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Research Article

Declining adult body size and contracted life history in an unexploited boreal lake trout (*Salvelinus namaycush*) population during a period of warming

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Abstract

Evidence of declines in fish body size with warming in the absence of exploitation is lacking. During a period of regional climate warming (1986–2016), we examined trends in growth, size-structure, and age-structure of an unexploited population of lake trout (*Salvelinus namaycush*) from a small Canadian Shield Lake. These data were evaluated against long-term annual air and water temperature data, ice-cover data, and prey fish densities for the same period. Over time, the size of young immature lake trout did not change, while mature fish became smaller. The age-at-maturity of the population decreased by 4 years (from 9 to 5 years) and the body condition of immature and mature fish also declined. Though the adult lake trout population doubled over time (125–280 individuals), and the production (P), biomass (B), and biomass turnover (P/B) was constant, the population shifted to smaller, skinnier, younger individuals. By contrast, the relative abundance, biomass, and mean size of the prey fish community remained unchanged. Together this suggests that warming correlates with the contraction of the population's life history.

Key words: temperature-size rule, climate change, freshwater fishes, boreal shield lake

Introduction

Rising global air temperatures over the past century have had widespread, often referred to as "universal", impacts on biodiversity (Gardner et al. 2011). The first two universal responses to warming are recognized to be shifts in species distributions (Perry et al. 2005; Chen et al. 2011) and changes in phenology (Stenseth and Mysterud 2002; Walther et al. 2002; Parmesan and Yohe 2003). Additionally, reports of declines in adult body size across a variety of species (Daufresne et al. 2009; Gardner et al. 2011; Sheridan and Bickford 2011) has prompted researchers to suggest this phenomenon may be a universal response to warming (Gardner et al. 2011). Given that body size affects nearly all metabolic and biological properties (Peters 1983; Schmidt-Nielsen 1984) and directly influences population- and food web-level dynamics and stability (Savage et al. 2004; Petchey et al. 2008; McCann and Rooney 2009), a more thorough understanding of the prevalence of warming-induced declines in body size in nature is required.

Temperature-related reductions in animal body size have been observed in both endotherms and ectotherms (Ashton et al. 2000; Yom-Tov and Geffen 2011; Gardner et al. 2011; Sheridan and Bickford 2011). Ectotherms are thought to be especially susceptible to warming because their body temperatures and consequently their metabolic rates and growth are dictated by their ambient environment (Fry 1947; Brett and Groves 1979; Ohlberger 2013). The general relationship between temperature and ectotherm growth is represented by a dome shaped curve, with growth increasing up to an optimum temperature, after which it rapidly declines. As a result, individuals/populations that are below their thermal optimum for growth would be expected to increase in growth with warming, while those at their thermal optimum would see growth declines (Ohlberger 2013). Of course, this relationship between temperature and growth is dependent on sufficient food availability and does not account for an organism's ability to behaviourally thermoregulate (Snucins and Gunn 1995), both of which vary in the wild.

The temperature-size rule (TSR) uses the expectations of the relationship between temperature and growth to describe an individual's phenotypic response to warming throughout ontogeny (Atkinson 1994). The TSR indicates that warmer temperatures should cause ectotherms of the same species to have a higher early growth rate, younger age-at-maturity, and smaller maximum adult body size (Atkinson

1994; Van der Have and De Jong 1996; Angilletta et al. 2004). Consequently, the TSR suggests that changes in size-at-age are dependent on the stage of ontogeny and how warming relates to the optimal growth temperature of that species/population (Ohlberger 2013). Similarly, life history theory predicts that a shift towards accelerated juvenile growth and earlier maturation should also be accompanied by increased instantaneous mortality rates (i.e., shorter lifespan) and reduced adult body sizes (Charnov 1993; Jensen 1996; Hutchings 2008). Metabolic and growth responses by ectotherms to warming are thought to be strongest in aquatic environments because oxygen—required for aerobic metabolism—is more limiting in water compared to air (Forster et al. 2012; Horne et al. 2017). Indeed, the Gill-Oxygen Limitation (GOL) hypothesis postulates that as fish get larger, their oxygen demand increases with volume at a higher rate than the (essentially) two-dimensional surfaces of their gills, leading to a decline in growth rate. Under warming, decreased oxygen availability and elevated metabolic demands are predicted to further reduce fish body size (Pauly 1981, 2019, 2021) and advance maturation (Pauly 1984; Morbey and Pauly 2022). While the GOL hypothesis has informed predictions of widespread body size declines in marine ectotherms with climate warming (Cheung et al. 2013), the generality of the temperature–size rule (TSR) in fish and its underlying mechanisms remain unresolved (Lefevre et al. 2017*a*, 2017*b*; Pauly and Cheung 2017, 2018; Audzijonyte et al. 2018).

Uncertainty around the universality of warming-induced shrinking in fishes is heightened by the fact that empirical studies of body size changes of wild populations in response to warming are mixed. A study by Daufresne et al. (2009) found reductions in the mean size and size-at-age of several marine and freshwater fish species sampled over periods ranging from 14 to 31 years. Likewise, a handful of studies have shown the body size and growth of several marine and anadromous fish species have declined over time with warming (Thresher et al. 2007; Baudron et al. 2014; Oke et al. 2020, 2022; Beaudry-Sylvestre et al. 2024). Though a recent study by Huss et al. (2019) observed that European perch (*Perca fluviatilis*) in an experimental lagoon exhibited increases in juvenile growth with 5–10 °C warming, this increase in size was maintained throughout their lifetime (inconsistent with the predictions of TSR). Similarly, the maximum length of dolly varden (*Salvelinus malma malma*) in the Chukchi and Beaufort seas has increased from 1969 to 2015 (Courtney et al. 2019). In two studies testing the TSR in freshwater systems using time-series and space-for-time approaches (Solokas et al. 2023; Warne et al. 2024), mixed results of changes in body size were found across several Northern Hemisphere fishes, with some species getting larger, some smaller, and others showing no change. However, because many of the species/populations in the above studies were exploited to various degrees, the potential contribution of harvest (i.e., fishing mortality) on body size and growth are difficult, if not impossible, to unravel (Olsen et al. 2004; Hutchings 2005; Waples and Audzijonyte 2016).

Unexploited fish populations inhabiting smaller temperate lakes are ideal for understanding warming-related impacts on body size and life history because there is no influence of harvest on mortality and body size, and the option for fish to emigrate is typically absent. One such fish is the cold-water predator lake trout (*Salvelinus namaycush*), a species whose native range encompasses oligotrophic lakes of the northernly half of North America (Martin and Olver 1980). Lake trout require cold-water for optimal growth and metabolic function (Martin and Olver 1980; Ryan and Marshall 1994; Evans 2007) making it a suitable species for studying the effects of warming in freshwater lakes. Lake trout populations are especially concentrated near the southern extent of its geographic distribution within the Boreal Shield ecozone, where they typically inhabit small, thermally stratifying lakes (75% of lakes <500 ha, median size 169 ha; Gunn and Pitblado 2004) with simple food webs (i.e., few competitors with only nearshore minnow species or offshore/deepwater *Mysis* or zooplankton as primary prey and no offshore prey fish species; Mills et al. 2002*a*). These small Boreal Shield lakes are responsive to rising air temperatures through increases in summer surface water temperatures (and therefore stratification intensity) and shifts in environmental seasonality that include reductions in the duration of ice-cover and longer open-water seasons (Keller 2007; Guzzo and Blanchfield 2017). In response to these shifts in phenology, lake trout perform behavioural thermoregulation to avoid water temperatures exceeding 15 °C. As a result, lake trout in small lakes are a likely candidate species to respond to warming as longer periods of warm water leads to reduced access to nearshore prey fish and in turn slower growth under these conditions (Plumb and Blanchfield 2009; Plumb et al. 2014; Tunney et al. 2014; Guzzo et al. 2017). Moreover, lake trout populations are known to exhibit plasticity in body size and age structure across a latitudinal gradient, with maximum body size and population production (i.e., the rate of biomass accumulation over time) increasing with latitude (Shuter et al. 1998; McDermid et al. 2010; Rypel 2014; Rypel and David 2017; Wilson et al. 2019). Therefore, it would be expected that changes in lake trout growth and corresponding life history traits (Charnov 1993; Hutchings 2008) in Boreal Shield lakes over a documented directional period of warming the past half-century may reflect shifts in water temperature phenology and seasonal diet shifts associated with warming.

