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RESEARCH ARTICLE

Shrinking body size and climate warming: Many freshwater salmonids do not follow the rule

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Abstract

Declining body size is believed to be a universal response to climate warming and has been documented in numerous studies of marine and anadromous fishes. The Salmonidae are a family of coldwater fishes considered to be among the most sensitive species to climate warming; however, whether the shrinking body size response holds true for freshwater salmonids has yet to be examined at a broad spatial scale. We compiled observations of individual fish lengths from long-term surveys across the Northern Hemisphere for 12 species of freshwater salmonids and used linear mixed models to test for spatial and temporal trends in body size (fish length) spanning recent decades. Contrary to expectations, we found a significant increase in length overall but with high variability in trends among populations and species. More than two-thirds of the populations we examined increased in length over time. Secondary regressions revealed larger-bodied populations are experiencing greater increases in length than smaller-bodied populations. Mean water temperature was weakly predictive of changes in body length but overall minimal influences of environmental variables suggest that it is difficult to predict an organism's response to changing temperatures by solely looking at climatic factors. Our results suggest that declining body size is not universal, and the response of fishes to climate change may be largely influenced by local factors. It is important to know that we cannot assume the effects of climate change are predictable and negative at a large spatial scale.

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KEYWORDS
body size, climate change, *Coregonus*, *Prosopium*, *Salvelinus*, somatic growth, *Thymallus*

1 | INTRODUCTION

Body size is an important organismal trait that plays a crucial role in reproductive fitness, physiology, and ecological interactions, driving the success and survival of species (Daufresne et al., 2009; Peters, 1983). Body size trends (i.e. increases or decreases in mean body size of individuals in a population over time) resulting from changing growth rates, shifting population age structure, or a combination of the two can influence population, community, and ecosystem level dynamics (Oke et al., 2020; Peters, 1983; Werner & Gilliam, 1984). Within a species, smaller body sizes lead to reduced fecundity and survival (Barneche et al., 2018; McPhee et al., 2016), which can alter competitive interactions and induce trophic cascades (Ahti et al., 2020; Delong et al., 2015; McGill et al., 2006). Large reductions in body size can result in populations that are less resilient to disturbances and more susceptible to collapse as the impacts of body size changes extend from individuals to population stability and ecosystem functioning (Clements & Ozgul, 2016; Su et al., 2020).

Due to the significance of body size across spatial and temporal scales, extensive research has been conducted to identify factors contributing to body size trends, with a particular focus on climate and warming (Baudron et al., 2014; Cline et al., 2019; van Rijn et al., 2017). Temperature directly influences biochemical reactions, such as metabolism, in cold-blooded organisms which ultimately affects body size through energy allocation to fitness-enhancing processes such as growth, activity, migration, and reproduction (Brown et al., 2004; Gillooly et al., 2001; Ohlberger, 2013; Peters, 1983). Thus, the response of growth to temperature has become well-established through the temperature-size rule (TSR), which predicts organisms in warmer temperatures will experience faster growth as juveniles but reach maturity at a smaller size (Atkinson, 1994). As climate change has led to rising global temperatures, the applicability of the TSR to wild populations has largely been supported by decreases in adult body size (Baudron et al., 2014; Daufresne et al., 2009; van Rijn et al., 2017), so much so that a reduction in body size has been proposed as a universal response to warming (Daufresne et al., 2009; Gardner et al., 2011; Sheridan & Bickford, 2011).

There are some exceptions to the universal expectation of shrinking body size with warming, particularly in fish (Audzijonyte et al., 2020; Jeffrey et al., 2017). For example, marine species that were larger at the warmer edge of their geographical distribution were more likely to become larger with warming (Audzijonyte et al., 2020), and body size trends of Pacific salmon (*Oncorhynchus* spp.) in Canadian waters, which showed marked declines throughout the 1950s and 1960s, have since halted or reversed

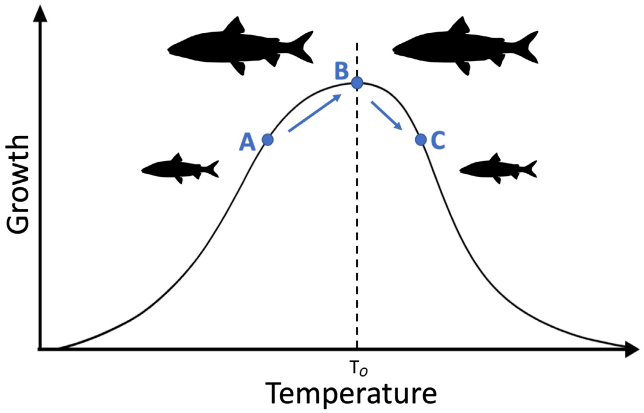

FIGURE 1 The dome-shaped relationship between temperature and growth, modified from Ohlberger (2013). Populations transitioning from temperature A to temperature B are expected to experience increases in growth while populations transitioning from temperature B to temperature C are expected to experience decreases in growth. T_O represents the optimal growth temperature. Image by Ellen Edmonson and Hugh Chrisp (illustration) and Timothy J. Bartley (silhouette) via PhyloPic (CC BY-SA 3.0).

(Jeffrey et al., 2017) even as the climate has continued to warm. A thermal growth curve is often used to explain these patterns by representing a unimodal relationship between growth and temperature within ectotherms (Figure 1), consisting of relatively linear increases in growth over a mid-range of temperatures before reaching a thermal optimum, beyond which growth decreases rapidly (Neuheimer et al., 2011; Ohlberger, 2013). Based on this relationship, populations that are below their thermal optimum are expected to experience faster growth as temperatures increase (Figure 1; A to B), and populations that are at or past their thermal optimum are expected to experience slower growth as temperatures increase (Figure 1; B to C) assuming no other size-selective pressures on body size are present. Additionally, if temperatures increase above the thermal optima, increased food availability and consumption can potentially counteract decreases in growth. However, such counteractions require ample food availability and consumption to support the increased metabolic costs accompanying increasing temperatures (Brown et al., 2004; Pennock et al., 2021; but see Wootton et al., 2022). Therefore, changes in food availability may cause the growth response of fish in wild populations to diverge from expectations based on laboratory studies.

Freshwater salmonids are a group of fishes whose growth is especially likely to be influenced by a warming climate. Salmonids, with their native distributions in the mid to high latitudes of the northern hemisphere, are especially vulnerable to warming

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because of their cold thermal ranges (Sauter et al., 2001). Northern latitudes are also experiencing faster rates of warming than other regions of the globe (Parmesan, 2006; Serreze & Barry, 2011) and thus salmonid populations may already be exposed to thermal stress. The effects of warming are further exacerbated in lake ecosystems, where spatially isolated populations may not be able to undergo geographic range shifts in response to changing conditions (Heino et al., 2009; Lynch et al., 2016). The combination of rapid rates of warming coupled with a narrow thermal range puts northern salmonid populations at high risk of climate-induced changes in growth.

