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RESEARCH ARTICLE

Growth and maturation of rainbow smelt (*Osmerus mordax*) at the northern limit of their distribution range (Lake Melville, Labrador): Support for the hypothesized temperature-size rule

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Rainbow smelt (*Osmerus mordax*), a small pelagic fish found throughout the northwest Atlantic Ocean, experienced a northward retreat of its distribution range over the 20th century and an overall decline in biomass in recent decades, both attributed to warming waters and habitat loss. In the Lake Melville estuary (Labrador, Canada), at the northern limit of its distribution range, smelt represents the main forage species and faces environmental changes from both climate warming and hydroelectric dams. This study aims to improve our understanding of the ecology of rainbow smelt and its vulnerability to climate and anthropogenic changes. We investigated hatching period, growth, and maturation of rainbow smelt in the Lake Melville estuary using trawl surveys and otolithometry. Growth and maturity from rainbow smelt in Lake Melville were then compared to southern populations to test the temperature-size rule, which stipulates slower growth and larger length-at-age of maturity at colder temperatures. In accordance with this rule, adult rainbow smelt in Lake Melville grew slower, matured up to 2 years later, and lived up to 3 years longer compared to southern populations. In contrast to it, larval growth rate was up to 3 times faster than values reported for a more southern population. Our results demonstrate that rainbow smelt in Lake Melville are well adapted to the short growth season and cold water temperatures prevailing at sub-arctic latitudes. Yet, if variation in life history across their range is a plastic response to thermal gradients, populations at their northern limits could benefit from a longer and warmer growth season.

Keywords: Growth, Temperature-size rule, Rainbow smelt, Phenology, Life history

Introduction

Rainbow smelt (*Osmerus mordax*) is a small forage fish found throughout the northwest Atlantic Ocean (Bradbury et al., 2006; Bradbury et al., 2008; Chase et al., 2019). Due to its variability in life history strategies, it can be found in both coastal and freshwater habitats ranging from Massachusetts, USA, to coastal Labrador, Canada, while also extending through the Laurentian Great Lakes and many other freshwater bodies (i.e., Lake Champlain; O'Brien et al., 2012; O'Malley et al., 2017; Dobosenski et al., 2020). The introduction of rainbow smelt to many North American lakes has also led to further dispersal into the Hudson Bay watershed (i.e., James Bay, Canada; Committee on the Status of Endangered Wildlife in Canada, 2018). Coastal rainbow smelt are anadromous, moving inland to spawn in freshwater tributaries just ahead of tidal influence (Bradbury et al., 2006; Enterline et al., 2020). Larvae are carried downstream by currents after hatching (Sirois et al., 1998; Bradbury et al., 2006).

Rainbow smelt dominates the forage fish assemblage within the seasonally ice-covered Lake Melville, the largest estuary of Labrador, despite being at the northern extent of its range (**Figure 1**; McCarthy, 2013; Hanson and Courtenay, 2020; Paterson et al., 2020). It funnels energy from lower trophic levels to top predators, such as gadids, salmonids, flatfish, and ringed seals (McCarthy, 2018). In addition to being one of the main prey of brook trout (*Salvelinus fontinalis*) and salmon (*Salmo salar*), both of which are harvested in Lake Melville, winter recreational

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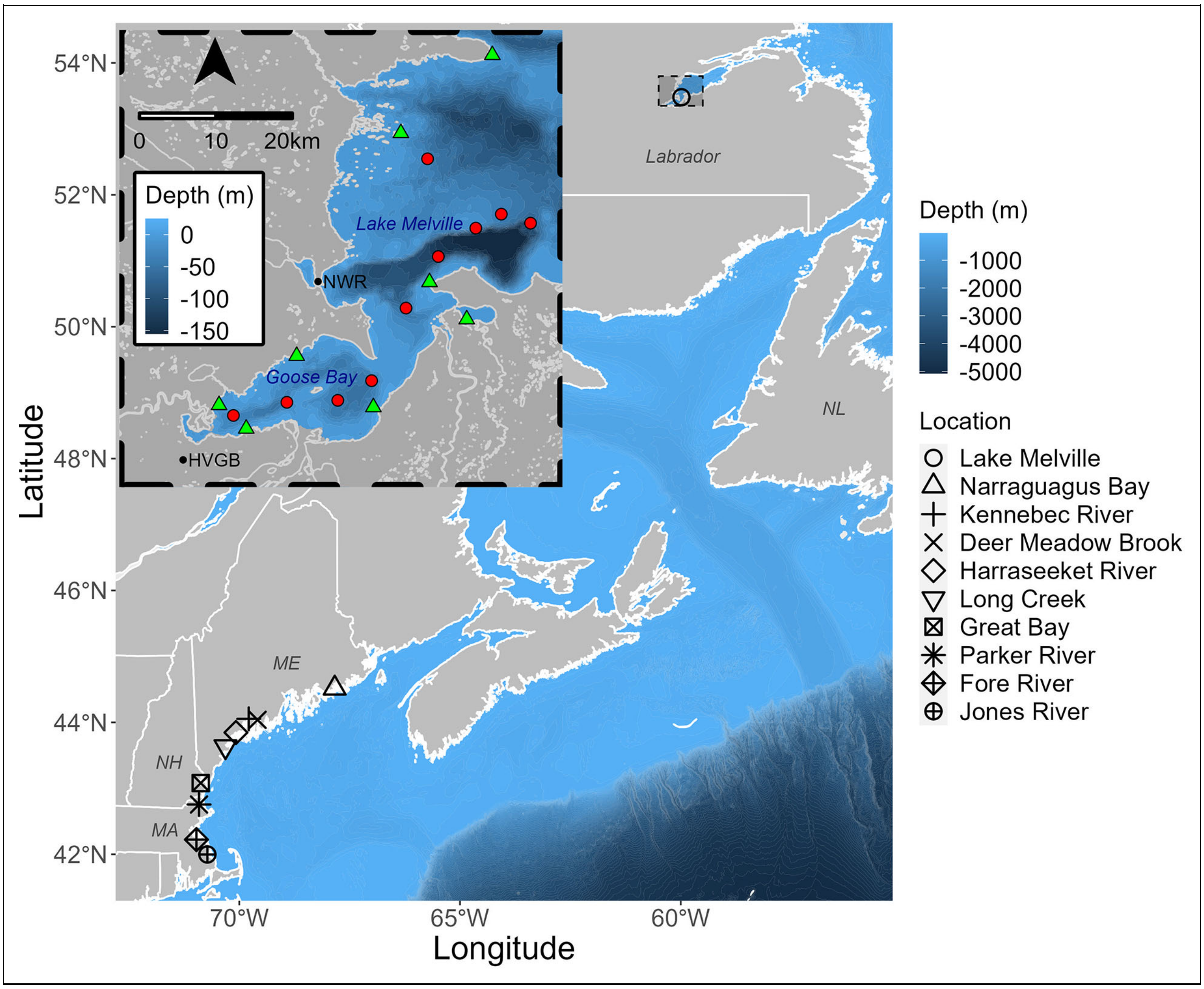

Figure 1. Map of sampling locations for adult rainbow smelt from North America. Inlay shows sampling locations for adults (green triangles) and larvae (red circles) within the Lake Melville System, Labrador (and Newfoundland, NL), Canada, which consists of Lake Melville (open circle) and Goose Bay. Black circles denote the towns of Happy Valley-Goose Bay (HVGB) and Northwest River (NWR). Other sampling locations are along the northeastern U.S. coast, from Massachusetts (MA) to New Hampshire (NH) and Maine (ME).

and subsistence fisheries directly target rainbow smelt; smelt is listed as one of the top five species consumed by local communities within the region (Wells, 2016). Despite its ecological and cultural importance, most aspects of the life ecology of the rainbow smelt population in Lake Melville remain unknown.

