Received: 26 May 2022 | Accepted: 24 September 2022

DOI: 10.1111/1365-2656.13833

Journal of Animal Ecology | BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Identifying mechanisms underlying individual body size increases in a changing, highly seasonal environment: The growing trout of West brook

Benjamin H. Letcher[1] | Keith H. Nislow[2] | Matthew J. O'Donnell[1] | Andrew R. Whiteley[3] | Jason A. Coombs[4] | Todd L. Dubreuil[1] | Daniel B. Turek[5]

[1]U. S. Geological Survey, Eastern Ecological Science Center, Silvio O. Conte Research Laboratory, Turners Falls, Massachusetts, USA

[2]US Forest Service, Northern Research Station, Amherst, Massachusetts, USA

[3]Wildlife Biology Program, Department of Ecosystem and Conservation Sciences, Franke College of Forestry and Conservation, University of Montana, Missoula, Montana, USA

[4]Department of Environmental Conservation, University of Massachusetts, Amherst, Massachusetts, USA

[5]Department of Mathematics and Statistics, Williams College, Williamstown, Massachusetts, USA

Correspondence
Benjamin H. Letcher
Email: bletcher@usgs.gov

Funding information
U.S. Fish and Wildlife Service; U.S. Forest Service

Handling Editor: Marlène Gamelon

Abstract

1. As air temperature increases, it has been suggested that smaller individual body size may be a general response to climate warming. However, for ectotherms inhabiting cold, highly seasonal environments, warming temperatures may increase the scope for growth and result in larger body size.
2. In a long-term study of individual brook trout *Salvelinus fontinalis* and brown trout *Salmo trutta* inhabiting a small stream network, individual lengths increased over the course of 15 years. As size-selective gains and losses to the population acted to reduce body sizes and mean body size at first tagging in the autumn (<60 mm) were not observed to change substantially over time, the increase in body size was best explained by higher individual growth rates.
3. For brook trout, increasing water temperatures during the spring (when both trout species accomplish most of their total annual growth) was the primary driver of growth rate for juvenile fish and the environmental factor which best explained increases in individual body size over time.
4. For brown trout, by contrast, reduction in and subsequent elimination of juvenile Atlantic salmon *Salmo salar* midway through the study period explained most of the increases in juvenile growth and body size.
5. In addition to these major trends, a considerable amount of interannual variation in trout growth and body size was explained by other abiotic (stream flow) and biotic (population density) factors with the direction and magnitude of these effects differing by season, age-class and species. For example, stream flow was the dominant growth rate driver for adult fish with strong positive effects in the summer and autumn, but flow variation could not explain increases in body size as we observed no trend in flow.
6. Overall, our work supports the general contention that for high-latitude ectotherms, increasing spring temperatures associated with a warming climate can result in increased growth and individual body size (up to a point), but

[Correction added on 17 November 2022, after first Online publication: In affiliation 5, the city name "Williamsburg" has been changed to "Williamstown".]

context-dependent change in other factors can substantially contribute to both interannual variation and longer-term effects.

KEYWORDS
Atlantic salmon, brook trout, brown trout, climate change, stream ecology, stream flow, stream temperature

1 | INTRODUCTION

Temperature drives the energetics and metabolic processes underlying somatic growth of species whose internal temperatures largely reflect environmental temperature (ectotherms; Forster et al., 2012; Ohlberger, 2013). These processes translate into effects on individual body size and population size structure, with major implications for population resilience and in the case of harvested populations (fisheries, forestry), economic value. Given the generality of observed and forecasted increases in environmental temperatures (Stocker et al., 2013), what are the likely impacts on body size and what can different sources of information (theory, laboratory and field experiments) tell us about mechanisms and consequences under climate change? Based on energetics, and extending more broadly into the Metabolic Theory of Ecology (MTE) (Brown et al., 2004; Gillooly et al., 2001), the baseline expectation of a warming environment is a reduction in individual ectotherm body size as an increasing proportion of the energy budget is devoted to temperature-driven increases in metabolic rate (Killen et al., 2010; Sheridan & Bickford, 2011) and physiological components of heat-related stress. These considerations, in conjunction with climate-related impacts on development and life history, have led to the suggestion that decreasing individual body size may be a broadly observed response to climate warming (Ohlberger, 2013; Sheridan & Bickford, 2011). Several studies have clearly demonstrated reductions in individual body size that were directly linked to a warming climate (Baudron et al., 2014; Forster et al., 2012; Ozgul et al., 2009), while others have found age-dependent (Huss et al., 2019; Smoliński et al., 2020) or season-dependent (Rogers et al., 2011) reductions in body size related to increasing temperature.

Fishes represent a valuable study system for research on this question, and the impacts of climate-driven changes in individual body size are particularly relevant for fish and fisheries conservation and management. As ectotherms, somatic growth and size are strongly temperature-dependent and thermal performance relationships for many species have been well characterized (Childress & Letcher, 2017; Dell et al., 2011; Payne et al., 2016). However, for most fishes, growth performance declines at low as well as high temperatures (Payne et al., 2016). In highly seasonal, high-latitude environments, this growth curve suggests that growth may be temperature limited and warming environmental temperatures may move fish closer to their growth performance optima and result in increased individual body size. Approaching the growth maximum of the parabolic growth curve may be particularly important during the spring season, where prey availability in both lentic and lotic environments tends to be high, temperatures have not yet reached summer maxima, and as a result fish often obtain a large percentage of their total annual growth (Bacon et al., 2005; Letcher et al., 2022).

