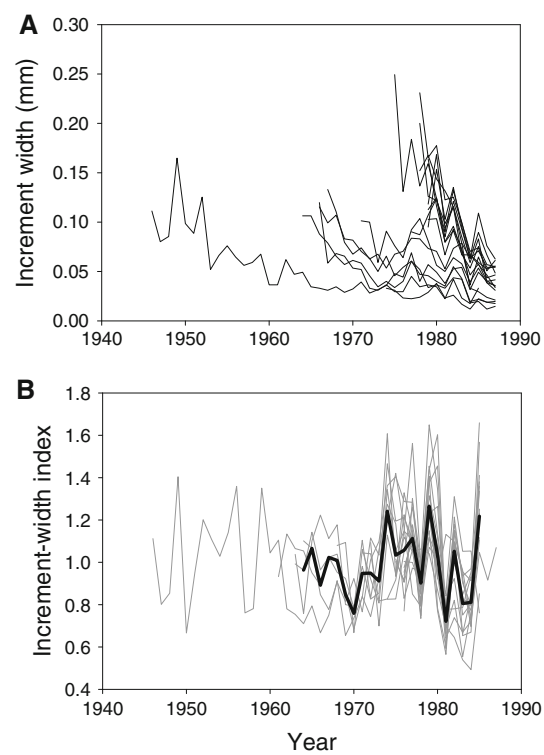

Fig. 3 **a** Measurement time series for all lake trout otoliths ($n = 17$). **b** Measurement time series after age-related growth declines had been removed. Also shown is the lake trout master chronology (*black line*; mean of all detrended individuals). Note the high level of synchrony among individuals

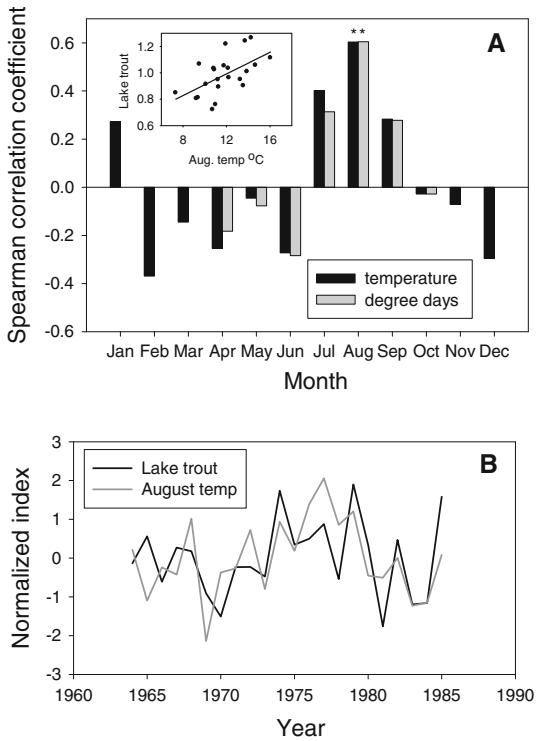

Fig. 4 **a** Spearman correlations between the lake trout master chronology and monthly mean air temperature and degree days from Bettles, AK. Degree days were calculated only for the months of April through October. *Asterisk* denotes significance at the $p < 0.01$ level. *Inset* The relationship between the lake trout master chronology and mean August air temperature at Bettles, AK. $r^2 = 0.32$ ($p = 0.005$). There was no significant autocorrelation in the residuals; DW = 2.39 ($p = 0.19$). **b** Lake trout master chronology and August air temperature. Both time series are normalized to a mean of 0 and standard deviation of 1

Sea (≅0.61 SIC; ≅0.24 MS), Pacific rockfish from the California Current Ecosystem (≅0.55 SIC; ≅0.2 MS), Pacific geoduck (*Panopea generosa*; formerly *P. abrupta*) along the British Columbia coast (≅0.72 SIC; ≅0.25 MS), and tree-ring data throughout Alaska (≅0.62 SIC; ≅0.25 MS) (Black et al. 2009; Matta et al. 2010). Thus, the degree of interannual growth variability and synchrony among lake trout individuals should be sufficient for developing exactly dated, environmentally sensitive chronologies. One important limitation was that the removal of age-related growth declines would have also removed any environmentally related trends equal to or greater in length than the measurement time series, which in this data set averaged 19.1 years. For this reason, trends exceeding approximately 15–20 years could not be resolved in the lake trout chronology. However, the chronology tracked interannual variability as well as some multiyear trends including a warming period from 1970 through 1976 followed by a cooling period that lasted until approximately 1984 (Fig. 4b).

Relationships between the lake trout chronology and climate were consistent with fish biology. For example, warmer temperatures are generally associated with accelerated metabolism and increased growth rates (Brett and Groves 1979). Another possibility was that temperatures could have indirectly affected growth by stimulating lower trophic productivity. Even slightly warmer air temperatures can stimulate production by decreasing lake ice cover and lengthen the growing season (Smol et al. 2005). Paleolimnological studies throughout the arctic indicate shifts in diatom species assemblage, an expansion of aquatic insect populations, and an abrupt increase in chlorophyll-a concentrations while temperatures have warmed over the last 200 years (Douglas and Smol 1999; Michelutti et al. 2005; Quinlan et al. 2005; Smol and Douglas 2007). Overall, a positive relationship between the otolith chronology and temperature suggests that cold temperatures limited lake trout growth in these high-latitude systems.