Here, we considered evidence of climate-induced trends in body size of 12 species of salmonids to better understand the commonalities of change across taxa and broad latitudinal ranges. The objectives of our study were twofold: (1) to identify population and species-specific trends in body size of lacustrine populations of freshwater salmonids and (2) to quantify the importance of environmental factors in driving observed trends. By quantifying patterns in body size across populations spanning northern latitudes, we were able to examine the influence of climate in relation to geographic range position to test how body size changes with range position and the local rate of climate warming. We hypothesized that (1) populations experiencing greater warming would have greater decreases in body size over time and (2) populations near the southern (warmer) edge of their species' range would have more negative body size changes due to temperatures already exceeding thermal optima. We also tested for a relationship between lake productivity, climate, and body size to determine if salmonids in highly productive lakes, with presumably higher food availability and thus the potential to counteract the effects of warming, would show smaller reductions or even increases in body size.

2 | METHODS

The methodology of this study consisted of a two-step approach. First, we determined changes in body size (i.e., body length) of salmonids over time using linear mixed models (LMMs). We then attempted to correlate changes in body length with biological and environmental variables through secondary regression analyses.

2.1 | Data

A total of 531,653 observations of length measurements were compiled from 208 lakes in the Northern Hemisphere (Budy et al., 2022; Magnuson et al., 2022; Figures 2 and 3 Step #1). To identify datasets and potential contacts, we searched the published literature and used snowball sampling in which collaborators who provided data were asked to recommend other researchers who may be able to provide additional datasets. State and provincial natural resource agencies and academic research sampling efforts provided much of the data, which date back to the 1950s and spanned a range of sampling gear types (Table 1, additional details in Tables S1 and S2). The final dataset included 770 populations (unique lake/species/gear combinations) across 12 species of salmonids [vendace (*Coregonus albula*, Linnaeus, 1758); cisco (*Coregonus artedi*, Lesueur, 1818); lake whitefish (*Coregonus clupeaformis*, Mitchill, 1818); common

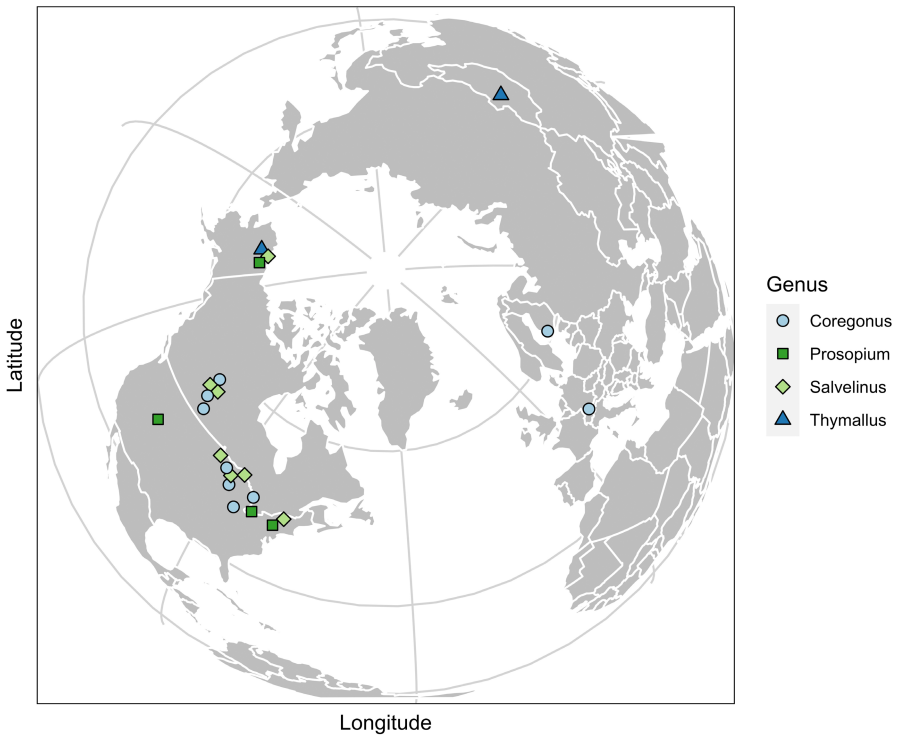

FIGURE 2 Map of study sites by genus including *Coregonus* (circles), *Proposium* (squares), *Salvelinus* (diamonds), and *Thymallus* (triangles).

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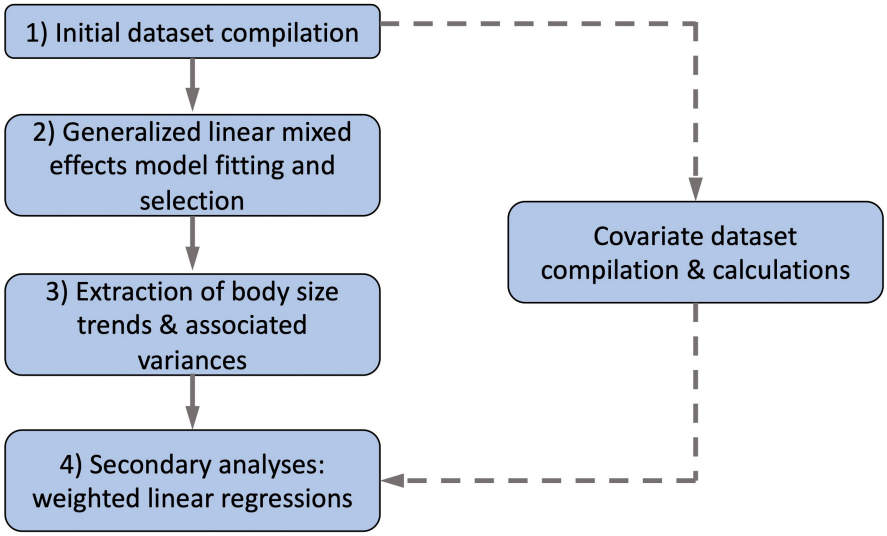

FIGURE 3 A flowchart describing the study methodology.

TABLE 1 Data compiled from long-term surveys.