While some empirical and modelling results have provided support for this prediction of larger body size in fishes under climate warming in high-latitude aquatic ecosystems (Huss et al., 2019; Rogers et al., 2011), others have emphasized important caveats, context dependencies and interactive effects (Lindmark et al., 2018). Using bioenergetics models, Hill and Magnuson (1990) found that warming temperatures would result in higher growth rates and larger body size in several fish species in the Laurentian Great Lakes of North America, but only if prey availability did not decrease. Empirical and modelling results associated with a long-term study of migratory brown trout in England (Elliott & Elliott, 2010) observed increasing growth and size at age with warming temperatures during the spring high-growth period, and made the key observation that increases associated with spring warming outweighed reductions in growth during summer even for quite large (>3°C) increases in water temperature. Similarly, for stream and river fishes, climate change can influence the frequency, duration, timing and magnitude of stream flow (Siddique et al., 2020) which may then influence individual growth and size, and long-term studies have found direct effects of flow, and flow and temperature interactive effects on individual growth and body size (Stoffels et al., 2020; Xu et al., 2010).

In addition to abiotic factors, climate change can also influence individual fish growth and body size via changes in survival and population density, which then translate into density-dependent effects on growth and size (Bassar et al., 2016; Lindmark et al., 2018). Ecological niches and habitat relationships of many fish species also change substantially over ontogeny, largely as a function of individual body size (Lindmark et al., 2018). Additionally, fish assemblages, particularly in freshwater habitats, have been heavily influenced by invasions (Leprieur et al., 2008) and extirpations (Burkhead, 2012), the pace of which has increased greatly in the Anthropocene and is expected to continue. Variation in these factors is likely to generate different responses to changing environmental temperatures and require the ability to integrate the stage-specific effects over the entire life history to assess population-scale implications (Peralta-Maraver & Rezende, 2020; Rogers et al., 2011; Sheridan & Bickford, 2011).

Long-term population studies, particularly those that have documented concordant increases in environmental temperature, can be particularly relevant and useful for identifying patterns and mechanisms

related to a changing climate (Huss et al., 2019; Smoliński et al., 2020; Stoffels et al., 2020). Effective long-term studies in this context share several critical features. First, analysis of the data must be able to determine the mechanisms (growth rate, size-selective mortality, phenology) underlying changes in individual body size, and the multiple biotic and abiotic factors (including environmental temperature, population density and community structure) that could additively or interactively drive variation in body size. For example, unprecedented rates of both invasions (Mačić et al., 2018) and extirpations (Singh, 2002) make it increasingly likely that while the climate warms, species assemblages will change significantly over the course of long-term studies, affecting interspecific interactions which may influence growth and body size (Reuman et al., 2014; Walter et al., 2017). Second, for highly seasonal environments, the pattern of somatic growth, and the intensity and direction of any size-dependent process including temperature effects on growth may differ strongly across seasons, making it imperative to understand season-specific changes and correlations. Finally, in strongly age- and size-structured populations, the direction, magnitude and mechanism of changes in body size may differ among age-classes (Lindmark et al., 2018) as a result of fundamental differences in thermal niches and thermal performance relationships and also differences in the interactions among vital rates (e.g. between pre-reproductive and adult life-history stages).

In this paper, we use a long-term, intensive study of non-migratory brook trout and brown trout in a small stream network to address the effects of changes in water temperature and other abiotic and biotic factors on individual body size. Our long-term (15 years), intensive (individually tagged fish, seasonal samples each year) approach allows us to ask the following fundamental questions:

1. Was there an observed trend in body size over the course of the experiment?
2. What mechanisms (phenology, size-selection, body growth) best explain trends in body size?
3. Which changes in abiotic (seasonal and annual temperature, flow) or biotic (interspecific or intraspecific density) factors are related to changes in body size? How do these factors interact?
4. How do trends in, and drivers of, individual body size differ between species and age classes?

Our goal is to provide a valuable case study and contribute to the emerging body of theoretical and empirical work on individual body size and population size structure in the context of a changing climate.

2 | MATERIALS AND METHODS

2.1 | Study area

2.1.1 | Field site

The study area is a small stream network in western Massachusetts, USA, consisting of a mainstem and three tributaries (Figure 1) embedded in mixed hardwood forest with a dense canopy and light farming and residential areas (watershed area = 11.8 km^2). The mainstem (West Brook; WB) is a third-order stream with an average wet width of 4.5 m. The streambed is mainly cobbles with sporadic bedrock and boulders. Stream habitat consists of mostly riffles with occasional glides and pools. While we also sampled the three tributaries, here we report on growth results only for the mainstem to simplify the presentation. The WB study area consisted of an approximately 1-km long reach (Figure 1). A small (approximately 0.5 m, depending on stream flow), but passable waterfall defined the bottom of the study area. The upstream boundary of the study area was open and fish could freely pass in either direction.

All study locations contained naturally-reproducing populations of brook trout *Salvelinus fontinalis* and brown trout *Salmo trutta*. Atlantic salmon *Salmo salar* fry were stocked into the WB in spring from 1997 through 2004; juveniles were present in the system until 2007. We do not present growth results for salmon here as they were not present for the duration of the study. Brook trout and brown trout life cycles and the timing of sampling in relation to life events are described in Figure 1 (below). The only other fish species found consistently in the study area was blacknose dace *Rhinichthys atratulus*, but densities were commonly low (<10 per 20 m section) and although effects of dace on trout growth are unknown, they are likely low as dace were rare and were commonly found in different microhabitats than trout. Trout were not stocked in the study area and fishing pressure was very low (<10 observed anglers during the study).