Both regional anthropogenic activities and global climate change are impacting the physical oceanography of Lake Melville. Its main tributary, the Churchill River, was harnessed twice for hydroelectric power, in the 1970s and 2020s (Bobbitt and Akenhead, 1982; Durkalec et al., 2016; Kamula et al., 2020). Seasonal variation in flow has consequently been altered significantly, with a marked increase in freshwater released in winter and a reduction in freshwater released in spring and summer (Durkalec et al., 2016; Kamula et al., 2020). The ecological impacts of changes in the hydrography of Lake Melville may be exacerbated further by the warm weather anomaly prevailing in coastal Labrador since the 1990s (Finnis and Bell, 2015; Kamula et al., 2020). Ultimately, such changes in the seasonality of freshwater inflow and surface temperatures could potentially impact the ecology and survival of forage fish, including rainbow smelt (Sirois and Dodson, 2000; Simonin et al., 2016).

Ectothermic species generally display intraspecific variations in growth and maturation across thermal gradients (Atkinson, 1995; Forster and Hirst, 2012; O'Malley et al., 2017). One phenomenon, dubbed the temperature-size rule (TSR; Atkinson, 1995), stipulates slower growth and delayed maturation at larger sizes in fish populations inhabiting colder, northern climates (Forster and Hirst, 2012). Accordingly, the length-at-age for anadromous populations of rainbow smelt has been observed to decline with increases in latitude (Enterline et al., 2012; Chase et al., 2019); however, these relationships were derived across a relatively narrow latitudinal range because of the paucity of information at the northern extent of their distribution. Testing the TSR across a broader range of rainbow smelt populations that include higher latitudes will improve assessments of the potential responses of rainbow smelt to forecasted changes in thermal regimes.

Larval survivorship rates have long been hypothesized as being correlated with size such that faster growing larvae are less vulnerable to risk of starvation and predation (Houde, 1987; Anderson, 1988; Miller et al., 1988). Because fish population dynamics are driven by survival of the early life stages, which are highly sensitive to environmental conditions (Fennie et al., 2023), documenting the early-life history and larval growth of a relatively understudied population provides critical information about the vulnerability of a species to environmental changes.

This study aims to improve our understanding of the ecology of rainbow smelt at its northern range limits and to predict its response to warmer temperatures. First, we document the life history (spawning period, hatching period, and age of maturity) and growth during both the larval and adult life stages for a population at the northern extent of the species' range: Lake Melville, Labrador. Second, we compare the adults in Lake Melville with other populations to test whether growth and maturity of rainbow smelt follow the TSR across a broad latitudinal range and to evaluate their potential responses to changing environmental conditions.

Materials and methods

Study area and design

Goose Bay and Lake Melville, collectively referred to as the Lake Melville System (LMS), are located in Central Labrador, Canada (**Figure 1**). The LMS is a semi-enclosed, seasonally ice covered estuarine fjard that connects to the Labrador Sea in the east and to Goose Bay in the west via two narrow, shallow glacial sills which limit the exchange of seawater with the North Atlantic (Durkalec et al., 2016; McCarthy, 2018; Kamula et al., 2020). Lake Melville is classified as a fjard and not a fjord because of its low topographical relief and irregular bathymetry (Kamula et al., 2020). The majority of freshwater that enters the LMS comes through 4 rivers: Goose, Northwest, Kenamu, and Churchill (Durkalec et al., 2016; Kamula et al., 2020). The Churchill River, which flows into the western side of Goose Bay, provides the majority (1700 $m^3 s^{-1}$) of freshwater to the system (Kamula et al., 2020). A defining characteristic of the LMS is the consistent low-salinity surface layer over a steep pycnocline that persists year round at depths of 10–15 m (McCarthy, 2013; Kamula et al., 2020; Small et al., 2023).

Due to logistical constraints and based on the prediction that the potential downriver effects of altered freshwater hydrology due to hydroelectric development (Upper Churchill Development and Muskrat Falls) would be most prominent closest to the inflow of the lower Churchill River, sampling effort was focused within Goose Bay and Upper Lake Melville. Sampling of rainbow smelt larvae was conducted from June 29 to July 12 in 2018 and July 4 to July 14 in 2019 at 10 stations distributed across the study area to create a cross-section between both basins (**Figure 1**). At each of the stations, a Bongo net, comprised of two adjacent 28 cm diameter ring nets with 335 μm mesh, was towed at a depth <10 m at 2 knots for 20 minutes to capture ichthyoplankton during the day. Samples were filtered through a 120 μm sieve. Larval fish were separated from zooplankton and were fixed in 95% ethanol that was replaced after the first 24 hours to prevent samples from becoming acidic (Sirois and Dodson, 2000).

Adult rainbow smelt were collected (n = 201) by local fishers with a fishing rod through the ice in February and March during the 2019 and 2020 recreational and subsistence ice fisheries. Additional samples (n = 66) were collected in August and September by Wood Environment & Infrastructure Limited during their 2019 net surveys using 15 m four-paneled experimental gill nets (mesh sizes: 5.1, 7.6, 10.2, and 12.7 cm). The nets were deployed at depths down to 3 m for a period of at least 16 hours, to ensure fishing occurred during dusk and dawn periods. Adult rainbow smelt were collected in Maine, New Hampshire, and Massachusetts (n = 10,714) by state fisheries resource spawning surveys in March–June 2008–2021 following methods described in Enterline et al. (2020). Rainbow smelt were collected using 3-chambered fyke nets (mesh size: 1.9 cm) placed downstream of the spawning grounds with the opening facing downstream to collect upstream traveling individuals. The nets were left to soak for 3-day intervals.