Here, we examine monitoring data from an unexploited lake trout population collected annually for over three decades (1986–2016) to document variability on individual growth, body size, and life history in relation to changes in climatic variables. Critically, the lack of exploitation allows us to negate harvest as a potential driver in temporal patterns in body size (Waples and Audzijonyte 2016). In a region of the Boreal Shield where mean annual air temperatures have risen by about 2 °C since 1970 (Guzzo and Blanchfield 2017), changes in lake trout growth, production, size-structure, and age-structure were evaluated against expectations from the TSR and life history theory, while also considering temporal patterns in lake trout abundance, thermal habitat, and the size and abundance of their preferred food, nearshore-littoral prey fish (i.e., minnows).

Materials and methods

Study site

Long-term monitoring data were collected from the IISD Experimental Lakes Area (IISD ELA), located in northwestern Ontario, Canada (49°40′N, 93°44′W). The IISD ELA (ELA hereafter) is a set of 58 small Boreal Shield lakes and their watersheds set aside for conducting aquatic research (Blanchfield et al. 2009). Our main study system was Lake 373 (hereafter L373), a long-term reference lake used to monitor regional variation. Closed to angling, L373 is a small (surface area 27.3 ha, maximum depth 20.8 m), single basin lake that contains a native, resident, self-sustaining lake trout population with no other predatory fish species present. In addition to lake trout, L373 also supports populations of northern redbelly dace (*Chrosomus eos*), finescale dace (*Chrosomus neogaeus*), pearl dace (*Margariscus nachtriebi*), slimy sculpin (*Cottus cognatus*), and white sucker (*Catostomus commersonii*). The lake also contains freshwater shrimp (*Mysis diluviana*), an important zooplankton predator and diet item for lake trout (Trippel and Beamish 1993). Small-bodied nearshore forage fish, *Mysis*, and Cladocera represent the major prey items for lake trout in L373 (Rodrigues et al. 2025), but the spatial and temporal diets of lake trout vary seasonally. When water temperatures are cool in fall through spring, lake trout can use the nearshore and feed on minnow species without having to go in waters above their thermal preference (15 °C). However, in summer, the nearshore exceeds lake trout's preferred temperatures and they occupy and feed primarily in the deep offshore area of the lake on *Mysis* and Cladocera (Guzzo et al. 2017; Rodrigues et al. 2025).

Air and lake temperatures and ice-cover

Daily air temperature and precipitation data collected at the Environment and Climate Change Canada Rawson Lake weather station at the ELA since 1969 were used to calculate mean annual air temperature for each study year and assumed to accurately reflect conditions ∼10 km away at L373. Annual dates of winter ice-formation and break-up (hereafter ice-on and ice-off dates, respectively) were monitored at Rawson Lake (also known as Lake 239, surface area 54 ha, maximum depth 30.4 m). Trends in Rawson Lake ice cover are comparable to L373, which on average has ice-off one day earlier and ice-on four days earlier than L239, largely a function of lake size (Higgins et al. 2021).

Water temperatures in L373 were monitored every 2–4 weeks during the open-water seasons during 1986–2016. Water temperatures were measured using a handheld probe at 1 m depth intervals from the lake surface to bottom (Guzzo and Blanchfield 2017). We used this temperature profile data to estimate the mean daily temperatures of the upper 6 m of the water column (hereafter denoted as the littoral zone), which along with the presence or absence of ice-cover has been shown to be important in directing the seasonal habitat use of lake trout in our study lake (Guzzo et al. 2017). Because adult lake trout sampled in the initial year of the study (1986) would have also lived through previous years, we used water temperature profile data collected bi-weekly from Lake 239 to extend our estimated littoral zone water temperature dataset for L373 back to 1970. A Pearson correlation between open-water mean daily littoral zone temperatures during the period of sampling overlap (1986–2016) between Lakes 373 and 239 yielded a correlation coefficient of 0.98 and was highly significant ($n = 5254$, $p < 0.001$).

We used ice-cover and water temperature profile data to estimate the length of each season over time based on the same criteria as Guzzo et al. (2017). Winter is defined as the period of ice-cover. Spring is the period from the day of ice-off to when the mean temperature of <6 m of water was ≤15 °C. Summer is the period when mean temperature of <6 m of water exceeded 15 °C and fall was the period when <6 m of water cooled below 15 °C until the lake froze over.

Fish population data

The fish community in L373 was assessed annually or biannually using standardized collection methods as part of the long-term fish monitoring program at the ELA during 1986–2016. Fish capture included catch-and-release methods with Beamish-style trap nets (spring and fall; both lake trout and prey fish) and short (<30 min) small-mesh evening gill net sets on spawning shoals (fall; lake trout only). Surveys (in terms of net design, timing, and general locations targeted within the lake) were consistent through time. Lake trout are almost exclusively captured in short set gillnets in the fall but catches in trap nets during both seasons occur. Only fall-caught fish were sampled for ageing structures. Because fall gillnetting targets fish on spawning shoals, this method tends to select individuals at or near maturity, despite using a relatively small mesh size (i.e., 25 mm). More details on the ELA fish monitoring program can be found in (Mills et al. 1987, 2000, 2002*a*, 2002*b*; Rennie et al. 2019). Fish collections were made with the approval of annual Scientific Collections permits from the Ontario Ministry of Natural Resources, under the authority of Fisheries and Oceans Canada prior to 2014, the University of Manitoba Animal Care Committee in 2014 (AUP F14-07) and the Lakehead University Animal Care Committee from 2015 onward (AUP 1464656).

Lake trout

Weight (g) and total and fork lengths (mm) of each lake trout captured were recorded; lake trout captured during fall not previously captured had the leading fin-ray of the pectoral fin removed for ageing. Fish were then marked with a season-specific braille-like batch mark on their dorsal fin by clipping dorsal fin rays in specific combinations and "rows" specifying a season of capture, and were tagged with Passive Integrated Transponder (PIT) in the skeletal musculature just below the dorsal fin on the left side of the fish, Carlin-style sew-on tags just anterior to the dorsal fin through the skeletal musculature of the fish or VIE tags behind the clear tissue of the left or right eye for future identification (Mills et al. 1987). VIE tags were only rarely used in Lake 373, and accompanied by Carlin-style sew-on tags due to occlusion (i.e., pigmentation over the tags) which excluded their use immediately after this issue was identified. Season-specific batch marks served as a backup means of identifying capture histories of fish in case of tag loss. In cases where tag losses were apparent (e.g., dorsal batch marks but no identifiable tag), fish were re-tagged and noted as such in data records. Previously-captured fish had tag numbers recorded. Fin rays from fish not previously captured were dried, embedded in epoxy and sectioned prior to mounting and ageing (Mills and Beamish 1980). Age-at-capture for previously tagged fish was determined by adding years from initial capture age (determined from fin rays) since first capture. Fin-rays were aged by a single reader prior to 2013. Ages determined by a second reader during 2014–2016 were only done after a blind assessment of previously-aged material to ensure consistency in age determination (Kennedy and Rennie, unpublished data; Mills and Beamish 1980; Mills et al. 2002*a*; Mills and Chalanchuk 2004).

Together, fall size- and age-at-capture data allowed for an estimation of fork length-at-age and weight-at-age for each sampled lake trout. The body condition (i.e., fatness) of lake trout was estimated as relative weight, which is expressed as a percentage of standard weight specific for lake trout applied to fish >280 mm total length (Piccolo et al. 1993). For each year, we retained only fish captured on spawning shoals during fall sampling and then calculated the mean (±1 s.d.) fork length, weight, and relative weight of all fish captured as well as age-specific estimates of these metrics. To obtain proxies for age- and size-at-maturity, we calculated the 20th percentile of lake trout ages, fork lengths, and weights captured on the spawning shoals during fall sampling each year (Cruz-Font et al. 2019; Rennie et al. 2019), while lifespan and maximum size were estimated as the 95th percentile of ages and sizes, respectively, using the same data (Purchase et al. 2005*a*, 2005*b*).