2.1.2 | Fish sampling

Here, we report on brook and brown trout growth rates for sampling that began in 2000 and continued through 2015. Sampling adhered to the U.S. Geological Survey (USGS) Eastern Ecological Science Center animal care and use policy (under IACUC 1997-01C). Scientific collection permits for fish sampling were obtained each year of the study from the Massachusetts Division of Fisheries and Wildlife, (series 97-15SCP). The study reach was divided into 47, contiguous 20-m long sections and each section was sampled consecutively from downstream to upstream. Sampling consisted of isolating the study section with temporary block nets at the top and bottom of the section and conducting two-pass backpack electrofishing (300–400 V unpulsed DC). Captured fish were anaesthetized, measured for length (±1 mm, fork length), and scanned for a tag and tagged if no tag was present and the fish was >60 mm. All fish, tagged and untagged, were measured. Although not reported here, we also weighed (g, wet weight) each fish and took an anal fin clip for genetic analysis. We used 12-mm full-duplex passive integrated transponder (PIT) tags for individual fish identification (Digital Angel). Tags were inserted through a thin abdominal slit made with a small scalpel (Gries & Letcher, 2002). Tagging mortality was rare and tagging has minimal impact on fish

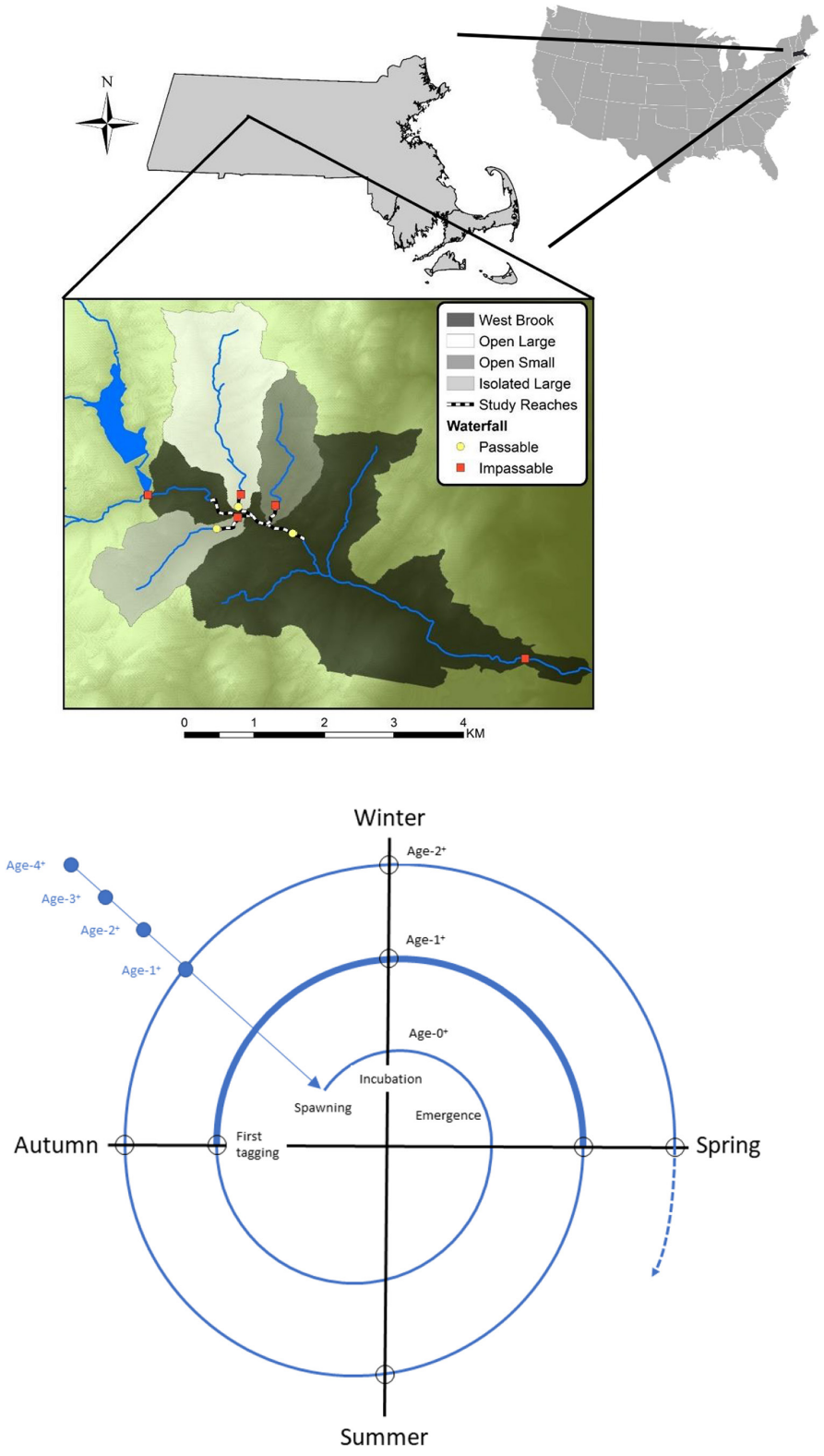

FIGURE 1 Map of the study area in Massachusetts, USA (above) and a representation of trout life cycles and our sampling strategy (below). In the map, the mainstem (West brook) and tributary watersheds are colour-shaded and the tagging study area is shown with black and white dashes. Impassible (square) and passable (circle) waterfalls are indicated on the stream network (blue lines). The map was made using ArcMap v10.8.1 and datasets included the National Hydrography Dataset (U.S. Geological Survey, 2020b), the National Elevation Dataset (U.S. Geological Survey, 2020a) and the National Hydrography Dataset Plus High Resolution Dataset for flow lines (U.S. Geological Survey, 2018). In the life cycle graph, the spiral represents aging across seasons (vertical and horizontal lines) from spawning through the spring of age-2+ (trout can live to age-4+, but we limit to age-2+ for simplicity). Spawning occurs between autumn and winter and embryos incubate in streambed gravels over the winter. Fry emerge from the gravel in early spring and are large enough to tag in the autumn of their first year (age-0+). Tagging samples are represented by open circles and the closed blue circles represent ages at which adults could contribute to spawning (here, age-1+ through age-4+). The thicker line on the spiral represents the range of ages used for 'growth year 0/1' described in the text.