Environmental data

Sea surface temperature (SST) over the study period was measured weekly by the Department of Environment and Climate Change, Newfoundland and Labrador, as part of their methylmercury monitoring program (Environment and Climate Change, 2022) at a depth of 1 m from the surface. A cubic spline was fit to the data to interpolate missing data points, and the temperature time series produced was used to estimate the SST at first hatch and to determine the spawning period, estimated as occurring 156.5 degree days before the hatching period (Gagnon, 2005). This number of degree days represents the average incubation period from six studies within North America. Because spawning is believed to begin when waters reach temperatures of 3–5°C (O'Brien et al., 2012), a threshold was set to exclude dates where temperatures were less than 3°C as the first day of the spawning period. Proportion of ice cover was determined by using daily ice data obtained from Canadian Ice Services and allowed for testing whether spawning within Lake Melville occurred near the date of ice breakup (Rupp, 1959; O'Brien et al., 2012). For this study, ice breakup dates were calculated as the first day where ice concentration reached <50% within the study area (e.g., Bouchard et al., 2021) and the optimal growth window for young-of-year smelt was calculated as the period from first hatching to the day of first ice formation (first appearance of ice in the study area). Ice concentration was calculated by dividing the area of ice coverage by the total study area. Daily atmospheric temperature data for the Lake Melville region were obtained from the Government of Canada's past weather and climate data resource and from the National Centers for Environmental Information (NCEI) Climate Data Online (CDO) for stations within the United States. The number of degree days (DD_i) was calculated as the sum of the number of days where the temperature was greater than 5°C in a given year and was averaged over a 5-year period (Chezik et al., 2014). Mean DD_i is used herein as a proxy for the length of the growing season.

Otolith analysis

A subsample of 200 larvae were selected to represent the size frequency distribution of all the larvae collected (5–13 mm). A minimum of 10 representatives from each station were selected from the 2019 sampling period ($n = 152$), while additional representatives were taken from the 2018 field season ($n = 48$). Fewer samples were used from the 2018 sampling season because more individuals were damaged during preservation. To account for the possibility that capelin larvae may have been caught in addition to rainbow smelt larvae, preanal myomere counts for each specimen were taken (48–51 for capelin; 42–48 for rainbow smelt; Fahay, 2007). No capelin were found during this process. Standard length of each larva was measured using a camera connected to an image analysis system, and no correction for shrinkage resulting from the preservation process was made (Sirois et al., 1998). Sagittal otoliths were removed with a pair of fine needles and mounted on a microscope slide using thermoplastic glue. Otoliths were then measured using an image analysis system connected to a light microscope (1000× magnification). The core radius, otolith radius, and width of every increment were measured for each otolith using calibrated ImageJ software. The age in days was inferred from the number of increment widths measured per otolith (Stevenson and Campana, 1992). All otoliths were measured twice in a random order, 3 months apart, and any otoliths with a discrepancy in number of increments greater than 10% were excluded from further analyses (Sirois and Dodson, 2000). A coefficient of variation was calculated to assess ageing precision (Campana, 2001). Hatch dates were determined for each larva by subtracting the number of daily increments (age in days) from the corresponding date of capture.

Sagittal otoliths from 267 adult rainbow smelt were analyzed in the Campana Lab at the University of Iceland. Otoliths were immersed in ethanol just prior to imaging, sulcus side down. While under a Leica S8 APO stereomicroscope at 16–40× magnification using reflected light, the growth increment sequence was photographed digitally at a resolution of 5760 × 3600 with an Olympus DP74 digital video camera. Calibrated CellSens software was used to measure otolith length along the long axis; the precision of repeated measurements was ±0.3%. Age interpretations were made from the digital image, which seldom required image enhancement. Known-age otoliths were not available, nor have age validation results been published for this species. Ageing precision was quantified using the coefficient of variation (Campana, 2001). Ageing of adult rainbow smelt from Maine, New Hampshire, and Massachusetts was performed using scales as described by Elzey et al. (2015).

Growth rates

A linear regression was performed on larval standard length and age for both seasons (2018 and 2019), and an average growth rate (mm day^{-1}) was calculated. In addition, the biological intercept method (Campana, 1990) was used to back-calculate larval length-at-age (L_t) using the following equation:

$$L_t = L_c + (O_t - O_c)(L_c - L_0)(O_c - O_o)^{-1}$$

where L is the standard length at capture (L_c), and O is the otolith radius at capture (O_c). A length at the biological intercept (L_0) of 5.81 mm was adapted from Sirois et al. (1998), and otolith radius at the biological intercept (O_0) was estimated from the observed core radius on the otoliths of each larva (Sirois et al., 1998; Leclerc et al., 2011).

The Von Bertalanffy growth function (VBGF) was applied to adult fish, ranging in age from 1 year to 8 years, to assess variation in the growth rates and size-at-age of males and females. The Von Bertalanffy growth equation is expressed as:

$$E[L][t] = L_\infty\left(1 - e^{-K(t-t_0)}\right)$$

where $E[L][t]$ is the fork length-at-age t, L_∞ is the average asymptotic length, K is the growth rate coefficient, and t_0 is the theoretical time when length is equal to zero if larval growth followed the same pattern as adult growth (Hopkins, 1992).

Gonad analysis

Gonads from each fish collected in February and March ($n = 201$) were removed, weighed, and imaged with a digital Single Lens Reflex (SLR) camera (resolution of 6000 × 4000). Each individual was characterized as mature or immature based on gonad presence and characteristics (i.e., color, texture, and size relative to body cavity) following methodology from Bucholtz et al. (2008). The age of maturity and length of maturity were then calculated for both sexes. The age and length of maturity are described herein as the age and length where 50% of the population is mature (A_{50} and L_{50}, respectively; Wheeler et al., 2009).

Comparison of growth across geographic range

Mean length-at-age for each age cohort was compared for data collected across the geographic range of rainbow smelt to examine whether they followed the TSR (**Table 1**). We used a generalized additive mixed model (GAMM; mgcv package, R version 4.3.1) to assess variation in length against sex, age, year, and DD_i. The GAMM was applied to *Age* to better capture the non-linear growth patterns of fishes, and *Location* was used as a random effect ($1|Location$) to capture the variability within each sampling location. Model predictions for each sex were plotted for each of the sampling locations.

Results

Environmental variables

Bottom depth at each station where larval and adult rainbow smelt were sampled varied from 30 m to

Table 1. Data for populations used to compare growth across varying number of degree days

Water Body	State/Province	Lat (°)	Long (°)	Year(s)	n	DD[a]	Resource
Lake Melville	Newfoundland	53.54	−60.01	2019–2021	267	144	This study
Narraguagus Bay	Maine	44.63	−67.75	2010	144	196	Gov ME[b] Unpublished data
Deer Meadow Brook	Maine	44.04	−69.59	2008–2010	648	216	Gov ME Unpublished data
Kennebec River	Maine	44.03	−69.81	2011–2012	518	219	Gov ME Unpublished data
Harraseeket River	Maine	43.83	−70.09	2009–2011	879	204	Gov ME Unpublished data
Long Creek	Maine	43.63	−70.31	2009–2012	513	226	Gov ME Unpublished data
Great Bay	New Hampshire	43.07	−70.87	2009–2021	4368	218	Gov NH[c] Unpublished data
Parker River	Massachusetts	42.75	−70.93	2009–2013	219	243	Gov MA[d] Unpublished data
Fore River	Massachusetts	42.22	−70.97	2013	2876	244	Gov MA Unpublished data
Jones River	Massachusetts	42.00	−70.72	2013	549	243	Gov MA Unpublished data

[a] Mean number of days with temperatures greater than 5°C over 5 years (i.e., growing season).