We estimated the annual abundance of adult lake trout by capture–recapture techniques based on individual fish capture histories. In cases of fish experiencing tag losses, the capture history was determined by interpreting the batch marks of the dorsal fin and matching it to a fish with that same capture history in the data file (ending on the last capture period according to the dorsal batch marks and never seen again). The fish in the database was therefore identified as a suspected tag loss event and removed from the capture history file to avoid double counting fish. Abundance was estimated using the POPAN formulation of the Jolly-Seber model (Jolly 1965; Seber 1965; Schwarz and Arnason 1996) in the R package *RMark* (White and Burnham 1999; Laake 2013) following methods described in detail in Rennie et al. (2019). Briefly, the method employs a maximum likelihood approach in a generalized linear modelling framework to estimate survival, capture probabilities, and, unique to the POPAN method, a probability of entry (defined as the fraction of the net births entering the system between time periods). The POPAN approach is a generalization of the Joly-Seber open population formulation applied to capture-recapture data that models births using a multinomal distribution from a superpopulation (Schwarz and Arnason 1996). To more clearly evaluate trends in survivorship and net births (i.e., recruitment to the adult population, derived from entry probability), we adjusted capture histories to examine fall captures only, where spring captures were assigned to the previous fall (making the reasonable assumption that adult fish captured in the spring were alive and in the lake in the previous fall). Goodness of fit and model selection was performed on fall-only models as described above. Model selection criteria indicated that the best model was one that used a model that treated apparent survival (0.86, 95% CI 0.85–0.88) and entry to the population (more commonly reported as net births, 41, 95% CI 38–44 in this case) as constant over time and catchability as a time-varying parameter to derive abundance estimates (Table S1, Fig. S1). Annual abundance estimates are derived from net births and survivorship (see Schwarz and Arnason 1996 for details). The assumptions of the model are that (a) unmarked animals in the population have the same probability of capture as marked animals, (b) tags are retained or that capture histories can be easily determined (as described above), (c), tags (and therefore capture histories) are read and interpreted properly, (d) sampling is instantaneous, and (e) survival is homogeneous for tagged and untagged individuals between capture occasions, and that the size of the study area is constant (Schwarz and Arnason 1996)). Annual estimates of lake trout biomass were calculated as the product of annual fall abundance estimates and mean weight of fall captures.

Estimates of adult lake trout production were calculated using the Instantaneous Growth Rate (IGR) method (Ricker 1946). Population production is defined as the amount of biomass elaborated per unit space per unit time (e.g., kg ha^{-1} year^{-1}). The IGR method determines the rate of biomass production of a population by summing estimated age-class specific production across two subsequent sampling periods to determine an annual population production estimate (Hayes et al. 2007). Generally, estimating production followed:

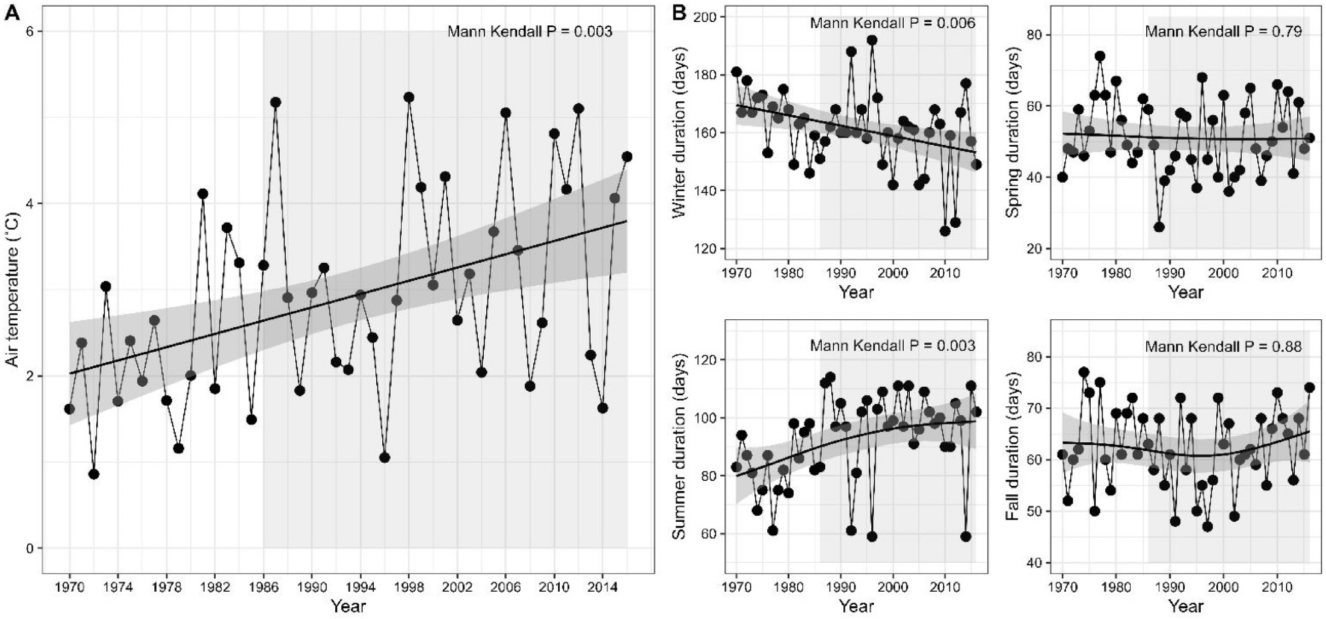
$$\widehat{P} \sum \widehat{G}\bar{B}$$

where $\widehat{P}$ is the sum of estimated production for all cohorts of a population between two subsequent sampling periods, $\widehat{G}$ is the instantaneous growth rate for a cohort from time t to $t + 1$ (i.e., $\widehat{G} = \log_e \bar{w}_{t+1} - \log_e \bar{w}_t$), with $\bar{w}_t$ representing mean cohort weight, and $\bar{B}$ is the mean cohort biomass from time t to $t + 1$ (i.e., $\bar{B} = (\widehat{B}_t + \widehat{B}_{t+1})/2$). Production estimates of the lake trout population were assigned to the second sampling period (i.e., $t + 1$) to better reflect the production of cohorts being modelled since lake trout size-at-age and abundance reflect those sampled in the fall during spawning. For example, if a single annual estimate of production was calculated using data from fall t and fall $t + 1$, production was assigned to the year $t + 1$ since most production occurred over the growing season of $t + 1$.

Prey fish

Prey fish monitoring data were examined to test if the size, relative abundance, and relative biomass of prey fish species and the total prey fish community changed over time. The individual fork lengths (mm) of each prey fish species captured during spring trap net sampling were recorded, as was their relative abundance, estimated from trap-net captures

Fig. 1. Annual variations in (A) mean annual air temperature (°C) and (B) season lengths based on presence or absence of ice cover and mean water temperatures <6 m depth being above or below 15 °C. The *P* values from Mann–Kendall tests of monotonic trends over the full time series (1970–2016) are indicated inside each plot. Trend lines (±95% CI) are from generalized additive models (GAMs) fit to each variable with year as the smoothed term fit using thin plate regression splines to help visualize trends. The grey shaded are indicated the period that fish monitoring occurred in the study lake.



as catch-per-unit effort (CPUE; units of number net^{-1} day^{-1}). Slimy sculpin was not included in our prey fish analysis as this species was not well sampled by the gear employed (i.e., trap nets set nearshore) and sample sizes were too low to be informative.

To assess changes in prey fish size over time we calculated the mean (±1 s.d.) and maximum (as 95th percentile) annual fork lengths of each individual prey fish species and entire prey fish community (combining data for all prey fish species). To assess changes in relative abundance of each species we calculated annual estimates of spring CPUE by dividing the total number of fish caught by the number of net days (i.e., # trap nets x # fishing days; Guzzo et al. 2014). Community CPUE was estimated by summing CPUE for all species to yield a total prey fish CPUE for each year. To assess changes in prey fish biomass over time (Biomass Per Unit effort or BPUE), the product of CPUE and a bootstrapped mean annual weight from spring captures for each species was calculated; a community estimate was summed across all species. Because prey fish weights are not measured as part of the regular fish monitoring program, the weight of each prey fish captured was estimated from fork length using length-weight regressions. Fork length and weight data for these regressions were collected from minnow trap sampling in L373 and Lake 442, another ELA reference lake (Paul Blanchfield, unpublished data; Kidd et al. 2007, 2014; Guzzo et al. 2014; Wellman et al. 2017). Resulting equations were: Finescale Dace $\log_{10}$(weight) = $\log_{10}$(total length) × 2.85–4.72; Pearl Dace $\log_{10}$(weight) = $\log_{10}$(fork length) × 2.94–4.91; Northern Redbelly Dace $\log_{10}$(weight) = $\log_{10}$(fork length) × 2.56–4.24. Because the resulting estimates of prey fish weights were not normally distributed, we bootstrap sampled the annual weight distribution of each species and the entire community 5000 times, using the number of fish captured that year as the sampling size and multiplied the annual means of these bootstrap distributions by the corresponding CPUE for that year to estimate relative biomass (BPUE; g trap^{-1} day^{-1}).