growth and survival (Gries & Letcher, 2002; Sigourney et al., 2005). Following recovery from anaesthesia, fish were returned to the approximate centre of the study section. Sampling occurred four times per year, corresponding roughly with the winter and summer solstice, and spring and autumn equinox. Depending on the number of fish captured and weather, a sampling occasion took between 7 and 25 days to complete. Longer sampling occasions typically resulted from floods causing unsafe and inefficient sampling conditions.

We installed PIT tag antennas (Zydlewski et al., 2006) at the top and the bottom of the study area to allow estimates of permanent emigration from the study site (see Horton et al., 2007; Horton & Letcher, 2008 for details). If a fish was last observed on an antenna, it was coded as a permanent emigrant.

Water temperature (±0.1°C) was recorded every 2 h using temperature data loggers (Onset Computer Corporation) housed in PVC pipe secured to a submerged rock. Stream level was also measured every 2 h using data loggers (Onset Computer Corporation) at the bottom of the study area. Continuous stream flow was estimated using a flow extension model (Nielsen, 1999) based on data from a nearby USGS stream gage (Mill River) (see Xu et al., 2010 for details).

2.1.3 | Field data summary

We present data from 62 sampling occasions from 2000 to 2015. Ice accumulation prevented winter sampling in 2002, 2005, 2007, 2012 and 2015 and led to incomplete sampling in 2003 (completed 30 of 47 sections) and in 2004 (completed three of 47 sections).

Overall, we tagged 8556 brook trout, 6389 brown trout and 5032 Atlantic salmon individuals in the WB. We captured these individuals 14,948 (brook trout) and 12,655 (brown trout) times. Approximately 25% of these captures were on consecutive occasions, allowing the possibility of direct calculation of individual growth rates at the scale of our sampling occasions. Non-consecutive occasions resulted from missing observations (fish not captured, but known alive); body sizes and growth rates for these occasions and intervals were estimated here using the growth model described below. Counting the number of sampling occasions between the first and last observation for each fish (including missing observations), we have in total 18,412 (brook trout) and 16,510 (brown trout) occasions for which we can estimate growth with the model.

2.1.4 | Definition of first growth year

As in a previous demographic analysis for brook trout (Letcher et al., 2015), we define 'age' based on growth and survival pattern differences between younger and older fish. In fisheries research, age is typically incremented on January 1, for example, fish in their first year before January = age-0+. In our study area, strong seasonal growth patterns result in marked size differences before and after spring. Based on these size differences, we chose to identify 'growth years' (g) based on size differences rather than on the calendar. Growth year '0/1' fish included fall age-0+ fish and age-1+ fish in the spring (before the spring growth spurt, includes the winter to spring growth interval). Growth year '1+' included all fish older than age-1+ in the spring.

2.2 | Capture MARK–recapture model

2.2.1 | Estimating survival and abundance

We used abundance estimates as input variables in the growth model. To estimate abundance, we simply divided total counts for each species on each occasion by the probability of detection. Detection was estimated using an hierarchical Cormack–Jolly–Seber (CJS) mark–recapture model (Kery & Schaub, 2011; Royle, 2008). As we were interested in detection on each occasion, we simplified a detailed CJS model (Letcher et al., 2015) by removing linear terms and retaining occasion-specific estimates in a hierarchical context. A CJS model estimates the alive state ($z_{i,t}$, 1 = alive, 0 = dead) and the probability of capture ($p_{i,t}$) for each individual (i) and sampling occasion (t) based on an encounter history of individual captures ($o_{i,t}$, 1 = captured, 0 = not captured for each t).

Capture probability is modelled as the probability of detection given the fish is alive at time t ($z_{i,t}$) and available for capture ($1-\eta_{i,t}$), where $\eta_{i,t}$ was an indicator of observed permanent emigration based on the PIT tag antenna data. $\eta_{i,t}$ equalled 1 when fish were observed for the last time on a PIT tag antenna at the top (upstream boundary) or bottom (downstream boundary) of the study area and equalled 0 otherwise. We also scaled p by the proportion of sections sampled during an occasion (ω); for the vast majority of samples, this equalled 1, but was <1 for the incomplete winter sampling occasions. Individual capture histories (o) provide data for the capture likelihood:

$$o_{i,t} \sim \text{Bernoulli}\left(p_{i,t} \bullet z_{i,t} \bullet \left(1-\eta_{i,t}\right) \bullet \omega_{s,y}\right) \quad (1)$$

where s = season [1:4] and y = year [2000:2015]. We estimated values of p as simple intercepts for each combination of s, y, g:

$$\text{logit}\left(p_{i,t}\right) = \beta_{s,y,g} \quad (2)$$

Intercepts were modelled in hierarchical context with a random effect structure across y:

$$\beta_{s,y,g} \sim N\left(muP_{s,g}, sigmaP_{s,g}\right) \quad (3)$$

with weakly informative priors $muP_g \sim N[0,1.5]$, truncated [−3.5,3.5], and $sigmaP_g \sim U[0,10]$.