Species	Scientific name	Number of lakes	Number of observations	Time period
Arctic Char	*Salvelinus alpinus*	5	2546	1991–2019
Arctic Grayling	*Thymallus arcticus*	3	233	1987–2019
Coregonus wartmanni	*Coregonus wartmanni*	1	27,240	1954–2020
Bonneville Whitefish	*Prosopium spilonotus*	1	5091	1990–2020
Brook Trout	*Salvelinus fontinalis*	4	25,896	1982–2020
Cisco	*Coregonus artedi*	161	142,423	1959–2020
Common Whitefish	*Coregonus lavaretus*	1	9282	1983–2019
Hövsgöl Grayling	*Thymallus nigrescens*	1	846	2009–2014
Lake Trout	*Salvelinus namaycush*	26	167,299	1956–2020
Lake Whitefish	*Coregonus clupeaformis*	38	139,797	1970–2020
Round Whitefish	*Prosopium cylindraceum*	3	2851	1972–2020
Vendace	*Coregonus albula*	1	8149	1989–2019

Note: Number of observations refers to the number of length measurements in the dataset for each species. Time period refers to the overall timespan available for each species, not necessarily the years of data available for each individual lake.

whitefish (*Coregonus lavaretus*, Linnaeus, 1758); *Coregonus wartmanni* (*Coregonus wartmanni*, Bloch, 1784); round whitefish (*Prosopium cylindraceum*, Pennant, 1784); Bonneville whitefish (*Prosopium spilonotus*, Snyder, 1919); Arctic char (*Salvelinus alpinus*, Linnaeus, 1758); lake trout (*Salvelinus namaycush*, Walbaum, 1792); brook trout (*Salvelinus fontinalis*, Mitchill, 1814); Arctic grayling (*Thymallus arcticus*, Pallas, 1776); Hövsgöl grayling (*Thymallus nigrescens*, Dorogostaisky, 1923)].

The initial dataset was filtered using several criteria to remove extremely small datasets ($n < 10$ observations), which might have limited our ability to estimate lake-specific trends, and lakes where fish populations had been intensively manipulated by researchers or fishery managers. We applied the following minimum criteria for inclusion in our analysis: survey data were required to include at least a total of 10 observations (individual fish) per gear type over a minimum of 5 years of sampling. Gaps in survey time series were permissible as long as the survey had included data from at least 5 years of sampling. Lakes were excluded if they had been experimentally manipulated, subject to removal efforts, or if any of the target species of salmonids had been significantly stocked (>20% of total recruitment) during the period of survey coverage. Only surveys with consistent gears and sampling protocols from year to year were used, and gears were considered to be survey-specific; that is, gears were not combined across surveys due to potential procedural differences. Because the survey methods were not directly comparable, individual trends for each survey were estimated and these trends, not absolute body size, were compared across surveys.

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2.2 | Initial LMM fitting and selection

We used the *lme4* package (Bates et al., 2015; R Core Team, 2020) to fit LMMs to test for body length trends over time (Figure 3 Step #2). A mixed-effects model was deemed the best approach because it can quantify the overall effect of year on body length while accounting for different gear types and any variation that may exist across lakes and species. We considered linear models appropriate given our interests in trends, rather than year-to-year variation. Additionally, no obvious nonlinearities were evident in the relationship between body length and year across populations in an initial examination of the data, justifying the assumption of a linear relationship. In the models explored, our response variable was length. Gear, lake, and species were included as categorical covariates. To facilitate model fitting, we centered and standardized years and lengths to a mean of zero and a standard deviation of one.

To identify potential model structures, we fit LMMs with and without year as a fixed covariate, and then used Akaike's information criterion (AIC; Akaike, 1974) to fit a set of plausible models (Table 2, additional details in Table S3; Burnham & Anderson, 2004). We treated lake and species as separate random effects to account for environmental and taxa-specific factors, which allowed us to investigate body length trends across populations. We then added gear as either a fixed or random effect to potential model options. The effect of year on length may vary depending on the gear used, making it plausible to include gear in the fixed effect structure. However, because there were many different gear types and these gears represent a subset of all potential gears that have been used, it was also plausible to treat gear as a random effect to reduce model degrees of freedom and facilitate model fitting. Additionally, we considered model options that nested gear within the lake random effect because many of the gears were lake specific. The full list of models tested can be found in Table S3.

We used hierarchical model selection to determine if the effect of year on body length differed among species (Gelman & Hill, 2007). Because the models included species as a covariate, we compared the full models that had an interaction between species and year (i.e., random slopes and intercepts for year for each species) to reduced models which did not include an interaction term (i.e., random intercept for each species; Table 2). The random intercepts for year for each species included in both models allowed the species to have different body lengths; the random slope for year for each species in the full models allowed the rate at which body length changes to differ for each species. We used AIC for model comparison to identify the most parsimonious model (lowest AIC) in explaining body length change over time across datasets. To examine the influence of very short time series, we also reran the LMM with populations that spanned a minimum of 10 years. This reduced the number of populations from 770 to 719 and excluded Hövsgöl grayling from the dataset.

2.3 | LMM estimate extraction

For secondary analyses testing for potential drivers of body size change, we obtained estimates of the effect of year on body length for each fish population (species/lake/gear combination) from the LMM selected above, along with their associated conditional variances, using best linear unbiased predictors (Figure 3 Step #3; Hadfield et al., 2010). To determine the conditional variances for each estimate of the effect of year on body length, we extracted the variance associated with the fixed effect of year on length, as well as conditional variances associated with each level of each random effect (Bates et al., 2015). For each overall slope (i.e., every unique species, lake, and gear combination) we calculated the total conditional variance by summing the variances for each level of each effect.

TABLE 2 Description of the models and their parameters, along with AIC, marginal R^2, and conditional R^2 values.

Model	AIC	ΔAIC	Marginal R^2	Conditional R^2
Year + (Year|Species) + (Year|Lake/Gear)	712697.6	0	.0043	.6891
Year + (1|Species) + (Year|Lake/Gear)	712796.9	99.3	.0053	.6888
Year + (Year|Species) + (Year|Lake) + (Year|Gear)	715874.5	3176.9	.0051	.7088
Year + (1|Species) + (Year|Lake) + (Year|Gear)	715968.2	3270.6	.0080	.7094
Year * Gear + (Year|Species) + (Year|Lake)	715994.5	3296.9	.4028	.6887
Year * Gear + (1|Species) + (Year|Lake)	716087.0	3389.4	.4056	.6887
⋮	⋮	⋮	⋮	⋮
1 + (1|Species) + (1|Lake/Gear)	724918.8	12221.2	0	.6667
1 + (1|Species) + (1|Lake) + (1|Gear)	727435.5	14737.7	0	.6397
Gear + (1|Species) + (1|Lake)	727458.8	14761.2	.4336	.6713

Note: Values for ΔAIC are the difference between that model's AIC and that of the best fit model. (*X*|*Y*) notation represents varying slopes and intercepts for the effect of *X* on fish body length for each *Y* and (1|*Y*) notation represents varying intercepts for fish body length for each *Y*. The dots indicate additional models that were tested but are not shown for brevity (additional details in Table S3).

Abbreviation: AIC, Akaike's information criterion.

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2.4 | Drivers of fish body size trends

The potential drivers of body size we investigated included six covariates: two metrics of average body size (one at the species level and one at the population level), range position, change in water temperature over the survey period, mean water temperature, and mean productivity.