[b] Government of Maine.

[c] Government of New Hampshire.

[d] Government of Massachusetts.

100 m, with a mean depth of 51 m (Table S1). The average temperature (and standard deviation, SD) within the top 10 m was 9.9 (±1.1)°C in 2018 ($n = 10$) and 11.4 (±1.4) in 2019 ($n = 10$), while the average practical salinity by conductivity within the top 10 m was 4.12 (±3.1) in 2018 and 1.2 (±1.1) in 2019 (Table S1). The low salinity surface layer persisted until a depth range of 10–15 m, depending on station, and a sharp pycnocline was observed at all stations at these depths. Atlantic-influenced water, with average temperature of 3.3 (±1.8)°C and practical salinity by conductivity of 18.1 (±4.3) in 2018 ($n = 10$) and 4.5 (±2.5)°C and 15.9 (±4.8) in 2019 ($n = 10$), was found below the pycnocline. Ice breakup within the study area occurred on May 31 for both years, while ice formation occurred on November 10, 2018, and November 14, 2019.

Hatch date and growth rate of larval rainbow smelt

The age of larvae sampled ranged from 0 to 10 days in 2018 and from 0 to 15 days in 2019. The ageing precision between both independent readings was 3.6%; of the 200 larval otoliths analyzed, 19 (9.5%) were removed from further analysis due to discrepancy in age determination. The back-calculated hatch dates varied between years with the earliest hatch dates being June 26 and June 22 in 2018 and 2019, respectively, while the latest observed hatch date was July 11 for both years. Estimated spawning periods ran from June 10 to June 28, 2018, and from June 3 to June 27, 2019, based on an estimated embryonic period of 156.5 degree days (Gagnon, 2005). Using the temporally interpolated SST values, temperature at first hatch was estimated at 7.3°C in 2018 and 8.9°C in 2019. Using ice concentration data and back-calculated hatch dates, the growth season was estimated to vary from June 26 to November 10 in 2018 and from June 22 to November 14 in 2019.

Standard length (*SL*) of larval smelt ranged from 5.15 mm to 11.20 mm in 2018 and from 4.94 mm to 13.10 mm in 2019. Average otolith increment width was 2.05 (±0.175) µm, while the average hatch mark diameter was 9.56 (±1.05) µm. Average length of larval age-0 fish was 5.65 (±0.41) mm in 2018 and 5.70 (±0.44) mm in 2019. The observed growth rate of larval smelt averaged 0.53 mm day^{-1} (linear regression, $R^2 = 0.82$), while the back-calculated growth rates for individual larvae ranged from 0.32 mm day^{-1} to 0.89 mm day^{-1} with a mean growth rate of 0.59 (±0.13) mm day^{-1} for data pooled from both seasons ($n = 181$). The estimated length at hatch (y-intercept) was 6.21 mm from the observed growth rates, and the mean back-calculated length at hatch was 5.87 (±0.16) mm (**Figure 2**).

Growth rate and maturation of adult rainbow smelt in Lake Melville

A total of 201 adult smelt were collected during the recreational and subsistence fishery and an additional 66 during gill net surveys in 2019 and 2020. There was a difference in size classes retained from the two different sampling methods. Fish caught during the recreational and subsistence fishery were larger with an average (±SD) length of 171 (±18) mm, while fish retained from the net surveys had an average length of 136 (±38) mm. Lengths ranged from 110 mm to 221 mm and 58 mm to 220 mm for these methods, respectively. The age of adult smelt ranged from 1 year to 8 years, and, at 1.2%, the ageing precision between independent readings was high (Campana, 1990). A linear relationship between fish length and otolith length was observed over the size distribution (Figure S1) and can be used for growth back-calculation. The overall fitted linear regression ($p < 0.001$, $R^2 = 0.88$) was:

$$FL = 0.94 + 0.0327(O)$$

where FL is fork length (mm) and O is otolith length (µm).