Similarly, survival was modelled as the probability of being alive at $t+1$, given being alive at t:

$$z_{i,t+1} = \text{Bernoulli}\left(\varphi_{i,t} \bullet z_{i,t}\right); t > f_i \quad (4)$$

where f_i is the first capture occasion.

$$\text{logit}(\varphi_{i,t}) = \beta_{s,y,g} \quad (5)$$

Survival intercepts were also modelled in hierarchical context with a random effect structure across *y*:

$$\beta_{s,y,g} \sim N(muPhi_{s,g}, sigmaPhi_{s,g}) \quad (5)$$

with weakly informative priors $muPhi_g \sim N[0,1.5]$, truncated [−3.5,3.5], and $sigmaPhi_g \sim U[0,10]$.

2.3 | Body size and growth analyses

2.3.1 | Size-dependent losses and gains

Body size distributions can be influenced by size-dependent losses (emigration, mortality) and gains (immigration, growth to taggable size) within and across cohorts. Within cohorts, losses and gains could vary by age and across cohorts they could vary from year to year. Here, we evaluated whether losses or gains could contribute to the observed increases in body size across years. Gains could lead to increased body sizes if larger fish entered the tagged population and the strength of this relationship increased over time. Likewise, losses could lead to increased body size if smaller fish were lost and the strength of the size-dependent loss increased over time. To evaluate the direction and strength in losses and gains, we coded each observation for each fish as either the first observation (gain) or the last observation (loss) and ran separate generalized linear models in R (binomial link function) for losses or gains. Independent variables included observed body length, cohort, species and an integer variable defining the combination of age in years and season (ageInSamples, 1–10 where 1 = age-0+ autumn and 10 = age-2+ winter). We conducted model selection using the Akaike information criterion (AIC) to identify a model for inference.

With the top model for both losses and gains, we report significance (*p*-values) for the interaction between body size and cohort where a detectable interaction indicates a change in the size-dependent relationship over time. Because the models include complex interactions among variables, we also present predicted values for losses and gains across age for the middle cohort (2008) to show the strength and direction of the size-dependent effects.

2.3.2 | Statistical model for body growth

For brook trout and brown trout independently, we modelled body size ($\ell_{i,t}$ = length) as the change in length $(\delta_{i,t})$ between consecutive sampling occasions:

$$\ell_{i,t+1} = \ell_{i,t} + \delta_{i,t} \quad (6)$$

Growth was modelled as:

$$\delta_{i,t} \sim N(\epsilon\delta_{i,t}, , sigma\epsilon\delta_{i,t}) \quad (7)$$

where $\epsilon\delta_{i,t}$ was mean expected seasonal growth and $sigma\epsilon\delta_{s,r}$ was the SD in expected seasonal growth rate. We multiplied $\epsilon\delta_{i,t}$ and $sigma\epsilon\delta_{i,t}$ by $d_{i,t}$ to account for unequal sample intervals among individuals. $d_{i,t}$ represented the number of days between sampling occasions for each individual. For an occasion when an individual was not captured, we used the median sample date of the capture occasion. We modelled $\epsilon\delta_{i,t}$ as a function of stream temperature (*T*), stream flow (*F*), body length (ℓ), and estimated abundances of brook trout (nBKT), brown trout (nBNT) and Atlantic salmon (nATS):

$$\begin{aligned}\epsilon\delta_{i,t} = {} & \beta_{0,g,s} + \beta_{1,g,s} \bullet T_{i,t} + \beta_{2,g,s} \bullet F_{i,t} + \beta_{3,g,s} \bullet T_{i,t} \bullet F_{i,t} + \beta_{4,g,s} \bullet {T_{i,t}}^2 \\ & + \beta_{5,g,s} \bullet {F_{i,t}}^2 + \beta_{6,g,s} \bullet cBKT_{s,y,g} + \beta_{7,g,s} \bullet \ell_{i,t} + \beta_{8,g,s} \bullet nBNT_{s,y,g} \\ & + \beta_{9,g,s} \bullet nBKT_{s,y,g} \bullet nBNT_{s,y,g} + \beta_{10,g,s} \bullet nATS_{s,y,g} + RE_i\end{aligned} \quad (8)$$

where β's were the intercept (subscript 0) or coefficients (subscripts 1:10), *T* and *F* were average temperature or flow for each individual's sampling interval ($d_{i,t}$), length was either observed or estimated (latent) depending on whether the individual was captured on occasion *t*, the estimated abundances derived from the detection model and *RE* was a random effect for individual growth. All input variables were standardized to mean = 0 and SD = 1. Although not reported here, the structure of Equation (8) was determined using model selection based on minimum AIC using a linear mixed model for growth with individual random effects.

We modelled the SD of growth ($sigma\epsilon\delta$) as a linear function of stream flow and temperature and their interaction. Initial analysis indicated that including length and the abundance estimates led to poor mixing during Markov chain Monte Carlo (MCMC) estimation so these variables were excluded from the estimation of $sigma\epsilon\delta$.

$$\log(sigma\epsilon\delta_{i,t}) = \beta s_{0,g,s} + \beta s_{1,g,s} \bullet T_{i,t} + \beta s_{2,g,s} \bullet F_{i,t} + \beta s_{3,g,s} \bullet T_{i,t} \bullet F_{i,t} \quad (9)$$

As with mean growth, βs was the intercept (subscript 0) or coefficients (subscripts 1:3) and *T* and *F* were mean temperature and flow of each individual's sampling interval. We used a random effect structure across growth year for all βs,

$$\beta s_{0:3,g,s} \sim N(\beta sMu_{0:3,s}, \beta sSD_{0:3,s}) \quad (10)$$

with non-informative priors for βsMu (N[0,30]) and βsSD (U[0,100]). Code for the growth model is available in Supporting Information.