Statistical analysis

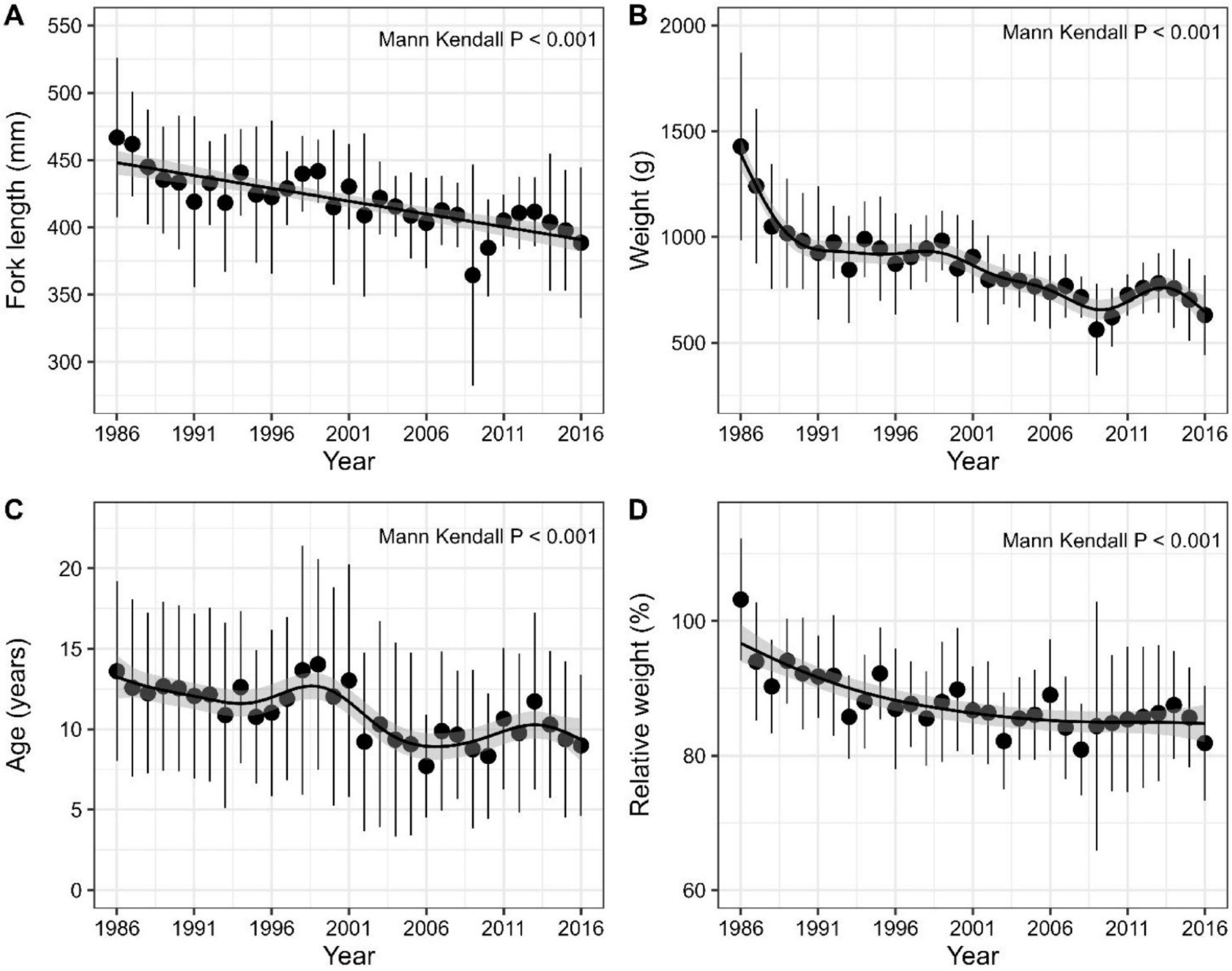
We used Mann–Kendall trend tests (Mann 1945; Kendall 1955) to test if monotonic trends (i.e., generally increasing or decreasing) occurred in time series of annual air temperatures, season length, water temperatures, and lake trout and prey fish data, with statistical significance defined as $p < 0.05$. To visualize patterns in the time series of each environmental and fish metric we added curves generated by fitting generalized additive models (GAMs) to each variable with year as the smoothed term fit using thin plate regression splines (Wood 2003). All data analyses were completed using the R Statistical Computing Software (v. 4.4.1; R Core Team 2024). Mann–Kendall tests were fit using the *MannKendall* function in the "Kendall" package (McLeod 2022) and GAMs were fit using the "mgcv" package (Wood 2017) through the *geom_smooth* function in the "ggplot2" package (Wickham 2016).

Results

Air and lake temperatures

Mean annual air temperatures at the Rawson Lake weather station increased by 2 °C (from approximately 2 to 4 °C) from 1970 to 2016 (n = 47, tau = 0.30, $p < 0.01$). Ice conditions at Rawson Lake mirrored trends in annual air temperatures (Fig. 1A). The period of ice cover (i.e., winter) declined over

Fig. 2. Annual variations in mean (±1 s.d.) (A) fork length (mm), (B) weight (g), (C) age (years), and (D) relative weight (%) (i.e., condition) of lake trout sampled in L373 each fall during 1986–2016. The *P* values from Mann–Kendall tests of monotonic trends over the time series are indicated inside each plot. Trend lines (±95% CI) are from generalized additive models (GAMs) fit to each variable with year as the smoothed term fit using thin plate regression splines to help visualize trends.