To test for potential differences in responses among species that varied in average body size, we used asymptotic length (L_∞) at the species level from von Bertalanffy growth models. To determine L_∞ values for each species, we averaged all L_∞ total length values listed in FishBase (Froese & Pauly, 2022) that were marked as not questionable and not from captive populations. If there was no information for the type of length measurement or whether it was from a captive population or not, we excluded that L_∞ value from the average calculation. Given the limited number of L_∞ values available on Fishbase for brook trout ($n = 2$), this species was removed from this analysis. To test whether among-population variation in mean body size influenced temporal patterns, we calculated the average body size for each population by taking the mean of the length measurements for each lake, species, and gear combination from our data. Examining relationships between body length trends and average body size determines whether species or populations of a certain size are more sensitive to changing conditions.

We calculated range position, a metric describing the latitude at which a population lies relative to the species' native range, to test whether populations more to the southern (warmer) edge of their range experienced faster body length changes. To determine range position, we used:

$$\mathrm{RP}_{\mathrm{lake},s} = \frac{\mathrm{Lat}_{\mathrm{lake}} - \mathrm{Lat}_{\mathrm{min},s}}{\mathrm{Lat}_{\mathrm{max},s} - \mathrm{Lat}_{\mathrm{min},s}},$$

where $\mathrm{RP}_{\mathrm{lake},s}$ is the range position of species s in a given lake, $\mathrm{Lat}_{\mathrm{lake}}$ is the lake latitude, $\mathrm{Lat}_{\mathrm{min},s}$ is the latitudinal minimum of the range of species s, and $\mathrm{Lat}_{\mathrm{max},s}$ is the latitudinal maximum of the range of species s. We took the latitudinal range of each study species from Fishbase (Froese & Pauly, 2022) and the latitude of the center of each study lake. Range position could vary from zero to one, with values closer to one representing more northerly populations. We treated the three endemic species included in our analysis that are only found in one lake (Hövsgöl grayling, *C. wartmanni*, Bonneville whitefish) as populations occurring in the center of their range, that is, a range position of 0.5.

To quantify the importance of climate in driving body size trends, we compared changes in surface water temperature over the survey period for each lake to the body length trends for the populations within that lake. Doing so allowed us to test whether populations that have experienced the strongest warming trends also showed the greatest body length changes. Although other temperature metrics (e.g., bottom temperature) may better reflect the temperature changes experienced by freshwater salmonids, surface temperature was the metric most widely available. Additionally, since growing seasons can vary from population to population and winter temperatures (i.e., ice duration) can indirectly influence body size through altered ecosystem dynamics (Feiner et al., 2022; Helland et al., 2011), we used mean annual temperatures rather than growing season temperatures. Lakes with a minimum of 5 years of surface temperature data corresponding to at least half of the time period covered by the body length data were included in the analysis; the decision to include or exclude the 53 populations without complete temperature datasets did not meaningfully change the results of the analysis. Daily surface water temperatures during survey periods for lakes in Minnesota, Wisconsin, and Indiana, U.S.A. were available from predictive models (Read et al., 2021). Of the lakes in our study from Minnesota, Wisconsin, and Indiana, only one, Green Lake in Wisconsin, had body length data that extended beyond the scope of the predictive temperature model; for Green Lake, the body length data extended 21 years prior to the modeled temperature data. For the Laurentian Great Lakes, satellite-derived average daily surface temperatures from the National Oceanic and Atmospheric Administration's Great Lakes Surface Environmental Analysis have been calculated since 1995 (NOAA CoastWatch, 2022). Year-round surface temperature data on the Great Lakes (Erie, Huron, Michigan, Ontario, Superior) for earlier years was not available, and so the body length data extended prior to temperature data (by 10, 25, 21, 3, and 24 years respectively). Water temperatures in Lake Constance, Germany have been sampled at least monthly since 1964, 10 years after the body length data began (IGKB, 2020). If surface temperature was measured more than once in a month, we took an average surface temperature value for that month before we calculated the yearly average. Due to missing months of data, 4 years were excluded (1965, 2000, 2009, 2013). For the remaining 36 lakes included in the original model, year-round surface temperature values were not available or accessible.

The change in temperature over the body length survey period for each lake was determined by calculating annual temperature means for each lake from the daily or monthly surface temperature data. We then fit linear regressions using annual mean temperature values to determine the rate of change of temperature for each lake over the years of interest. Using the number of years in each body length survey period and the rate of change of temperature for each lake, we calculated the overall temperature change for each lake. Rather than determining the difference between the mean temperature from the first year of the body length survey period and the last year of the body length survey period, obtaining the change in temperature via the mean rate of change allowed us to account for any potential temperature anomalies.

Similarly, overall mean temperature and mean productivity were included as covariates to characterize how relative temperature and productivity of the lakes related to body length trends. We used the same temperature data collected to calculate temperature change to calculate the overall mean temperature for each lake. We used mean chlorophyll-*a* values as a proxy for primary productivity, assuming the among-lake variation in chlorophyll-*a* values is greater than within-lake variation over the body length survey period (i.e., the trophic states of the majority of the lakes included in the

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analysis remained relatively constant over the period of observation). Satellite-derived summer surface chlorophyll-*a* values for 2017–2020 were available for all lakes in Minnesota, and we calculated an overall mean value for each lake across all 4 years (Minnesota LakeBrowser, 2022). Additionally, we used mean 2020 summer surface chlorophyll-*a* values for the Wisconsin lakes included in the Northern Temperate Lakes Long Term Ecological Research program (Magnuson et al., 2019a, 2019b). Summer chlorophyll-*a* data were also available for Säkylän Pyhäjärvi, Finland during 1989–2019 (Finnish Environment Institute, 2021) and Lake Constance, Germany during 1980–2019 (IGKB, 2020), from which we calculated the overall mean. If more than one measurement was taken in a month, we first calculated the monthly mean before calculating the overall mean. Data were not available or accessible for the remaining 45 lakes included in the original analysis.

2.5 | Secondary regressions

To test for factors influencing the rate of body length change estimated across populations in our dataset, we chose a two-step approach over stepwise model selection (Figure 3 Step #4). A consistent dataset is needed to perform stepwise model selection, but not all covariates of interest were available for all the lakes included in the models, as previously detailed. Therefore, we conducted separate secondary analyses on subsets of the lakes based on availability of covariate data.

We determined the impact of each covariate on trends in body length using separate weighted linear regressions using population-specific estimates of body length change from the LMM as the response and each covariate as the predictor. We used the inverses of the conditional variances in body length change as weights so populations with more uncertain body length trends (higher variance) had less influence in the analyses. We included species as a categorical factor and tested the interaction between species and the covariate of interest in the weighted linear regressions to determine if any effect of the covariates differed by species. All statistical analyses were performed using the open-source statistical software R (R Core team, 2020).