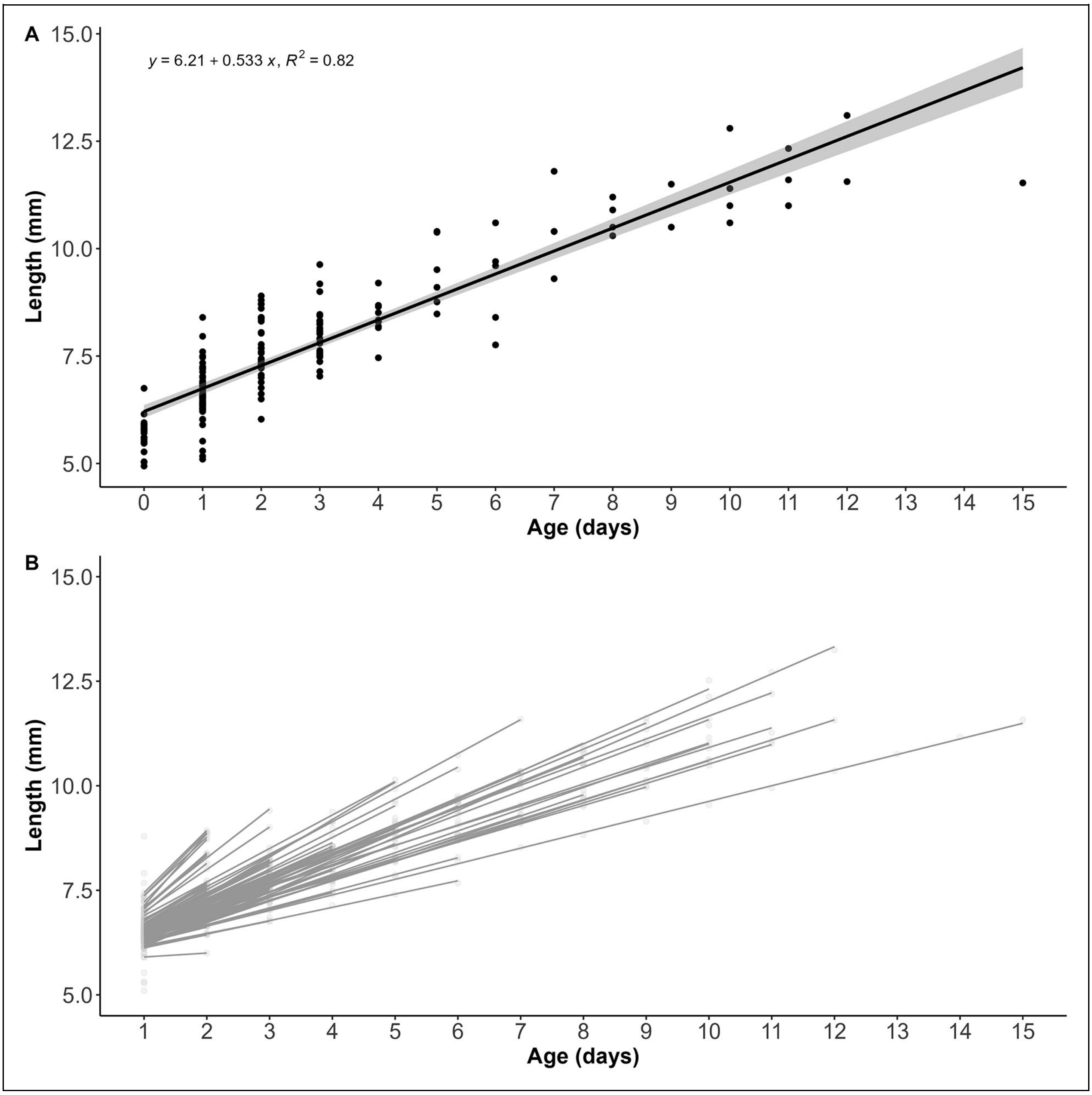

Figure 2. Growth rates of larval Lake Melville rainbow smelt. (A) Observed growth rates and (B) back-calculated growth rates for larval rainbow smelt caught in Lake Melville, Labrador, in 2018 and 2019. Gray shading (A) represents the 95% confidence interval.

Visual inspection of VBGF plots revealed clear sex differences in length-at-age and growth rate (**Figure 3**). Adult female length was larger than that of adult males for each age cohort after A_{50}. Thus, VBGF curves varied between males and females, with female $L_\infty = 269.1$, $K = 0.182$, and $t_0 = 1.569$, and male $L_\infty = 203.8$, $K = 0.347$, and $t_0 = 0.702$. Maturation also varied between sexes, with females maturing later and at a larger size than males. Female age of maturity (A_{50}) was estimated at 4.2 years, with a corresponding length of maturity (L_{50}) of 166.7 mm. Male A_{50} and L_{50} were lower, reaching values of 3.6 years and 151.2 mm, respectively (**Figure 4**).

Comparison of adult growth across geographic range

Mean length-at-age was strongly influenced by an increase in mean DD*i* for both sexes (p-values: <0.001). Mean length-at-age was lower in populations residing in colder climates at higher latitudes (**Figure 5**; **Table 2**). The GAMM that best explained the variation in length was:

$$TL_i \sim \text{meanDD}_i * Sex_i + s(Age_i) + (1|Location_i)$$

where TL_i represents the total length of individual *i*, mean DD_i is the number of days >5°C per annum averaged over a 5-year period (Chezik et al., 2014) for the location where

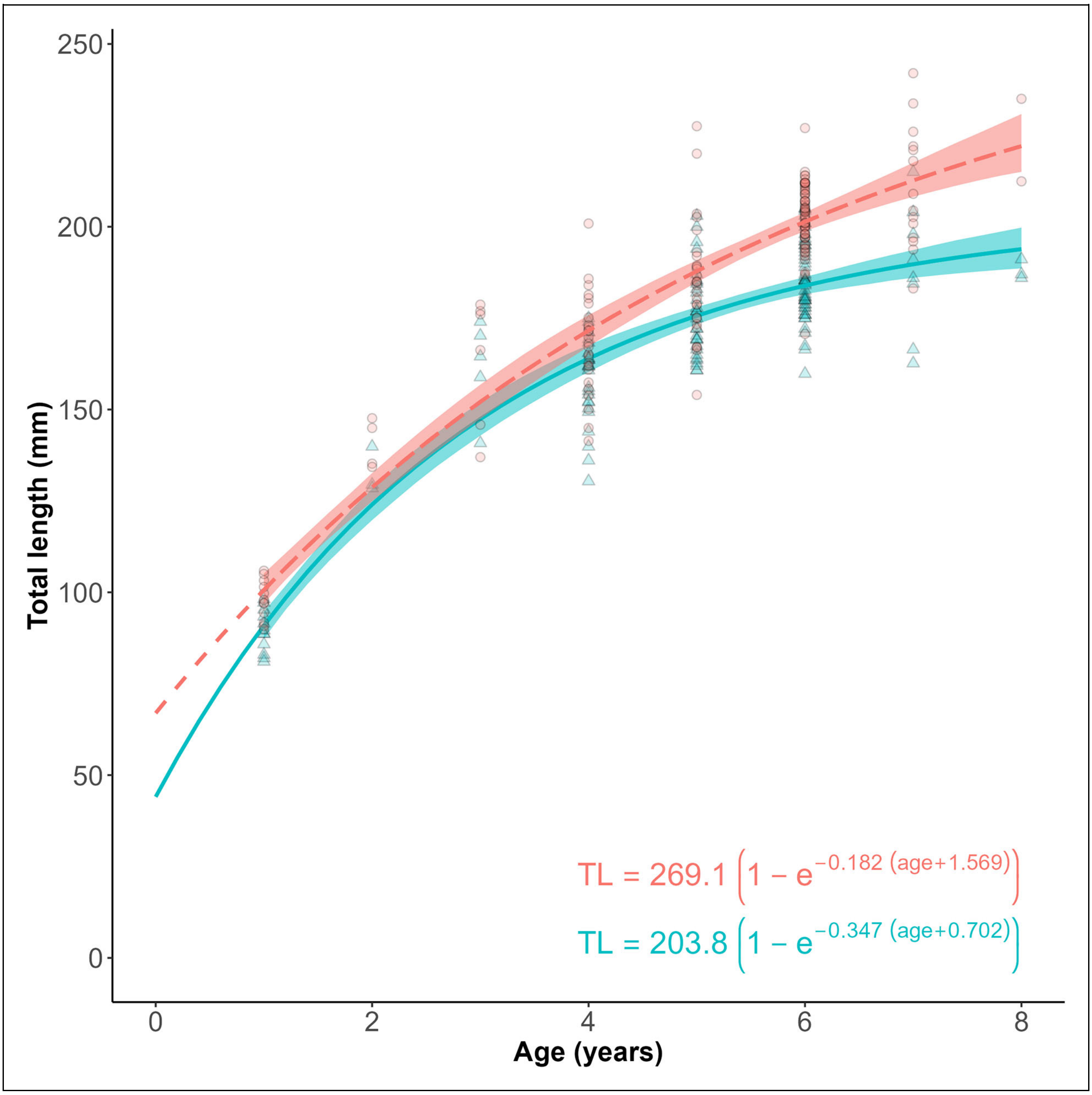

Figure 3. Von Bertalanffy growth curves for Lake Melville rainbow smelt. Blue triangles represent individual male rainbow smelt; solid blue lines represent the male growth curve. Red circles represent individual females; dashed red lines represent the female growth curve for rainbow smelt caught within the Lake Melville System, Labrador, during 2019 and 2020.

individual *i* was sampled, and *Sex* is a categorical variable (male or female). Latitude correlated strongly with mean DD*i* (correlation coefficient = −0.927) and was removed from the model.