2.4 | Model fitting

2.4.1 | Parameter estimation

We used the programming environment 'nimble' (de Valpine et al., 2017) within R (Plummer et al., 2006) to code the model and to draw posterior samples for the parameters. We ran three chains

with 25,000 burn-in and 25,000 evaluation iterations. Chains were thinned to retain every 10th iteration. We assessed chain mixing using the 'potential scale reduction factor' (Brooks & Gelman, 1998) from the 'CODA' package in R (values <1.1 indicate good mixing). We used overdispersed initial values for all parameters, except in the survival model where initial values of z were set to 1 from the occasion of the first capture for each fish to the occasion of the last capture (NA otherwise).

2.4.2 | Goodness of fit

We used posterior predictive checks for each species to assess goodness of fit (Gelman et al., 2004; Rubin, 1984). These checks involve comparing observed data (ℓ) with predicted data. Predicted lengths for each individual and occasion were generated during parameter estimation. From these data, we estimated Bayesian p-values (Gelman, 2003) for each species. Bayesian p-values are the proportion of predicted data that are above observed data; values near 0.5 signify lack of bias in estimates. From these data, we also calculated root mean square error (RMSE) as an index of error in the estimates. To test how well the model could predict unobserved samples, we randomly left out 10% of the observed data in a cross-validation exercise and calculated RMSE for those data.

2.4.3 | Predicted values

Based on parameter estimates, predicted growth rates across model variable ranges (±1.5 SD) indicated patterns in main effects and two-way interactions. To show trends without predictions of parameter uncertainty, we used mean parameter estimates across MCMC runs.

2.4.4 | Sensitivity

To identify relative effects of model variables on growth rate, we calculated sensitivities using simulated growth across variable ranges (±1.5 SD). We projected growth by replicating the growth model (Equation 8), including variable interactions, random effects, estimates of SD in growth and estimates of uncertainty among MCMC runs. We ran projections for all combinations of the variables in Equation (8) at values of [−1.5, 0, 1.5] for each of the five variables, for a total of 243 combinations per replicate. To simulate parameter uncertainty, we ran 100 replicates, each with parameter estimates from a random non-replaceable draw of the MCMC posteriors. Reflecting field conditions, we projected growth for 500 fish for each species with starting lengths drawn from a normal distribution (mean = 72 mm, SD = 9 mm) over 10 sampling occasions.

To estimate the effect of each variable on simulated growth, we calculated 'relative importance' (RI) using the calc.relimp function from the RELAIPMO R package. RI is the R^2 contribution of each variable in a linear model. As RI is based on R^2, estimates can be sensitive to variable ordering (Chevan & Sutherland, 1991). We used the 'lmg' option in calc.relimp() which estimates RI over all possible variable orderings. We report RI values for each species at three levels of organization, (1) across ages and seasons, (2) across seasons for each age and (3) for each age and season separately.

Finally, we evaluated the extent to which the range of observed stream temperature, flow or Atlantic salmon density (±1.5 SD) alone could account for the range of observed body sizes. Selecting predictions for low or high values of flow or temperature with all other variable values set to 0, we plotted predicted size trajectories from 100 randomly selected MCMC iterations against observed size ranges to examine whether temperature, flow or salmon ranges were sufficient to explain observed size ranges.

3 | RESULTS

3.1 | Survival model

Average probability of detection (±SD) across seasons and years was 0.56 ± 0.15 for brook trout and 0.52 ± 0.14 for brown trout. Detection was highest in the autumn (0.64) and lowest in the spring (0.50) (Figure A1). Average probabilities of survival (season^{-1}) were also similar for brook trout (0.62 ± 0.16) and brown trout (0.66 ± 0.16) and were highest in the spring (0.73) and lowest in the summer (0.57). Average survival was 0.65 in both the autumn and the winter.

3.2 | Patterns over time

Stream flow was highly variable over time (Figure 2), in contrast to stream temperature which increased in all seasons. Temperature increases were statistically significant in spring (0.15°C/year) and summer (0.09°C/year) (Figure 3).

Estimated total abundance and abundances of each species were highly variable over time (Figure 4, see Figure A1 for probabilities of detection used to estimate abundances). There was no trend in brook trout and brown trout abundances over time (slopes not detectably different from 0), while abundances of Atlantic salmon declined (reflecting the cessation of stocking in 2004).

Average body lengths of both trout species increased over the course of the study (Figure 5), with yearly increases averaging 1.90 mm/year and ranging between 0.34 and 3.62 mm/year across ages and seasons. On average, yearly increases in length (±SD) were greater for Brown trout (2.26 ± 0.96) than for brook trout (1.53 ± 0.76). Yearly increases were greater for older fish (Figure A2) and increased faster with age for brown trout (intercept = 0.61, slope = 0.30, p-value < 0.0001, r^2 = 0.87, N = 10) compared to brook trout (intercept = 0.46, slope = 0.20, p-value < 0.01, r^2 = 0.55, N = 10).