3 | RESULTS

3.1 | Body length trends

We found a significant, positive influence of year on length over time. The most parsimonious model of length by AIC criteria included year as a fixed effect and random intercepts and slopes for year for each gear nested within lake, as well as random intercepts and slopes for year for each species (Table 2; additional details in Table S3). The fixed effect estimate of year on length was significantly positive, indicating an average increase in total length of 0.046 mm per decade ($p = .005$, 95% confidence interval [CI] = 0.013, 0.076). The individual slope estimates, which take into account the random effects, indicated high variability in trends among populations and species, with two-thirds increasing in size over time (Figure 4). The marginal R^2 value for the year effect was very low (<1%), as lake, gear, and species random effects in our top model explained ~69% of the variation in body length trends. However, models that included year provided overwhelmingly better fits to the data than those that did not (Table 2). Additionally, the other top model structures, although different in structure and AIC support, also indicated consistent increases in length over time. Results from the additional analysis examining the influence of short time series can be found in Table S4. Hereafter, only the analyses of the best model selected by AIC will be discussed.

The full model with a random slope and random intercept for year for each species also resulted in a better fit compared to a reduced model with only a random intercept for each species (ΔAIC = 99.3), indicating the effect of year on body length differed by species. Taking the mean estimate of the population level body length trends for each species revealed eight of the 12 species increased in size overall (Figure 5).

3.2 | Covariate analyses

Of the six covariates investigated, two were found to be significant ($p < .05$) while all disagreed with our hypothesized relationships based on the TSR (Table 3). A weighted linear regression of asymptotic length (L_∞) on body size trends did not reveal a significant relationship between asymptotic length at the species level and body length changes (slope estimate = 0.00199, $p = .750$, 95% CI = −0.01028, 0.01427) indicating larger species of fish were not necessarily more sensitive to changing conditions (Figure 6a). The model included species, which was found to be a significant factor (analysis of covariance [ANCOVA], $p = .004$); no interaction term was included because the asymptotic length values were species-specific. However, a weighted linear regression of population average body size (data average) on body length trends did reveal a significant relationship (slope estimate = 0.00021, $p = .016$, 95% CI = 0.00004, 0.00038), highlighting the differential effects of changing conditions at the population level and showing that larger-bodied populations are experiencing greater increases in body length (Figure 6b). For example, a population with an average body length of about 200 mm experienced an average of 0.10 mm/decade increases in growth, while a population of the same species with an average body length of about 400 mm experienced an average of 0.29 mm/decade increases in growth. This model also included species, which was a significant factor (ANCOVA, $p = .006$) while an interaction between species and population average body size was not significant (ANCOVA, $p = .277$).

For range position, seven of the 12 species were only sampled at one latitude or within a very narrow latitudinal window in our dataset. For the other five species, coverage of each species' range captured in the dataset varied from 4% for brook trout to 80%

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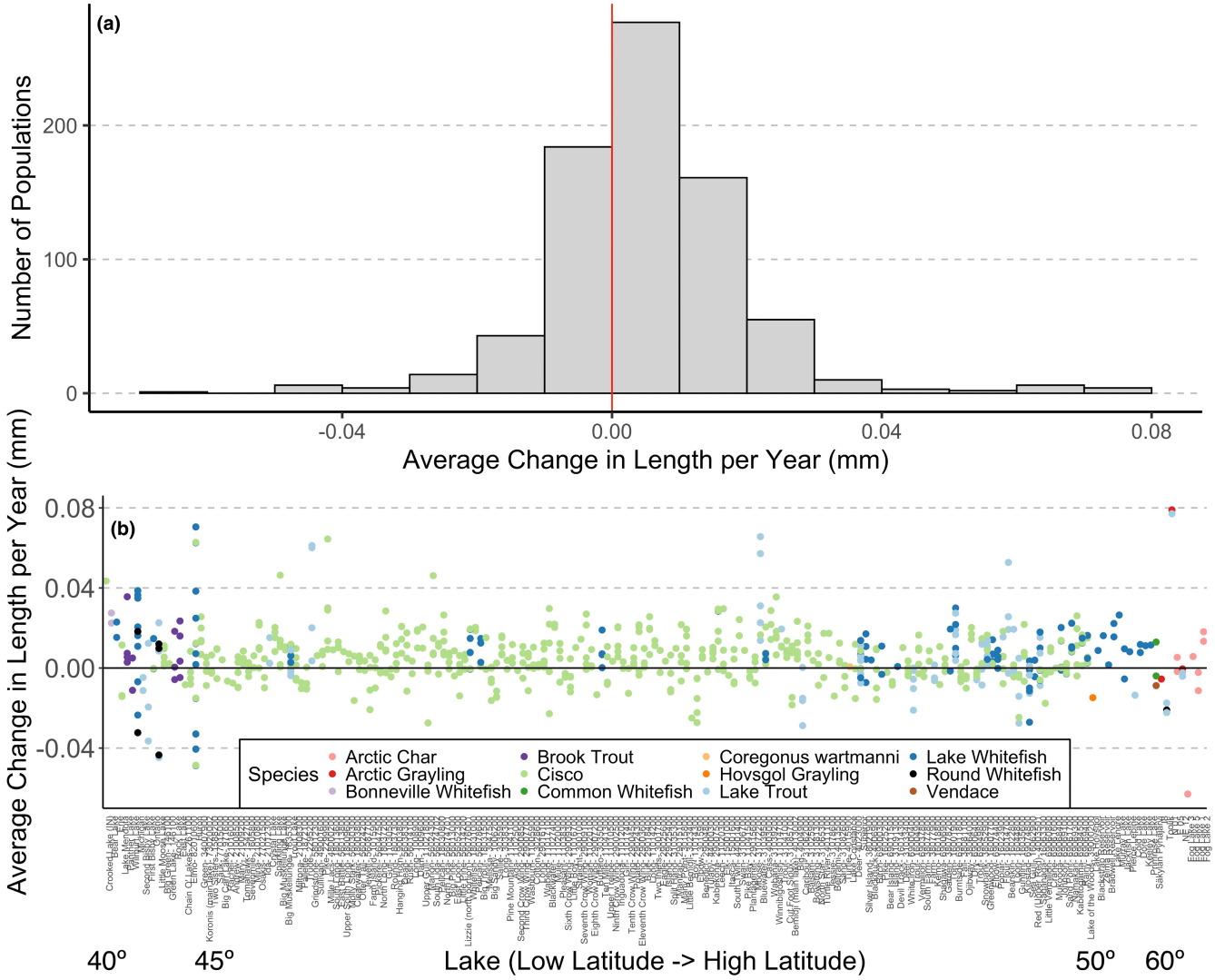

FIGURE 4 Average change in length (mm) per year at the population level for the best-fit model. Each population represents a unique species/lake/gear combination. The top panel represents the number of populations binned by 0.01 mm changes in length per year (a). The bottom panel includes a point for each population, colored by species and arranged by lakes on the *x*-axis moving south to north (b). Populations with values above 0, about 67% of the study populations, increased in length over time while populations with values below 0 decreased in length over time.

for round whitefish. A weighted linear regression for the effect of range position on body size trends was not significant (Figure 6c; slope estimate = −0.15397, p = .119, 95% CI = −0.34756, 0.03961), with species identified as a significant factor (ANCOVA, p = .009) but no interaction between the two predictor variables (ANCOVA, p = .538). These results indicate that relative position within a species range did not affect body length trends.