Discussion

Temperature-size rule in rainbow smelt populations

The TSR states that individuals inhabiting low temperature environments grow slower yet attain a larger length-at-age of maturity than populations in warmer habitats (Aguilar-Alberola and Mesquita-Joanes, 2014). When comparing 10 adult rainbow smelt populations ranging from 42.00°N to 53.54°N, their mean length-at-age generally decreased with a decrease in mean DD*i* and an increase in latitude (**Figure 5**; **Table 1**). Lake Melville rainbow smelt also matured at total lengths of 151 mm and 166 mm for males and females, respectively, while in more southern populations (i.e., Massachusetts), individuals matured at total lengths of approximately 126 mm for both sexes combined (Chase et al., 2019). Lake Melville rainbow smelt matured after the age of 3 years for males and 4 years for females, while in more southern populations the earliest reported age for maturation was 1 year (Enterline et al., 2012; O'Malley et al., 2017; Chase et al., 2019). Lake Melville rainbow smelt also lived longer, reaching a maximum age of 8 years, while in more southern regions, the observed maximum ages ranged from 5 years to 6 years. Because (i) mean length-at-age of adult rainbow smelt

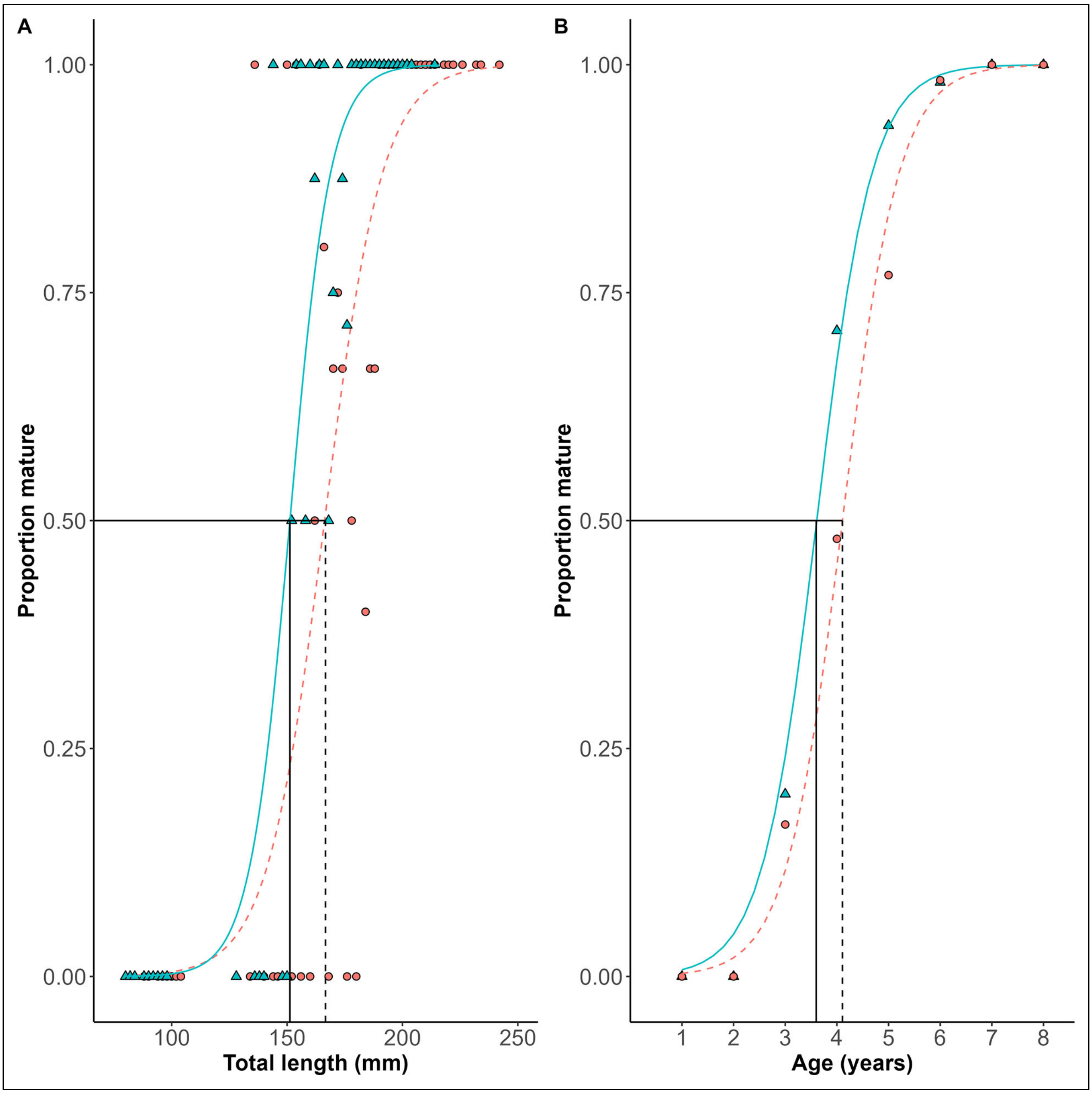

Figure 4. Maturity ogives for adult male and female Lake Melville rainbow smelt. (A) Length of maturity and (B) age of maturity for adult Lake Melville rainbow smelt. Solid blue lines represent maturity curves; blue triangles represent proportion mature at each length and age category for males. Dashed red lines represent maturity curves; red circles represent proportion mature for each length and age category for females. Solid black solid represent the age and length at 50% maturity for males; dashed black lines represent the age and length at 50% maturity for females.

decreased with DD*i* and with an increase in latitude (**Figure 5**) and (ii) length-at-age of maturity was larger in Lake Melville than in southern populations, we conclude that rainbow smelt populations adhere to the TSR across their observed latitudinal range.