Although it was not evident in this data set, effects of temperature on fish growth may be positive only up to a certain point should fish metabolic demands increase more rapidly than lake productivity (Mac 1985; Russell et al. 1996). Using a modeling approach, McDonald et al. (1996) estimated that a 3 °C rise in summer temperature at the high-latitude Toolik Lake, AK, would cause an eightfold increase in energetic demand for young-of-the-year lake trout, a rise that could not be supported by projected increases in lake productivity. Consistent with this finding, Mac (1985) demonstrated that captive lake trout selected warmer temperatures when accompanied by higher food rations (Mac 1985). Thus, the relationship between trout growth and temperature could become negative should conditions warm beyond a certain threshold. Future work will be useful in identifying key thresholds at which the growth of lake trout declines as a consequence of lake productivity, food availability, population density, or other factors.

Correlations between the lake trout chronology and temperature were highly ($p < 0.01$) significant, yet, these climate-growth relationships were relatively weak compared with those noted in other studies. For example, bottom temperatures explained more than 80 % of the variability in a yellowfin sole growth-increment chronology developed in the eastern Bering Sea (Matta et al. 2010). Part of the explanation may be the lack of local climate records in the Chandler Lake area. Bettles and Hadley CRUT3 climate data provided an indication of relative, region-wide changes in temperature and precipitation from year-to-year. Moreover, these data represented the terrestrial environment and may not have adequately captured such critical variables as water temperature or seasonal ice cover. To our knowledge, there are no water temperature or seasonal ice cover records in the Alaskan

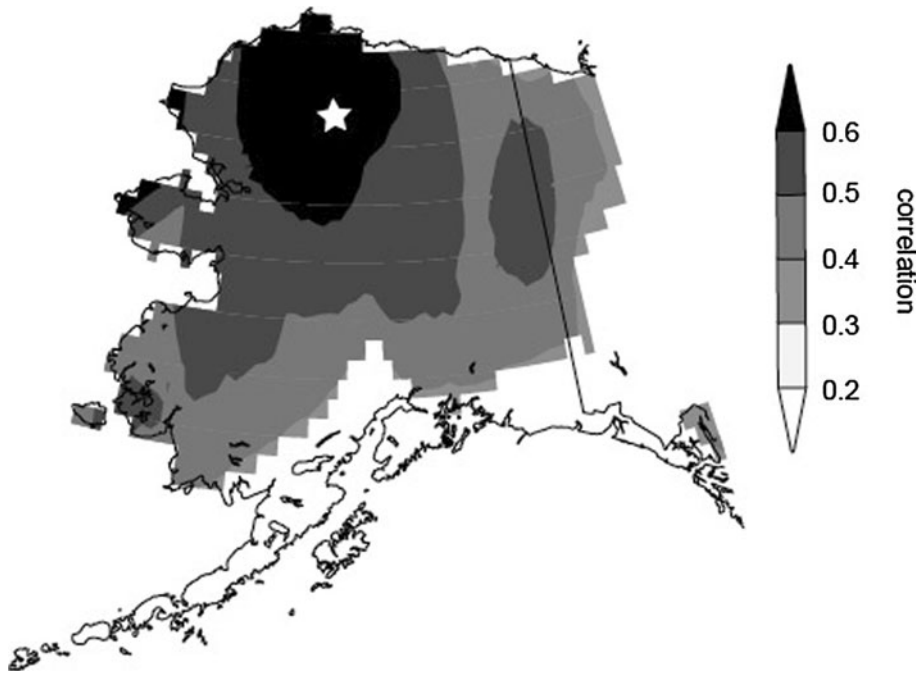

Fig. 5 Correlation between the lake trout master chronology and Hadley CRUT3 gridded land surface temperatures. *Star* notes location of Chandler Lake

arctic that overlap with the 1964–1988 lake trout chronology, though climate-growth relationships could be better assessed with an updated collection, or fish obtained from lakes farther to the south where instrumental records are more widely available. An additional consideration was that the lake trout chronology lacked long-term trends despite evidence of warming in high-latitude ecosystems. Yet, this could be explained by the fact that the detrending process used to generate the chronology removed low-frequency variability. Furthermore, no significant ($\alpha = 0.05$) linear trends were evident in the Bettles temperature or precipitation data over the relatively short 1964–1985 interval (data not shown). Sustained trends may be more apparent over longer time intervals.

In summary, the results from this analysis demonstrated that an exactly dated, environmentally sensitive lake trout chronology could be developed, and at a site above tree line where other long-term biological indicators are particularly scarce. Perhaps the greatest limitation was lake trout lifespan, which restricted chronology length and the ability to resolve long-term (multidecadal) trends. Moreover, had samples with unknown dates of death been available, they could not be have been crossdated into the chronology given the high probability of spurious matches. Chronologies could, however, be lengthened and low-frequency variability preserved if fish were live-collected across a range of dates and techniques such as regional curve standardization were applied to construct the chronology (Esper et al. 2002). Despite these drawbacks, lake trout do provide a novel means by which to examine long-term responses of arctic and subarctic freshwater ecosystems to environmental variability, and in regions for which such continuous biological records are particularly scarce.

Acknowledgments We thank Jason Dunham and two anonymous reviewers for comments that improved this manuscript. Any use of trade names or products is for descriptive purposes only and does not imply endorsement of the US Government.

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