Our analyses attempting to characterize the effects of productivity and temperature on body length trends yielded similar results. Mean chlorophyll-*a* was not related to body length trends (Figure 6d; slopes estimate = −0.00012, p = .938, 95% CI = −0.00326, 0.00301) and species was not a significant factor (ANCOVA, p = .651). However, mean water temperature was positively and significantly correlated with body length trends (Figure 6e; slope estimate = 0.01926, p = .032, 95% CI = −0.00330, 0.02925). Populations in warmer waters showed more positive body length trends. Species was a significant factor in the mean temperature regression (ANCOVA, p = .040) but the interaction between species and mean temperature was not significant (ANCOVA, p = .253).

Study lakes experienced a range of water temperature changes over the survey periods (Table 3), with 137 of the 172 lakes with temperature data experiencing temperature increases. In general, lakes with longer survey periods experienced larger temperature changes. The change in temperature experienced by the study lakes during the time period covered by each survey did not have a significant relationship with body length trends (Figure 6f; slope estimate = 0.01753, p = .286, 95% CI = −0.01468, 0.04973). Species was not a significant predictor of the effect of water temperature change on body length trends, and thus not included in this regression (ANCOVA, p = .139).

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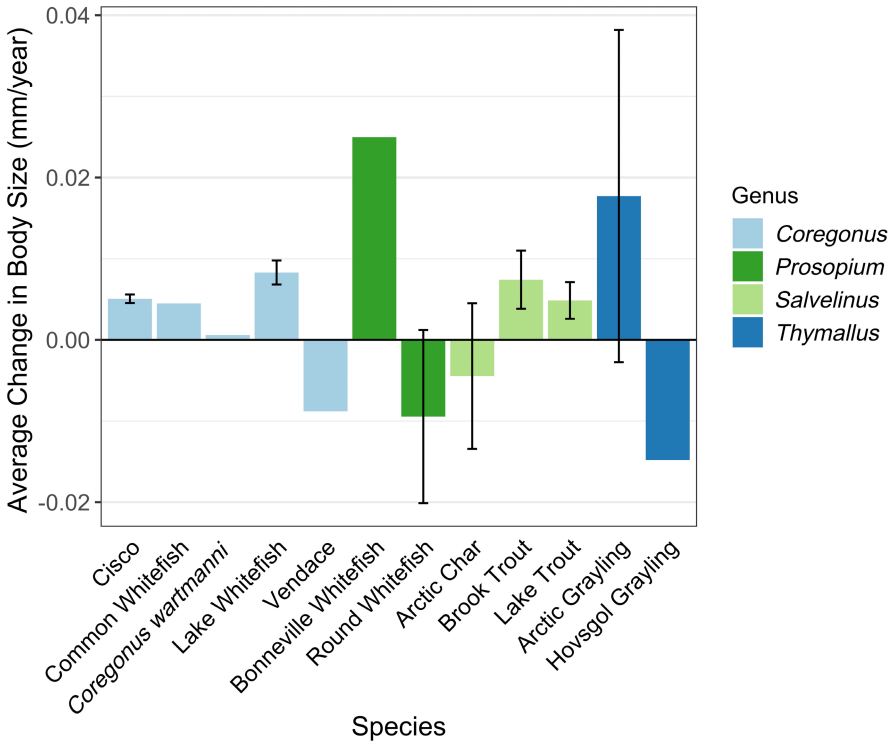

FIGURE 5 Average change in length (mm) per year for each species. Error bars indicate standard error. Common Whitefish, *Coregonus wartmanni*, Vendace, Bonneville Whitefish, and Hövsgöl Grayling are represented by a single population and thus do not have error bars.

4 | DISCUSSION

Our findings demonstrated an overall increase in the length of freshwater salmonid populations in lakes over recent decades. Our study is the first to our knowledge to identify an underlying trend in salmonid body size across freshwater populations. Only a handful of previous studies have focused on fish body size in freshwater systems, and the resulting trends, examined at smaller geographic scales, have not been conclusive (Jeppesen et al., 2012; Rypel et al., 2016). Most studies have investigated the applicability of Bergmann's rule (Belk & Houston, 2002; Rypel, 2014) or focused on management implications (Holbrook et al., 2021; Rypel et al., 2016) rather than attempt to disentangle drivers of body size changes. Importantly, none have identified a group of freshwater fishes with a consistent response toward larger body size as we have with freshwater salmonids.

In contrast, a wide variety of studies on marine and anadromous species have overwhelmingly called attention to declining body size over time (Daufresne et al., 2009; Oke et al., 2020; Ulaski et al., 2021; van Rijn et al., 2017). Of those studies that specifically tested for temporal and spatial trends in body size changes with warming temperatures, about half were heavily focused on salmon in the northeast Pacific and these consistently found anadromous salmon species were migrating to the ocean earlier and attaining smaller sizes overall (Cline et al., 2019; Lewis et al., 2015; McPhee et al., 2016; Ohlberger, 2013; Oke et al., 2020). However, Cline et al. (2019) found warmer lake temperatures were driving the decreased duration of freshwater residency in juvenile sockeye salmon (*Oncorhynchus nerka*), potentially indicative of faster freshwater growth in lakes consistent with the increasing trends in freshwater salmonid length we observed. Studies of marine fishes also largely indicated decreases in body size (Baudron et al., 2014; Daufresne et al., 2009), although some recent studies have highlighted that not all fish species were shrinking with warming (Audzijonyte et al., 2020; Berggren et al., 2021).

Although the overall pattern of increasing length was statistically significant and models containing a trend in length performed substantially better, the magnitude of this trend was small and there was substantial variation among species and populations within a species. At the population level, changes in fish body length ranged from 0.63 mm/decade decreases to 0.79 mm/decade increases, with more than two-thirds of populations experiencing increases. When made relative to size, the changes in length correlate to a range of 0.3% decreases in body length per decade to 0.4% increases in body length per decade. Compared to other studies, such as Oke et al. (2020) who found 2%–8% declines in body length of Pacific salmon over 20 years, our results provide little evidence of biologically relevant body size changes occurring in lakes. However, our results do provide support for the differential effects of changing conditions on body length across fish species and across organisms, as has been found in a range of studies of fish body size trends at different spatial scales (Audzijonyte et al., 2020; Jeppesen et al., 2012; van Rijn et al., 2017). As in other studies, changes in body length differed among species, a pattern also observed in Australian coastal reef fishes (Audzijonyte et al., 2020) and in the Mediterranean Sea (van Rijn et al., 2017). Similarly, Jeppesen et al. (2012) observed variable responses in body size of fish species to warming across 24 European lakes, with any changes in body size being system- and species-specific. Among the species in our analysis, trends in length were most negative for Hövsgöl grayling (−0.15 mm/decade) and most positive for Bonneville whitefish (+0.25 mm/decade). However,

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TABLE 3 Description of the covariates tested, our initial hypotheses, and the estimated coefficients and *p*-values from the weighted linear regression analyses.