Within the Lake Melville population, sexual size dimorphism was observed with females not only maturing later and at a greater size than males (**Figure 3**), but also growing larger than males post-age of maturity (**Figure 4**). This phenomenon has also been reported in other populations, for example, New Brunswick (McKenzie, 1958) and Massachusetts (Chase et al., 2019), and is likely selected for due to the strong correlation between female size and fecundity, egg size, and clutch size (Han and Fu, 2013). Rainbow smelt face a trade-off where smelt that mature later may realize a lower lifetime reproductive potential (i.e., fewer potential reproductive events), but are less exposed to mortality than individuals that mature earlier (Chase et al., 2019). However, a study of over 100 species from varying latitudes suggests that the relationship between fecundity and mass (i.e., reproductive scaling) increases with latitude (Alvarez-Noriega et al., 2023). Therefore, individuals in more northern regions, where there is less risk of natural mortality (i.e., mortality excluding fishing;

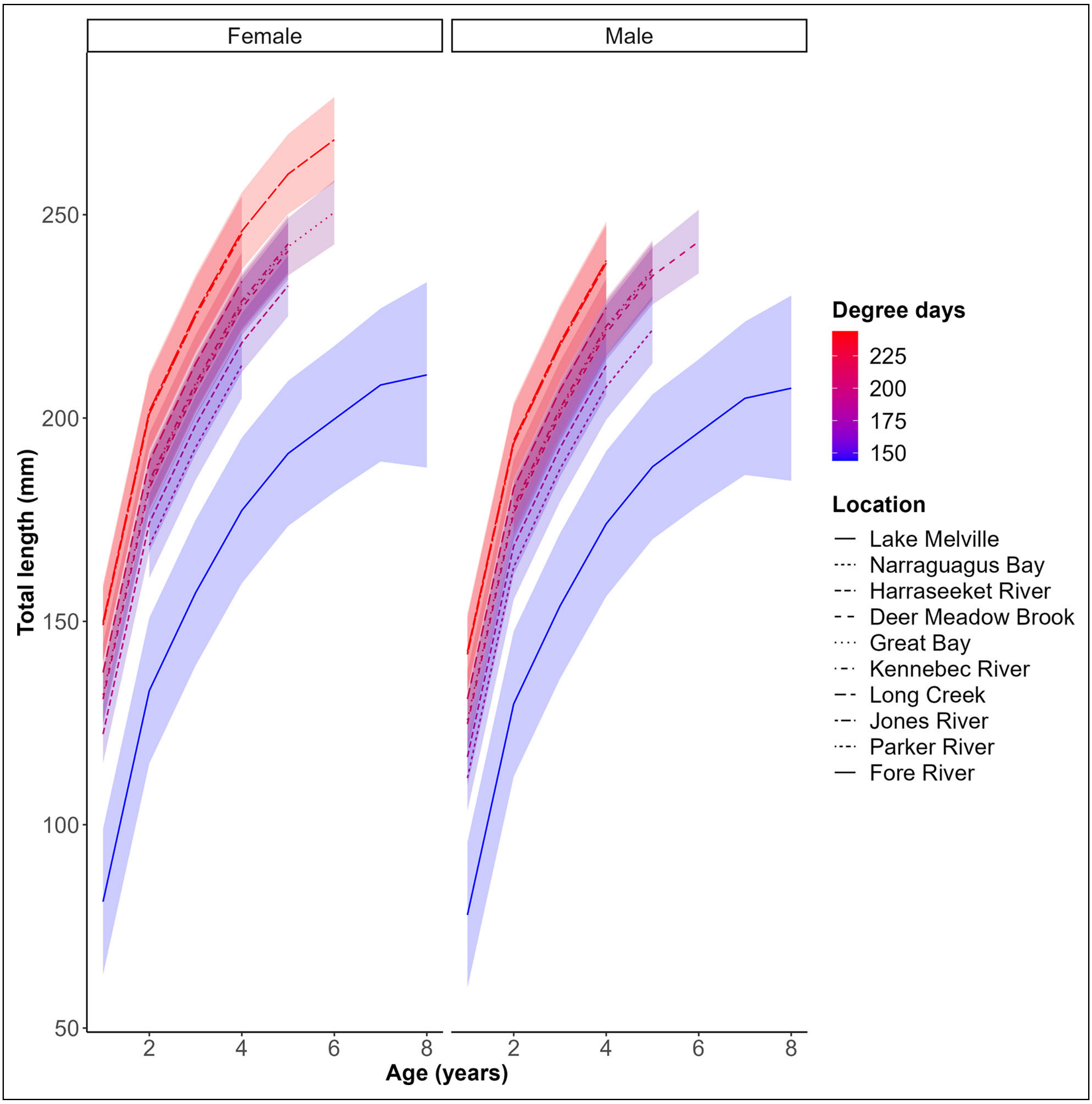

Figure 5. Mean length-at-age for rainbow smelt from varying thermal regimes. Mean length-at-age for both sexes, where the color gradient represents number of degree days, shaded areas represent the 95% confidence interval, and line type represents the sampling region. Locations are ordered by increasing number of degree days from top to bottom. See **Figure 1** for map locations.

Table 2. Results from the generalized additive mixed model (GAMM)

Parameter	Coefficient	SE	95% CI	t/F	df	df (error)	p-Value
Intercept	26.59	25.76	−23.91, 77.08	1.03	na[a]	10,934	0.302
meanDD[b]	0.69	0.12	0.45, 0.92	5.8	na	10,934	<0.001
Sex	2.43	4.26	−5.91, 10.78	0.57	na	10,934	0.568
meanDD*Sex	−0.04	0.02	−0.08, 0.00	−2.09	na	10,934	0.036
s (Age)	na	na	na	5045	5.44	na	<0.001

[a] Not applicable (na).

[b] Mean number of days with temperatures greater than 5°C over 5 years (i.e., growing season).

Alvarez-Noriega et al., 2023), delay maturation to a time when they can produce more offspring and subsequently produce proportionally more than similar-sized individuals in more southern regions (Alvarez-Noriega et al., 2023). Therefore, fish that live longer can mature later and compensate for reproductive output.

Ecology of early life stages of rainbow smelt at the northern limits of their range

Rainbow smelt align their reproductive cycle with seasonal change in temperature (Rupp, 1959; Ayer et al., 2005; O'Brien et al., 2012; Chase et al., 2019), and they time their spawning runs with spring ice breakup when temperatures reach 3–5°C (Rupp, 1959; O'Brien et al., 2012). First hatch occurs 10–32 days (Ayer et al., 2005; Simonin et al., 2016), or an average of 156.5 degree days (Gagnon, 2005), after spawning. The spawning period for Lake Melville smelt thus began in early June in both 2018 and 2019, later than in more southern regions where rainbow smelt spawning typically begins in early March (Chase et al., 2019). This later spawning period subsequently led to later hatch dates within the Lake Melville population and a shorter larval growth season. Lake Melville rainbow smelt began hatching in late June, one month later than the reported dates for a more southern anadromous population (Sirois and Dodson, 2000). In the St. Lawrence Estuary, the hatching period ran through May (Sirois and Dodson, 2000). Our findings, however, were comparable to hatching dates reported in Newfoundland populations, where the water is colder (mean spring estuarine temperature of −2.7°C) and seasonal sea ice is present. For example, anadromous rainbow smelt in the Salmonier River (47°N) hatch from early June to late July (Bradbury et al., 2006). Later spawning and hatching periods in Lake Melville coincide with the ice breakup and warming of surface waters, which did not occur until late May. These results are also consistent with an incubation period strongly correlated with temperature (Gagnon, 2005; Simonin et al., 2016).