Overall, observed growth rates (Figure A3) were highly seasonal, with at least 4-fold higher growth in the spring (0.43 mm/

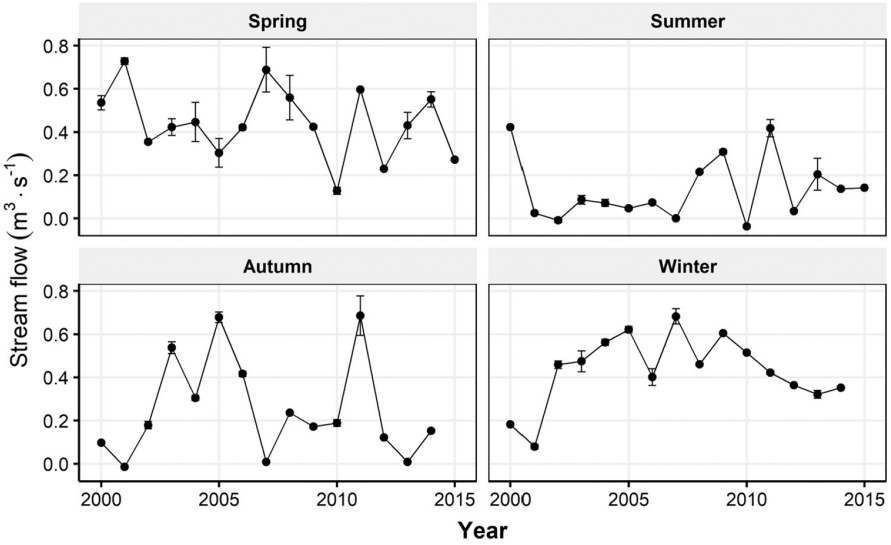

FIGURE 2 Average (±SD) stream flow ($m^3\ s^{-1}$) for each season over the course of the study in the West brook, Massachusetts, USA.

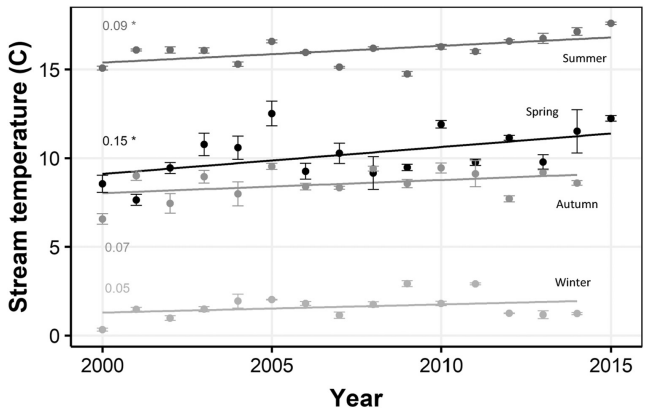

FIGURE 3 Average (±SD) stream temperature (°C) for each season (the range of dark grey to light grey corresponds to spring, summer, autumn, winter) over the course of the study in the West brook, Massachusetts, USA. Lines represent linear regressions and numbers near the beginning of each set of points are slopes (* signifies *p*-values <0.05).

day ± 0.11 [mean ± SD]) compared to the other three seasons (summer = 0.11 ± 0.88, autumn = 0.12 ± 0.070, winter 0.067 ± 0.048). Growth was also about 70% higher for younger fish (growth year 1) compared to older fish and brown trout grew about 8% faster than brook trout.

Although average growth rates tended to increase across years for most combinations of age and season (Figure 6), growth increases were only detectable over time in the spring for age-1 fish. On average, growth rate increased 0.0025 ± 0.0037 mm/day, and growth increases were slightly higher for brown trout (0.0028 ± 0.0037) compared to brook trout (0.00223 ± 0.0039). Growth rate increases were substantially higher than average for both species in the spring (~0.01 mm/day).

3.2.1 | Size-dependent gains and losses

For both gains and losses, the top model (gains ΔAIC = 17, losses ΔAIC = 33) included full interactions among all independent variables. The lack of detectable interactions ($p > 0.05$) between body size and cohort indicated that the relationships between body size and gains or losses were not changing over time. Furthermore, the direction of predicted body size effects indicated that gains or losses should lead to smaller body sizes with higher gains of smaller fish across ages (Figure 7 above) and generally higher losses of larger fish (Figure 7 below).

3.3 | Modelled growth

The 'potential scale reduction factor' indicated good mixing (values were <1.1) for all parameters. Bayesian *p*-values (0.52 for both species, Figure A4) suggested no bias in body size estimations, and RMSE values of 4.76 mm (brook trout) and 4.81 mm (brown trout) indicated low variation in estimated body sizes. RMSE increased to 6.55 mm (brook trout) and 6.54 mm (brown trout) for the observations that were left out of estimation during cross-validation (Figure A4).

3.4 | Parameter estimates

Reflecting growth rate observations (Figure A3), intercepts from the growth model were greatest in the spring, higher for younger fish and generally higher for brown trout than for brook trout (Figure A5, Table A1). Estimated standard deviation in growth was also higher in spring than in the other seasons, was very low in the winter and was typically lower for younger fish in the spring and autumn, especially in brown trout (Figure A5).