Variable	Hypothesis	Coefficient value	*p*-value	Minimum value–maximum value
Species level				
Maximum average body size (L_∞)	(−); larger species experience more negative body size changes	.002	.75	208–907 mm
Population level				
Average body size (data average)	(−); larger-bodied populations experience more negative body size changes	.0002	**.016**	58–667 mm
Range position	(+); more northern populations experience more positive body size changes	−.1540	.119	0.034–0.913
Average chlorophyll-*a*	(+); populations in more productive lakes experience more positive body size changes	−.0001	.938	1–28.5 μg/L
Average water temperature	(−); populations in warmer waters experience more negative body size changes	.0193	**.032**	6.56–12.8°C
Temperature change	(−); populations with water temperature increases experience more negative body size changes	.0187	.255	−0.36 to +1.43°C/decade

Note: The minimum and maximum values of each covariate are also shown. Bold *p*-values indicate significance at $\alpha = .05$.

both species are endemics represented by a single population in our analysis and thus, the observed trends may have been influenced by local conditions.

We attempted to explain species and population level variability in our study by examining multiple covariates related to taxonomic differences and climate. We found a significant positive relationship between average body size and body length trends; larger-bodied populations are getting larger over time. Our finding agrees with Audzijonyte et al. (2020), who found maximum body size in tropical marine fish species was positively correlated with changes in length as temperatures warm but contradicts what has been found in mammals and experimental studies of aquatic species, which showed more significant declines in body size among larger-bodied organisms in response to warming (Forster et al., 2012; Hantak et al., 2021).

Additionally, our results contrast with the relationship between temperature and growth predicted by thermal growth curves. We hypothesized populations experiencing warmer average water temperatures would exhibit more negative changes in body size (Figure 1b,c) than colder populations (Figure 1a,b). However, our results show a weak trend in the opposite direction; populations that reside in warmer water temperatures on average are experiencing more positive changes in body length. While the populations spanned much of the latitudinal range of these salmonid species, mean temperatures were generally below thermal optima derived from laboratory studies and thus may only be providing a limited window into the effects of warming on salmonid growth. Moreover, even though 137 of the 172 lakes experienced warming over the survey periods, change in water temperature was not a significant predictor of changes in body length, further highlighting the complexities associated with the response of fish to temperature changes. Notably, it is possible that although surface temperatures are changing, hypolimnetic temperatures are not yet being affected to the same degree and thus behavioral thermoregulation, maintained by moving between temperature regimes within a lake, buffered any temperature-induced changes in growth we predicted. Warming surface waters combined with a consistently cold hypolimnion would provide a wider range of temperatures available to

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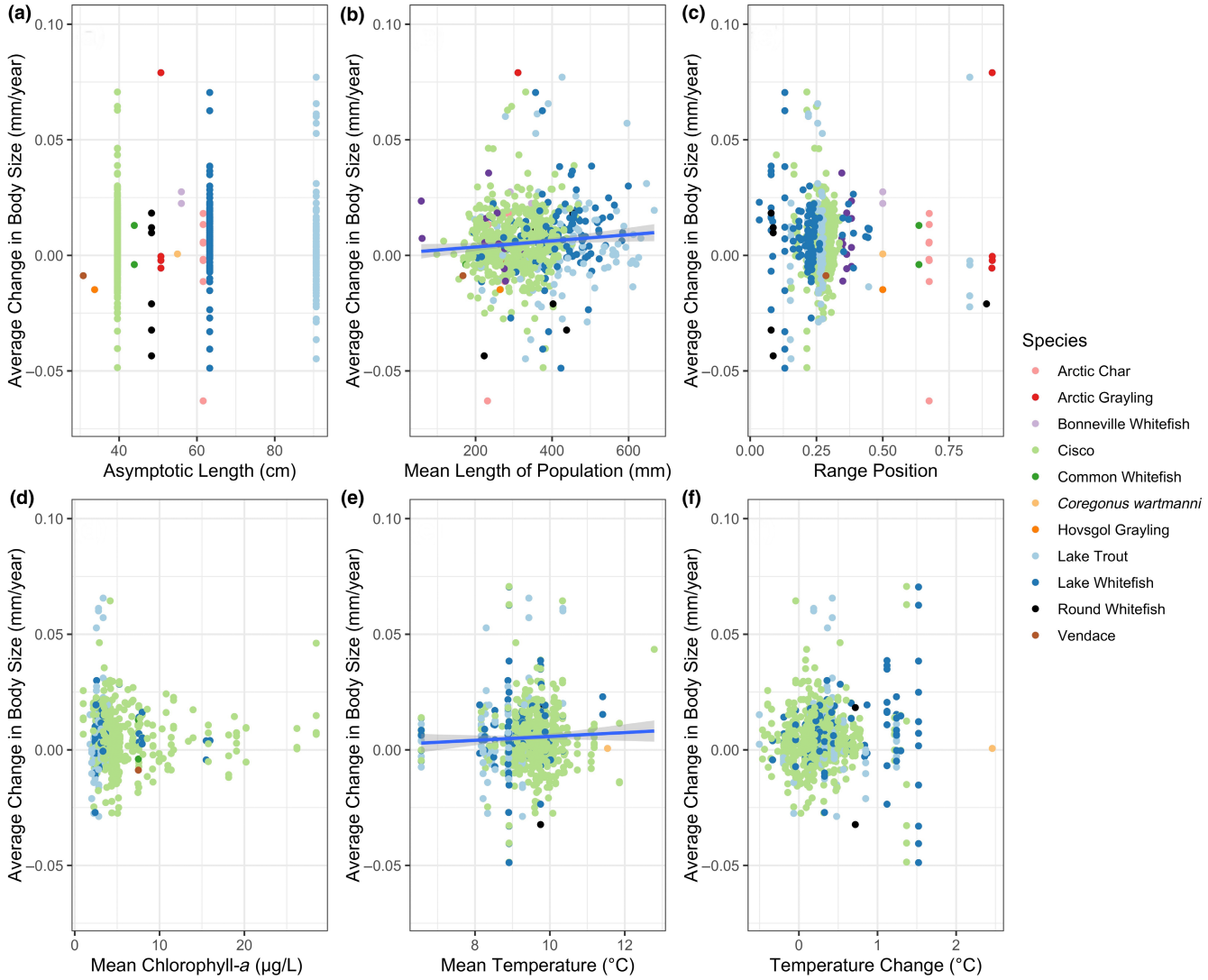

FIGURE 6 Biplots of body size change estimates in length (mm) per year regressed against environmental covariates: asymptotic length (a), mean length of population (b), range position (c), mean chlorophyll-*a* (d), mean surface temperature (e), and surface temperature change (f). Trend lines are only shown for significant relationships ($p < .05$).

vertically migrating salmonids. Warmwater habitats, such as the epilimnion of lakes (Jensen et al., 2006) or the lower mainstems of large rivers (Armstrong et al., 2021) may be critical for achieving high growth rates in salmonids even as they seasonally exceed the thermal optimum of these species.