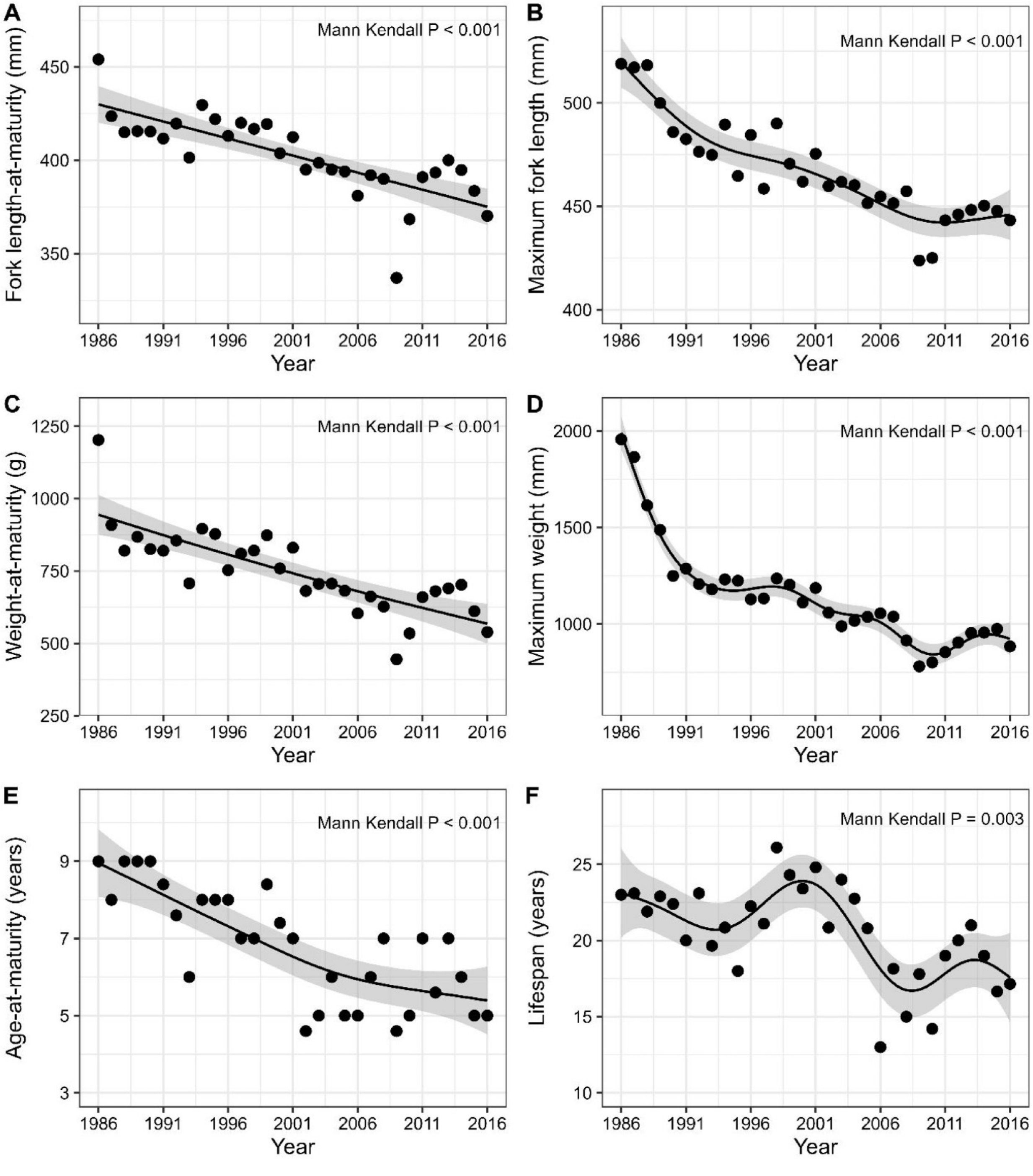
time ($n = 47$, tau $= -0.29$, $p < 0.01$), with the average days of ice cover dropping from 170 in 1970 to 155 in 2016 (Fig. 1B). These periods of ice cover would be expected to be on average 3 days longer on L373 each year but would be expected to have exhibited a similar trend over time as Rawson Lake (Higgins et al. 2021). In contrast, the summer period—defined as that when <6 m water depth (i.e., littoral zone) exceeds 15 °C—became longer over time ($n = 47$, tau $= 0.37$, $p < 0.01$; Fig. 1B). In other words, summer (as defined here and predicted from the reported trend above) was approximately 15 days longer in 2016 compared to 1970. No monotonic trends in the length of the spring or fall seasons were observed during 1970–2016 (spring: $n = 47$, tau $= -0.03$, $p = 0.80$; fall: $n = 47$, tau $= 0.02$, $p = 0.88$) (Fig. 1B).

Lake trout population data

Mean body sizes of adult lake trout captured in L373 declined between 1986 and 2016 (fork length: $n = 31$, tau $= -0.67$, $p < 0.01$; mass: $n = 31$, tau $= -0.76$, $p < 0.01$), with the sharpest drop in the earlier years of the study. Mean annual fork lengths decreased by from 450 mm in 1986 to under 400 mm in 2016 (Fig. 2A), while mean body mass declined by >50% over this period (Fig. 2B). Similarly, mean age of the population was also found to decline over time ($n = 31$, tau $= -0.50$, $p < 0.01$), with lake trout captured in the latter years of the study being on average 5 years younger (9 years old) than at the start of the study (14 years old; Fig. 2C, Fig. S2). The greater decline in fish weight compared to fork length resulted in the mean relative weight (i.e., body condition or fatness controlling for length) of lake trout decreasing ($n = 31$, tau $= -0.56$, $p < 0.01$) by almost 20% over the study period (Fig. 2D).

Over time, first time spawners in L373 were on average four years younger, half the weight, and >10% smaller in fork length compared with the beginning of the study period (Fig. 3). Age-at-maturity declined over the study ($n = 31$, tau $= -0.59$, $p < 0.01$), representing an average decrease from age 9 to age 5 (Fig. 3E). Similarly, weight-at-maturity declined, from

Fig. 3. Annual variations in (A) fork length-at-maturity (C) weight-at-maturity, and (E) age-at-maturity, as well as (B) maximum fork length, (D) maximum weight, and (F) lifespan of lake trout sampled in L373 each fall during 1986–2016. The *P* values from ManN–Kendall tests of monotonic trends over the time series are indicated inside each plot. Trend lines (±95% CI) are from generalized additive models (GAMs) fit to each variable with year as the smoothed term fit using thin plate regression splines to help visualize trends.



1000 to 500 g ($n = 31$, tau $= -0.63$, $p < 0.01$), while length-at-maturity declined ($n = 31$, tau $= -0.64$, $p < 0.01$), from 450 to 375 mm (Figs. 3A, 3C, and 3E). Together these data indicate that lake trout over time matured at younger ages and smaller sizes, with lower body condition (i.e., decline in weight was greater than that of fork length).

The maximum size and lifespan of adult lake trout in L373 decreased throughout the 31-year study period. Maximum fork length and weight declined 75 mm and 1000 g, respectively, between 1986 (525 mm and 2000 g) and 2016 (450 mm and 1000 g (fork length: $n = 31$, tau $= -0.76$, $p < 0.01$; weight: $n = 31$, tau $= -0.76$, $p < 0.01$; Figs. 3B and 3D). Similarly, the oldest lake trout captured each fall declined by six over the study period years ($n = 31$, tau $= -0.37$, $p < 0.01$) from age 23 in 2016 to age 17) in 2016 (Fig. 3F).

Shifts in the mean annual size-at-age and relative weight-at-age of lake trout were also observed, but the magnitude of these changes varied by age, with strongest declines in older fish (Fig. 4, Fig. S3). Younger lake trout (≤6 years old) did not exhibit obvious changes in fork length- or weight-at-age over time (Fig. 4). In contrast, older, mature lake trout (≥8 years old) underwent declines in both fork length- and weight-at-age. Most age classes underwent declines in relative weight over time and like size, the magnitude of these declines increased with fish age (Fig. 4).

Coincident with changes towards younger, smaller adults, the abundance of adult lake trout in L373 more than doubled from just over 125 in the first few years of the study up to 280 in the latter years of the study ($n = 31$, tau $= 0.84$, $p < 0.01$; Fig. 5A). The increase in adult abundance was strongest at the start of study and levelled off by the late 1990s. Despite this increase in abundance over time, the biomass of adult lake trout did not exhibit a directed trend ($n = 31$, tau $= -0.01$, $p = 0.95$), but rather an inverted dome pattern over time, with lows between 6 and 7 kg ha^{-1} at the start and end of the time series, and a peak of ~10 kg ha^{-1} in 1995 (Fig. 5B). Lake trout production averaged 0.37 ± 0.19 kg ha^{-1} year^{-1} (range 0.06–0.76) over the study period and did not exhibit a trend through time ($n = 31$, tau $= -0.02$, $p = 0.91$; Fig 5C). Similarly, the population biomass turnover (P/B) did not demonstrate a trend through time ($n = 30$, tau $= -0.03$, $p = 0.85$), averaging 0.05 ± 0.02 and ranging from 0.01 to 0.1 over the study period (Fig. 5D).

Prey fish population data

Over the study, the mean (±1 s.d.) fork lengths of prey fish species Pearl Dace, Finescale Dace, and Northern Redbelly Dace were 62.3 ± 3.58 mm, 48.9 ± 2.59 mm, and 39.7 ± 2.44 mm, respectively. None of the individual prey fish species underwent changes in mean fork length or relative abundance (CPUE) during the study period (fork length–Pearl Dace: $n = 28$, tau $= 0.21$, $p = 0.13$; Finescale Dace: $n = 24$, tau $= -0.17$, $p = 0.24$; Northern Redbelly Dace: $n = 26$, tau $= -0.19$, $p = 0.19$ and relative abundance–Pearl Dace: $n = 29$, tau $= -0.02$, $p = 0.87$; Finescale Dace: $n = 29$, tau $= 0.11$, $p = 0.43$; Northern Redbelly Dace: $n = 29$, tau $= -0.02$, $p = 0.88$; Fig. 6). In terms of relative biomass, neither Pearl Dace ($n = 28$, tau $= 0.01$, $p = 0.98$) nor Northern Redbelly Dace ($n = 26$, tau $= -0.03$, $p = 0.83$) showed trends over time, but Finescale Dace increased modestly over the course of the study ($n = 24$, tau $= 0.35$, $p = 0.02$; Fig. 6).