In contrast to adults, rainbow smelt larvae from the Lake Melville population exhibited a higher growth rate than the population in the St. Lawrence Estuary, the other anadromous population with available data. Larvae had an observed growth rate of 0.53 mm day^{-1} and a mean back-calculated growth rate of 0.59 mm day^{-1}, while within the St. Lawrence Estuary (48°N), where the growth season is approximately 2 months longer (Galbraith et al., 2012), observed growth rates ranged from 0.13 mm day^{-1} to 0.33 mm day^{-1} and back-calculated growth rates ranged from 0.16 mm day^{-1} to 0.26 mm d^{-1} (Fortier and Legget, 1982; Leprise and Dodson, 1989; Sirois and Dodson, 2000).

The counter-gradient growth hypothesis could explain the faster growth rates of rainbow smelt within Lake Melville. This hypothesis stipulates that fish larvae in cold habitats are adapted for rapid increases in growth at warm temperatures during the brief growing seasons found in these regions (Conover and Present, 1990; Conover et al., 1997). With hatching beginning in June–July and the onset of ice formation in mid-November, Lake Melville smelt larvae have a shorter window to exceed the critical size threshold for winter survival (approximately 141 days post-hatch; Sirois and Dodson, 2000; Arendt and Reznick, 2005). The shorter growth season within Lake Melville, coupled with improved overwinter survival for larger individuals, selects for faster growth during the larval stage (Conover and Present, 1990; Conover et al., 1997). Freshwater populations of rainbow smelt have similar growth patterns. For instance, Bérubé (2005) observed an inverse relationship between larval growth and thermal gradients of latitude for populations within Quebec, Canada, with northern populations realizing an increase in growth up to 0.19 mm day^{-1} compared to more southern populations. Future studies should test if the counter-gradient growth hypothesis holds for larval anadromous rainbow smelt in other populations than those presented here.

Potential effects from climate and anthropogenic change

The Lake Melville region has been experiencing a warm weather anomaly since the 1990s (Finnis and Bell, 2015; Kamula et al., 2020), and temperatures are expected to continue to rise. We demonstrate that the rainbow smelt population of Lake Melville follows the TSR. If this variation in growth across their range is a plastic response to thermal gradients, populations at the northern limits could benefit from a longer and warmer growth season. Similar to other fish species, warmer temperatures would likely increase adult growth rates and result in a decrease in age and length at maturity and overall longevity (Kuparinen et al., 2011; Trip et al., 2014). Younger and faster growing mature rainbow smelt would increase their lifetime reproductive potential (Chase et al., 2019). Furthermore, rainbow smelt are well adapted to a variety of temperature regimes, possessing antifreeze proteins for survival in cold climates (Driedzic and Short, 2007; Hanson and Courtenay, 2020), while also being capable of surviving at temperatures up to 20°C (Ayer et al., 2005). The temperatures observed during this study were within the preferred temperature range for smelt, as the SST range for the growing season was 7–12°C. Conditions can thus warm up and remain within the environmental envelope occupied by the species in this region. However, whether Lake Melville populations respond positively will depend on complex ecological processes (e.g., food availability or phenology) and whether these populations are locally adapted to colder water conditions. These complexities will be difficult to disentangle without targeted experimentation (e.g., common garden experiments; Kuparinen et al., 2011).

In addition to increasing temperatures, inflow to the Lake Melville System has been altered via the construction of the Upper Churchill Hydroelectric Development in the mid-1970s and the Muskrat Falls hydroelectric facility in the 2020s (Durkalec et al., 2016). Operation of these dams will further modify the spatial and temporal thermal regime within Upper Lake Melville. For example, on the North Tyne River in Wales (UK), water retained in the Kiedler Reservoir during the spring and summer was 1–3°C colder than downstream rivers, while water retained in the fall and winter was 1–4°C warmer than downstream rivers (Archer, 2008). Water density is highest near 4°C, leading temperature-stratified reservoirs to flip from warmest water on bottom in the winter to coldest water on bottom in summer (Heggenes et al., 2021). Large-scale hydroelectric facilities generally draw water from this bottom layer to feed directly to the power plant (Heggenes et al., 2021). Thus, water released from hydroelectric facilities in the spring will cause a decrease in downstream temperature while water released in the fall will lead to an increase in downstream temperature (i.e., lower summer maxima and higher winter minima; Archer, 2008; Clarke et al., 2008; Casado et al., 2013). Cold water inflow in the spring may offset the impacts of temperature increase due to climate change, mitigating some of the impacts of increased temperature on the growing season, whereas warmer inflow in the fall, compounded by warming atmospheric temperatures, are likely to extend the growing season by delaying ice formation and seasonal cooling of downstream waters (McCarthy, 2013; Heggenes et al., 2021). The impacts on Lake Melville rainbow smelt due to compounding thermal changes could include alteration in timing of life history processes due to cold water inflow in the spring, and physiological changes such as increased growth and earlier maturation due to a warmer and longer growing seasons (Li et al., 2016). While the variation in rainbow smelt life history and growth across its geographic range suggests that they can tolerate a broad range of water temperatures, predicting the future of the species at the northernmost limit of its range will require understanding changes in the whole marine ecosystem.

Data accessibility statement

All data collected during this study are available on the Polar Data Catalogue under CCIN 13159: Zooplankton and ichthyoplankton samples from Lake Melville, Labrador. The dataset can be accessed at https://www.polardata.ca/.

Maine data are available by request from the Maine Department of Marine Resources, Bureau of Sea Run Fisheries. For more information see https://www.maine.gov/dmr/science/species-information/smelt.

Massachusetts data are available by request from the Massachusetts Division of Marine Fisheries. For more information see https://www.mass.gov/info-details/marine-fisheries-technical-reports?_gl=1*izf433*_ga*ODgyNDMxODYxLjE3MzEzNDY1ODg.*_ga_MCLPEGW7WM*MTczMTM0NjYwNS4xLjEuMTczMTM0NzcwMy4wLjAuMA.

New Hampshire data are available by request from the New Hampshire Fish and Game Department. For more information see https://www.wildlife.nh.gov/saltwater-fisheries-new-hampshire/marine-fisheries-research-surveys-and-reports.

Environmental data for Lake Melville are accessible through the Government of Canada's past weather and climate data resource online database: https://climate.weather.gc.ca/historical_data/search_historic_data_e.html.

Environmental data for stations within the United States are accessible through the National Centers for Environmental Information (NCEI) Climate Data Online (CDO): https://www.ncei.noaa.gov/cdo-web/datasets.

Supplemental files

The supplemental files for this article can be found as follows:

Figure S1. Linear relationship between fish length and otolith length for rainbow smelt caught in Goose Bay and Lake Melville.

Table S1. General information collected for each station within Goose Bay and Lake Melville, Labrador.

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Competing interests

The authors declare no competing interests.

Author contributions

Contributed to conception and design: JS, MC, MG.
Contributed to acquisition of data: JS, TS, MG, MC, JM, CE, BCC.
Contributed to analysis and interpretation of data: JS, MG, PS, DC, CE.
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Drafted and/or revised the article: All authors.
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