Because our findings at the population level differed from theoretical predictions for changes in body size, it is also plausible that local factors result in different underlying curves and thermal optima for each population. Thermal optima, or optimal growth temperatures, have been found to differ across species and life stages with increasing temperatures often leading to increased growth in juveniles but decreased growth in adults, in accordance with the TSR (Ikpewe et al., 2021; Ohlberger, 2013). Optimal growth temperatures also have been found to differ within species in experimental studies, with optimal growth temperature negatively correlated with body size such that larger individuals within a species have colder thermal optima (Lindmark et al., 2022). Additionally, local adaptations to temperature may exist, which can affect the response of growth to temperature changes (Jutfelt, 2020; Seebacher et al., 2015). Thus, the optimal growth temperature for a population may be dependent on species, life stage, and individual body size amongst other local factors, resulting in differential growth responses to changing temperatures.

Furthermore, prevalent assumptions in growth models that (1) temperature is the primary driver of growth and (2) food consumption is a fixed proportion of maximum consumption have led to optimal growth temperatures being called into question for salmonids (Railsback, 2021). We attempted to investigate the role of food availability in fish body length trends via mean summer chlorophyll-*a* values as a proxy for productivity. However, we did not find a significant relationship between mean chlorophyll-*a* concentrations and trends in length and therefore could not draw any conclusions about the relationship between temperature, food availability, and body size changes. The use of mean productivity is a limitation of our data; it revealed that more productive lakes did not tend to exhibit more

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positive trends in length than less productive lakes, but it did not provide information about any potential relationship between productivity trends and body length trends. It is plausible that productivity may have increased in a lake over the survey period and thus was able to support more growth, but mean productivity values were not able to identify such a pattern. Additionally, food availability to secondary consumers depends on more than just primary productivity. Competition for food resources is a large driver of how much an individual fish consumes, leading to density-dependent growth. Such constraints have been identified in numerous species of fish spanning both marine and freshwater species (Lorenzen & Enberg, 2002; Post et al., 1999; Ward et al., 2017), potentially disrupting the positive correlation we hypothesized between growth and productivity (food availability) as metabolic costs increase with warming (Brown et al., 2004; but see Wootton et al., 2022). Density-dependent growth resulting from intraspecific food competition is known to be a strong driver of body size trends in vendace, one of our study species (Sarvala & Helminene, 2021). If perceived optimal growth temperatures are due to the assumptions made about food consumption in growth models (Railsback, 2021), they may not be widely applicable for wild populations where food availability, foraging abilities, and energy intake are variable, and likely to also vary with temperature.

Thus far, we have focused on changing growth rates as the mechanism behind changes in body length; however, trends in mean body length cannot always be directly interpreted as changes in growth. Shifting population age structure also produces trends in body size as a result of trends in recruitment and mortality (Ohlberger, 2013; Oke et al., 2020). As recruitment and mortality fluctuate, changes in mean age can drive changes in average body size, resulting in perceived trends in individual length without changes in growth. For example, Hansen and Nate (2014) found recruitment, along with growth, were strong drivers of walleye (*Sander vitreus*) population size structure in Wisconsin lakes. Additionally, natural and fishing mortality play relevant but competing roles in fish body size changes, as predation mortality tends to be lower in larger fish, while fishing and size-selective harvest target larger individuals (Allendorf & Hard, 2009; Olsen & Moland, 2011). The impact of harvest on body size is dependent on the degree of exploitation in a particular system, and thus size-selective harvest is likely an important factor in systems where fishing mortality considerably exceeds natural mortality (Stokes & Law, 2000). In fact, Berggren et al. (2021) found mortality trends to be a stronger factor driving size distributions of northern pike (*Esox lucius*) than variation in growth, and Fugère and Hendry (2018) suggested harvest may be a stronger selective agent than natural processes. Mortality may play an increasingly large role in driving body size trends as conditions continue to change because increasing temperatures have been linked to an increase in mortality (Brown et al., 2004). In addition to shifting size structure, mortality and recruitment can indirectly influence body size through population fluctuations; when mortality is high, density-dependent growth restrictions relax, potentially allowing for more growth and larger body sizes as has been the case with vendace in Säkylän Pyhäjärvi (Sarvala et al., 2020; Sarvala & Helminene, 2021). Data limitations prevented us from investigating recruitment and mortality trends as potential drivers of changes in mean body length as age data were not available for most of the populations analyzed, nor were estimates of fishing pressure or fishing mortality rates. However, we note fishing mortality has been linked to declining body size of the Hövsgöl grayling (Free et al., 2015), the species in our analysis that exhibited the most negative trend in length.

Furthermore, the time series included in our analyses were of varying lengths, which resulted in an unbalanced design accounted for with the use of mixed effects models. Nevertheless, the length of the time series could result in different effects (Claireaux et al., 2022). However, a coarse comparison of body length change estimates and time series lengths suggested no correlation between the two ($p = .401$, $R^2 = .0009$), nor did a comparison of the coefficient of variation and time series lengths ($p = .140$, $R^2 = .0028$). Additionally, although the sampling programs used consistent gears, consistent gear selectivity is not guaranteed because of potential changes in body condition. A change in body condition and therefore body depth changes gear selectivity (Holbrook et al., 2021), and it is plausible that fish are undergoing changes in weight rather than length in response to changing conditions.

Our study focused on 12 species of coldwater salmonids but the impacts of changing body size extend beyond populations to influence community and ecosystem level functioning (Ahti et al., 2020; Ohlberger, 2013; Werner & Gilliam, 1984). Body size trends and subsequent population size structure changes not only affect the species undergoing the changes (Barneche et al., 2018; McPhee et al., 2016; Peters, 1983) but also its predators, prey, and competitors (Delong et al., 2015; reviewed in Ahti et al., 2020). Other species that interact with the freshwater salmonids in our analysis are likely to be exhibiting their own variable responses to a changing climate. How changes in body size across organisms and ecosystem levels will alter the functioning of that ecosystem remains largely unknown. However, it is known that changing body size can alter the economic value of aquatic ecosystems, thus affecting humans that rely on them and the relative food security they provide (Oke et al., 2020). Our results provide further evidence that the 'shrinking of fishes' noted in marine environments (Cheung et al., 2013) may not be a universal phenomenon that extends to freshwater. Broad generalizations about the response of body size to climate warming obscure important variation that may help us better understand the mechanisms driving body size changes in freshwater systems, responses of coldwater species to warming conditions, and the repercussions for entire ecosystems and the humans that depend upon them.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and R code (data preparation, analyses, and figures) have been deposited in a Github repository (https://github.com/marysolokas/Salmonid-Body-Size) and are available in Zenodo (https://doi.org/10.5281/zenodo.7582537).

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