Discussion

Consistent with the TSR, we found that during a period of warming, an unexploited lake trout population exhibited reductions in maximum adult body size and lifespan (Atkinson 1994; Ohlberger 2013). The lake trout population also underwent decreases in the mean body size, age, and condition of adults, as well as a loss of the oldest and largest fish and a reduction in the age and size of first-time spawn-

Fig. 4. Annual variations in scaled mean annual (A) fork length-at-age (B) weight-at-age, and (C) condition-at-age, as well as (B) maximum fork length, (D) maximum weight, and (F) lifespan of lake trout (aged 2–20 years old) sampled in L373 each fall during 1986–2016. Trend lines are from generalized additive models (GAMs) fit to each age class with year as the smoothed term fit using thin plate regression splines to help visualize trends. Note that the data from each age class has been scaled (i.e., centered) around a mean of zero so that comparisons in the relative change in each metric over time can be made between age classes.

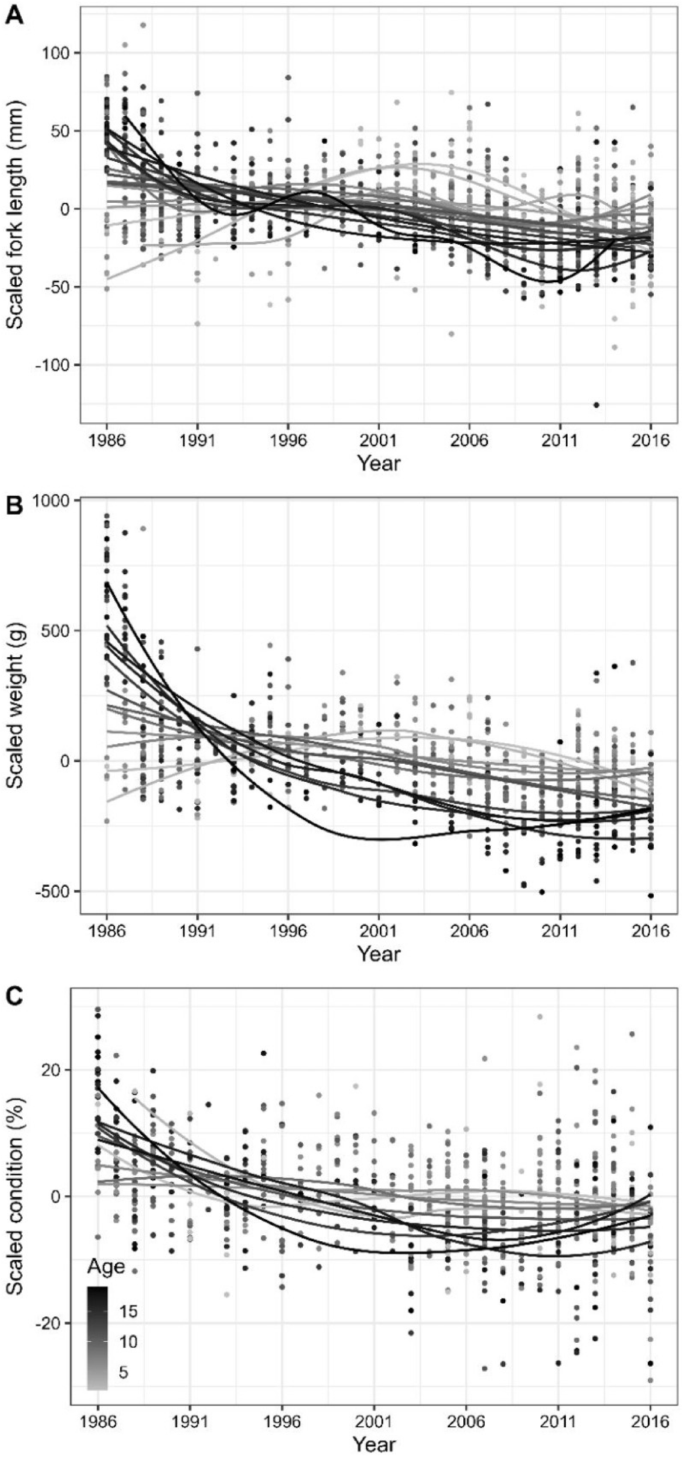
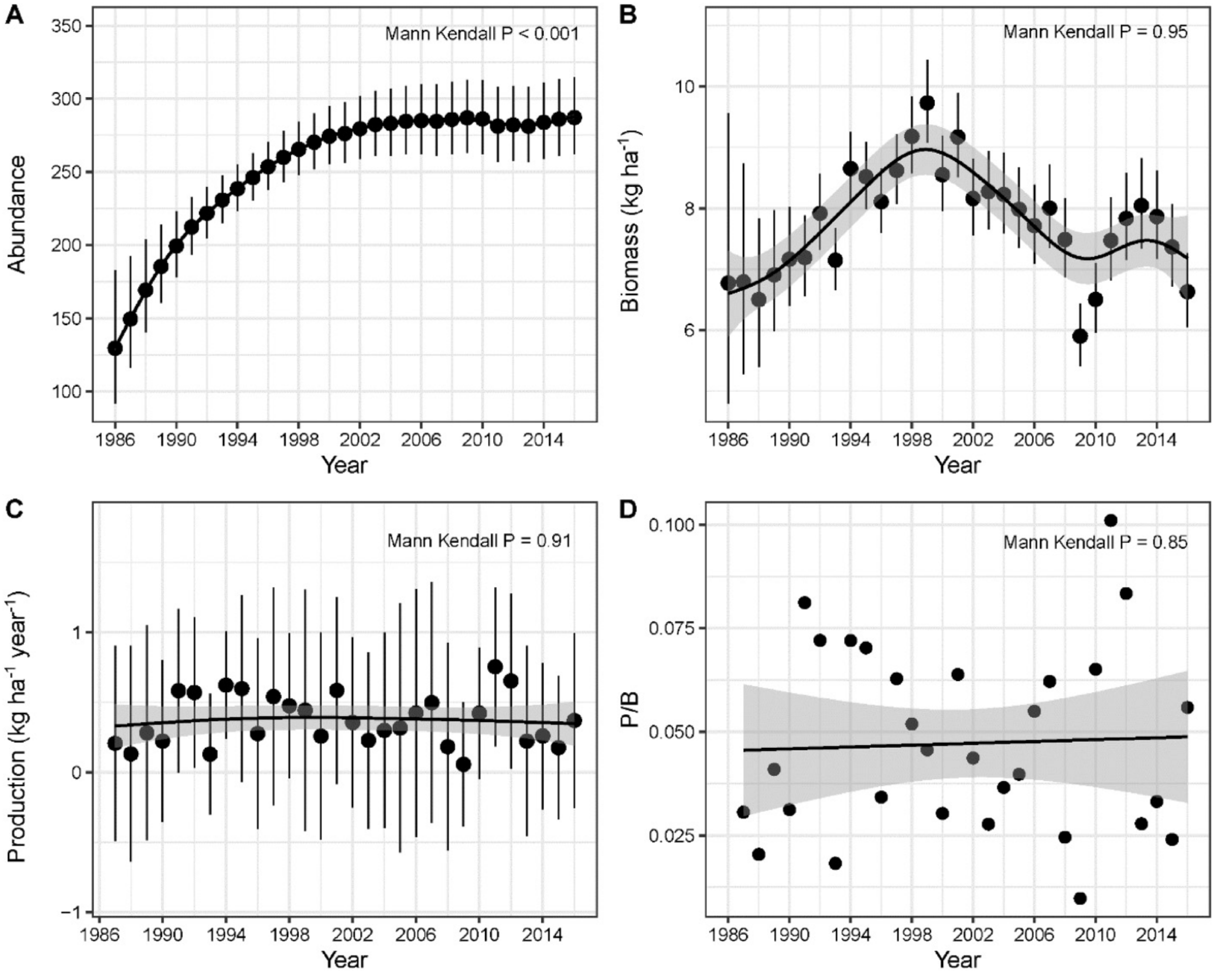


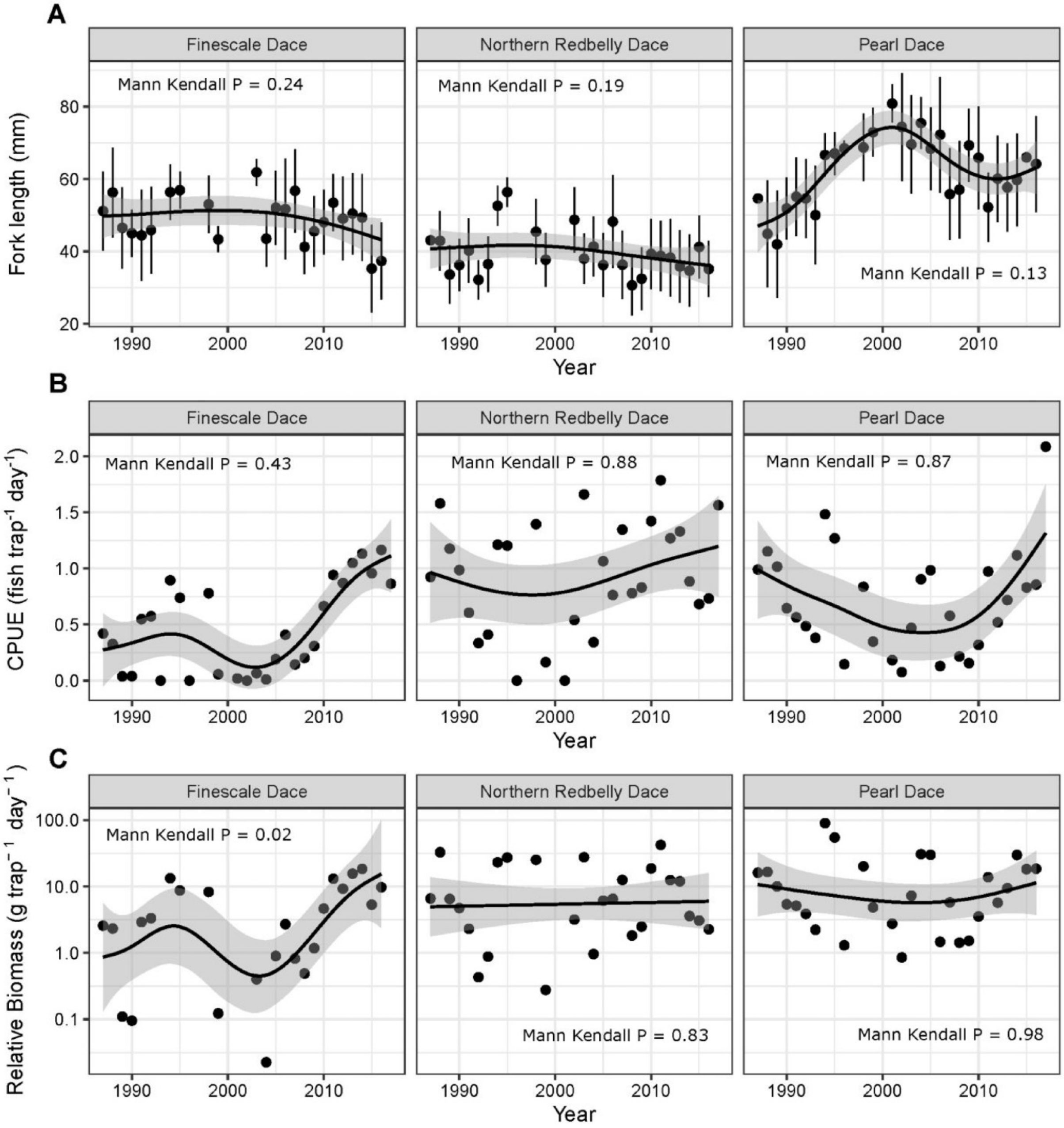
Fig. 5. Annual variations in estimates (±1 s.d.) of adult lake trout (A) abundance, (B) biomass density (B), (C) production (P), and (D) biomass turnover (P/B) in L373 during 1986–2016. Note that a production estimate and in turn P/B is not available for 1986. The *P* values from Mann–Kendall tests of monotonic trends over the time series are indicated inside each plot. Trend lines (±95% CI) are from generalized additive models (GAMs) fit to each variable with year as the smoothed term fit using thin plate regression splines to help visualize trends.



ers. During this size-structure shift, the abundance of the adult population doubled, while its biomass, production, and biomass turnover (P/B) were variable over time. As a result, the lake trout population is now comprised of a greater number of smaller, skinnier, younger individuals compared to 31 years prior. In contrast to the expectations of larger juvenile body size with the TSR, we did not find that size-at-age of young lake trout increased over time. Our data indicate that as age and size at maturation decreased, lifespan and maximum size decreased, consistent with expectations of life history invariants (Charnov 1993; Hutchings 2008). We highlight that the study population may represent an extreme example of the impacts of warming on lake trout, as the study lake did not contain offshore prey fish and the energetic costs experienced in this lake are among the highest observed for this species (Cruz-Font et al. 2019).

Our data suggest that a key contributing mechanism to these changes in life history was a reduction in access to high-quality littoral prey due to changing seasonality (increased duration of the summer stratification period, limiting access to nearshore-littoral zone) and potentially increased intraspecific competition, rather than a decline in available littoral prey. Though our mark-recapture models indicated that constant survivorship models outperform those with time-dependent survivorship, other data considered together indicates a potential change in the mortality rate of this population. The mean age of the lake trout population, which is often used as an index of lifespan (Brown et al. 2004; Munch and Salinas 2009), decreased over time, indicating that mortality may have potentially increased over this period. This shift is predicted to occur in response to earlier maturation age since life history invariants predicts age-at-maturation and mortality to be negatively correlated, with age-at-maturation decreasing with increasing rates of mortality (Charnov 1993; Hutchings 1993, 2008). However, increases in adult mortality may also be a consequence of limited food availability associated with reduced access to littoral energy during longer summers, which may especially impact the largest body sizes. Body condition is known to reflect changes in food availabil-

Fig. 6. Annual variations in mean (A) fork length (±1 s.d.), (B) catch-per-unit-effort (CPUE), and (C) relative biomass of prey fish in the L373 during 1986–2016. The *P* values from Mann–Kendall tests of monotonic trends over the time series are indicated inside each plot. Trend lines (±95% CI) are from generalized additive models (GAMs) fit to each variable with year as the smoothed term fit using thin plate regression splines to help visualize trends. Note that in panel C, the *y* axis is $\log_{10}$ scaled to allow a common axis range to be used across each species plot.



ity in salmonids (Rennie and Verdon 2008) including lake trout (Rennie et al. 2019). Increased intraspecific competition for resources may have contributed to observed declined in body size, as the adult lake trout population doubled over time; however, the biomass did not exhibit a trend over time, peaking in 1999 and declining to levels similar to the start of the time series.

In fisheries facing heavy, long-term exploitation, sustained selection against the largest individuals of the population has been shown to lead to an evolutionary response of smaller mean size, earlier maturity and an overall compression of life cycles (Gadgil and Bossert 1970; Ernande et al. 2004; Olsen et al. 2004). However, the short duration of the response in our population suggests the observed response is phenotypic in nature; assuming lake trout spawned somewhere between ages 5 and 9 years, only four to five generations of new spawners would have occurred by 2016 since the beginning of the study period in 1986. This would be a short period for the evolution of earlier maturation to occur, especially if only small (and variable) increases in mortality occurred. This finding of plastic maturity with warming is supported by studies that have found that maturation is linked to factors like temperature, oxygen, and growth rate, rather than being set by age (Policansky 1982, 1983; Morbey and Pauly 2022). As such, should climate patterns reverse, we would expect the population structure and life histories of lake trout in L373 to return to background conditions over a similar timeframe. Moreover, evolution for earlier maturation would depend on variation in age-at-maturity to exist among individuals within the population, which may be limited due to the small size of the lake and limited number of spawners (Brown et al. 2008; Hilborn and Minte-Vera 2008). The observed changes seen in this study of earlier maturation and reduced maximum size over a period of warming are consistent with others which have examined differences in populations across latitude; decreases in age-at-maturity and maximum size are expected with warmer environments/decreasing latitude (Rypel 2014; Weber et al. 2015).

While an expanded open-water period over time may be considered to positively influence lake trout growing conditions due to temperatures near physiological optima existing for longer, potential reductions in littoral prey access due to longer summers over time may be outweighing any such benefits. Longer open-water seasons typically extend the period when lake water temperatures remain within the optimal range for lake trout growth (10 ± 2 °C; Christie and Regier 1988; Ryan and Marshall 1994; Evans 2007). This also reduces the period when lake trout growth is expected to be negligible or negative due to thermal effects on their physiological conditions, such as in winter (Shuter et al. 2012). However, our findings combined with those of Guzzo et al. (2017) on the same population, suggest that longer summers experienced by lake trout in L373 over time counteract these physiological optimization effects on growth for adult and juvenile fish by restricting access to energy rich nearshore prey for longer periods (Guzzo et al. 2017). This reduced access is particularly troublesome for our study population as the lake does not contain offshore prey fish like cisco (*Coregonus artedi*). As a result, growth efficiency for adults is reduced during longer summers by forcing them to feed on smaller prey (i.e., *Mysis*), or forcing nearshore forays into warm water to feed (Sellers et al. 1998; Morbey et al. 2006) which could also impact growth (Guzzo et al. 2019).

The longer summers observed over time should not directly impact the ability of juvenile fish to feed on their main prey item *Mysis* (Trippel and Beamish 1993; France and Steedman 1996), which are confined to the hypolimnion during this season (Paterson et al. 2011). This is supported by our study, which showed no clear change in growth rates of immature/juvenile lake trout. However, evidence that the adult population has increased in abundance and that warming increases the tendency for adult lake trout to feed on *Mysis* suggests that competition between life stages (i.e., between juveniles and adults) is heightened with warming. This increasing reliance on offshore prey by lake trout over time may have contributed to observed reductions in *Mysis* densities observed in L373 during 2002–2008 (Paterson et al. 2011). However, given that predator-prey size ratios between smaller, immature lake trout with *Mysis* are lower, their foraging efficiency (and therefore growth efficiency) will be less affected compared to adults forced to resort to feeding on these small prey.

Over a period when there was the loss of the largest, most fecund, and most experienced spawners, there was an increase in abundance, while biomass stayed relatively constant, suggesting that the carrying capacity for lake trout is a function of biomass. Our biomass estimates were in line with those of (Mills et al. 2002*b*), who estimated the mean biomass of L373 population during 1986–1999 to be 7.8 kg ha^{-1} (our estimates range from 5.9 to 9.7 kg ha^{-1}), providing confidence in our independently-derived estimates. This is supported by the findings of Fry (1939), who noted that lake trout populations with smaller mean sizes are often in higher abundance than those with greater mean sizes. This idea of biomass-based carrying capacity makes sense from a bottom-up perspective (i.e., prey supply) because lake trout is the only top predator in the study lake, and its gross consumption increases with weight (Brett 1971; Stewart et al. 1983). This is similarly supported by estimates of lake trout population production, as the estimates were low and relatively constant over time, despite substantial increases in abundance and declines in mean body size. Similarly, biomass turnover (P/B) estimates, are low although inconsistent over time, suggesting that the population from a production and P/B perspective is relatively stable (Rypel et al. 2018).

Trends in prey fish densities and mean size failed to provide an explanation for the reductions in adult body size found here as both metrics did not show any trend over time, despite being the preferred prey for lake trout. Additionally, the mean size of prey fish (both at the species and community level) remained relatively constant over time. This suggests that bottom-up scaling, where warming-induced reductions in prey fish size led to smaller consumer body sizes (Sheridan and Bickford 2011), was not a cause of the declines in lake trout body size in this lake. We did however find a slight increase in the relative biomass of finescale dace over time, while the other dominant minnow species remained unchanged over time.

While interactions among age classes over time may be influencing the size-structure of the lake trout population in L373, a sum of available evidence suggests this may not be the case. The age distributions of long-lived fishes can exhibit temporal fluctuations due to sporadic recruitment, where once a strong cohort becomes established, it can dominate the population until it is either fished out or dies off–a phenomenon known as the “storage effect” (Warner and Chesson 1985; Secor 2000, 2007). Therefore, it is possible that as a dominant age class establishes and moves through the population over time, its cannibalistic and competitive (i.e., density dependent) interactions may alter the growth rates, sizes at maturity, and maximum sizes of younger cohorts (De Roos and Persson 2013). However, based on the annual age distribution of the L373 lake trout population (Figs. S2 and S3) and the trend observed in mean age, there is no clear indication of a single dominant age class or cohort moving through the population over time. Moreover, temporal trends in both mean size and age of lake trout in L373 (Fig. 2) suggest that cycles in size and age distributions may occur, but these are to a much lower magnitude compared to the negative trends observed over time (Fig. 4). Finally, an analysis of lake trout recruitment across several ELA lakes (including L373) showed no evidence of highly variable recruitment in lakes not undergoing experimental manipulations (Mills et al. 2002*a*).

While our study focused only on a single population, we note that data from other lakes within the IISD-ELA show similar trends (Figs. S2–S4). Lake trout in Lake 224, which is like L373 both biologically and physically, also showed decreases in the size-at-age of mature fish during 1976–2000, during a period where active baitfish harvest was ongoing in this lake. However, post-2000, baitfish harvest stopped, and the minnow population increased, and adult lake trout size rebounded to levels found in the late 1970s, suggesting that increases in prey density may trump warming-induced body size declines (Fig. S4), despite expected similar shifts in season duration in this lake (Guzzo and Blanchfield 2017). Similarly, the maximum size of lake trout also decreased from 1981 to 2006 in Lake 468, which is much larger than L373 and contains the pelagic prey fish cisco (Fig. S5). Although we chose not to focus on these lakes in the study because of a lack of available data for prey availability, lake trout ages, water temperatures and impact of minnow harvest (Lake 224), the general agreement in trends among data from L373 and Lakes 468 and 224 prior to the year 2000 provides some corroboration to our findings. Our findings were in contrast with recent studies that examined body size and temperature relationships for this species. As part of a larger analysis, Solokas et al. (2023) found evidence that lake trout were getting larger over time. However, most observations in this dataset were from Lake Superior, where the lake trout population has been subject to exploitation and strong recovery efforts over the past decades and the prey base within the lake has undergone large changes, making it difficult to infer impacts of temperature on body size. In contrast, a study by Warne et al. (2024) examined among-population variation in maximum body size of lake trout in Ontario lakes found no relationship with the corresponding growing degree days experienced by those populations while accounting for fishing pressure, spatial variation, lake characteristics and prey availability. Taken together this highlights the difficulty in trying to isolate the impacts of warming on fish growth and life history and the importance of long-term reference sites when studying global change.

Lastly, we acknowledge that the primary goal of this study was to quantify long-term changes in the growth, body size and life history of an unexploited lake trout population over time and how this related to observed climatic and environmental variation over that same time. Our findings provided clear evidence that over a period of regional warming and altered seasonality, the lake trout population in our study lake underwent a clear structure shift towards a larger, younger and smaller population with a compressed life cycle. While we have discussed the potential causes of these changes, we hope that our study inspires future studies that employ bioenergetic simulations, novel stock assessment models, and other approaches to try to isolate the mechanisms behind the changes in growth and life history found here.

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Copyright

Data availability

Data and R code to reproduce the results of this paper have been deposited in the open-access repository Zenodo (https://doi.org/10.5281/zenodo.17237900). All raw datasets used in this study are also available on request through IISD ELA (https://www.iisd.org/ela/researchers/data-requests/).

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Michael D. Rennie served as Associate Editor and Guest Editor of the "Commemorating the work and ideas of Jeff Hutchings" collection at the time of manuscript review and acceptance; peer review and editorial decisions regarding this manuscript were handled by another editorial board member.

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Formal analysis: MMG, HAM
Funding acquisition: PJB, MDR
Investigation: MMG, PJB, MDR
Methodology: MMG
Project administration: PJB, MDR
Resources: MDR
Supervision: PJB
Validation: MDR
Visualization: MMG
Writing – original draft: MMG
Writing – review & editing: MMG, PJB, HAM, MDR

Competing interests

The authors declare no competing interests.

Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2024-0393.

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