It can be challenging to interpret parameter estimates in models with interactions, but some patterns emerge including (1) similar effect sizes

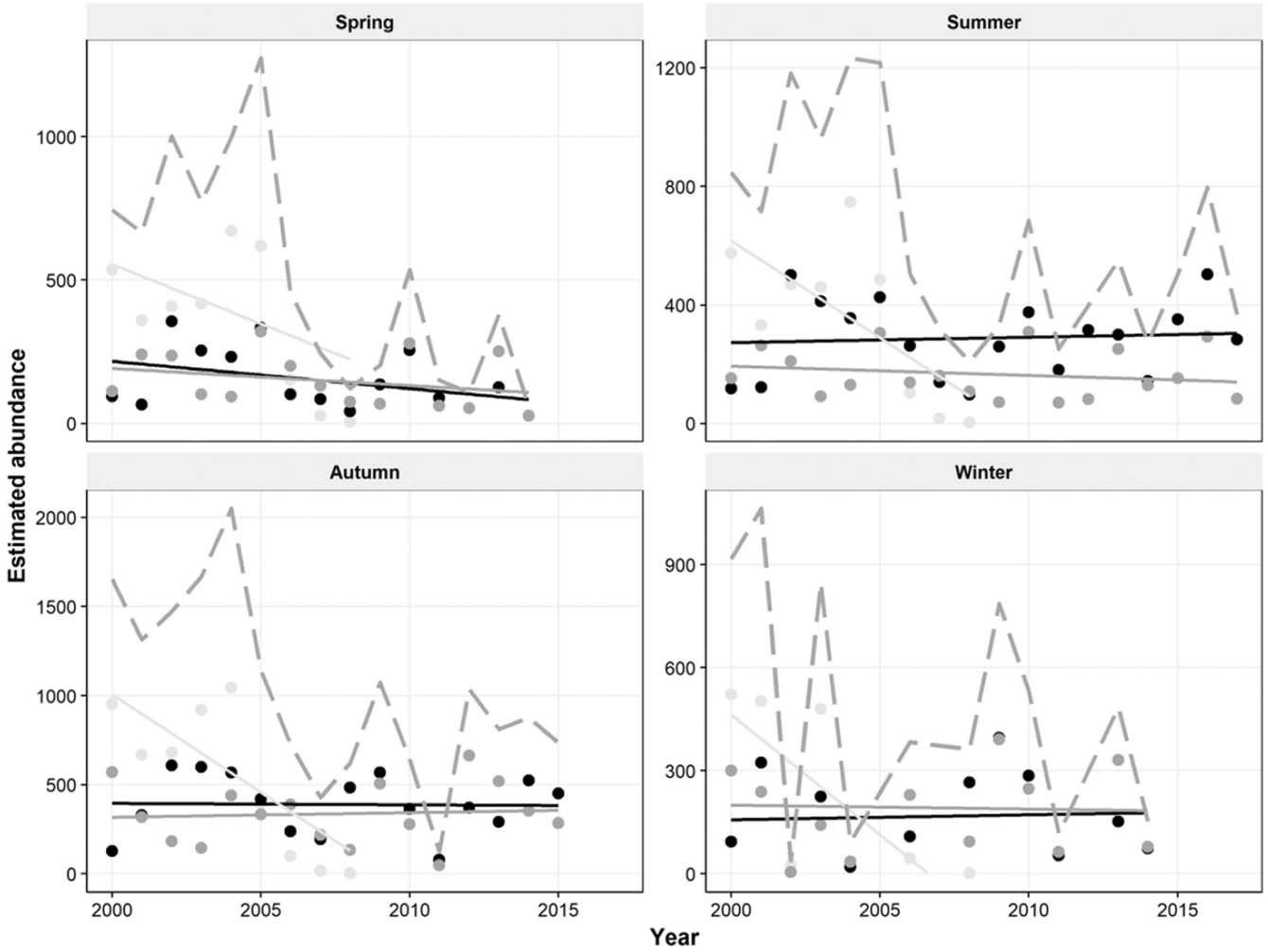

FIGURE 4 Estimated abundances over time for brook trout (black), brown trout (grey), Atlantic salmon (light grey) and the sum of all three species (dashed line). Solid lines represent linear regressions of abundance over time for each species. Atlantic salmon fry were no longer stocked after 2004.

and directions between species, (2) a strong positive effect of temperature in the spring but not in the other seasons, (3) strong positive effects of flow in spring and summer and negative effects in the winter, (4) a negative interaction between temperature and flow in the spring, (5) negative squared flow and temperature estimates in the spring, (6) positive effects of body size for young fish but negative length effects for older fish, and (7) and variable effect directions for brook trout abundance and generally negative effects of brown trout and Atlantic salmon abundance (Figure A5). Similarly, patterns in the parameter estimates for the standard deviation of growth included (1) mixed effects of temperature with strong positive effects in the spring and negative effects in the winter for brown trout, (2) strong positive effect of flow in the summer for both species and (3) a positive interaction between temperature and flow in the summer (Figure A6). Interactions among parameters and size trajectory predictions can be explored with a web application available here: https://usgs.gov/apps/ecosheds/#/westbrook-trout/predictions.

3.5 | Predictions

Predicted growth main effects mirrored parameter estimates (Figure A7), while predicted interaction plots revealed strong interactions between flow and temperature in the spring and weaker effects in the other seasons (Figure 8). With warm temperatures in the spring, maximum growth occurred at intermediate flows, but as temperatures cooled, greater flow was required to reach maximum growth (Figure 8). Patterns in predicted spring growth as a function of flow and temperature were similar between species for growth year 0 fish but differed substantially for growth year 1 fish, where maximum growth at a given temperature occurred at lower flow rates for brook trout, especially at warmer temperatures (Figure 8). Nonlinearities in growth were weak in seasons besides spring and interactions between flow and temperature generally resulted in faster growth with warm temperatures and higher flows (Figure 8).

3.6 | Growth rate sensitivity

Analysing growth rate variance sensitivities by growth year across seasons revealed marked differences between age groups and between species for younger fish (Figure 9). For older fish, flow alone explained a very large proportion of the growth variation (>75%) for both species. In contrast, flow explained relatively little growth variation for growth year 0/1 fish (Figure 9, top). For

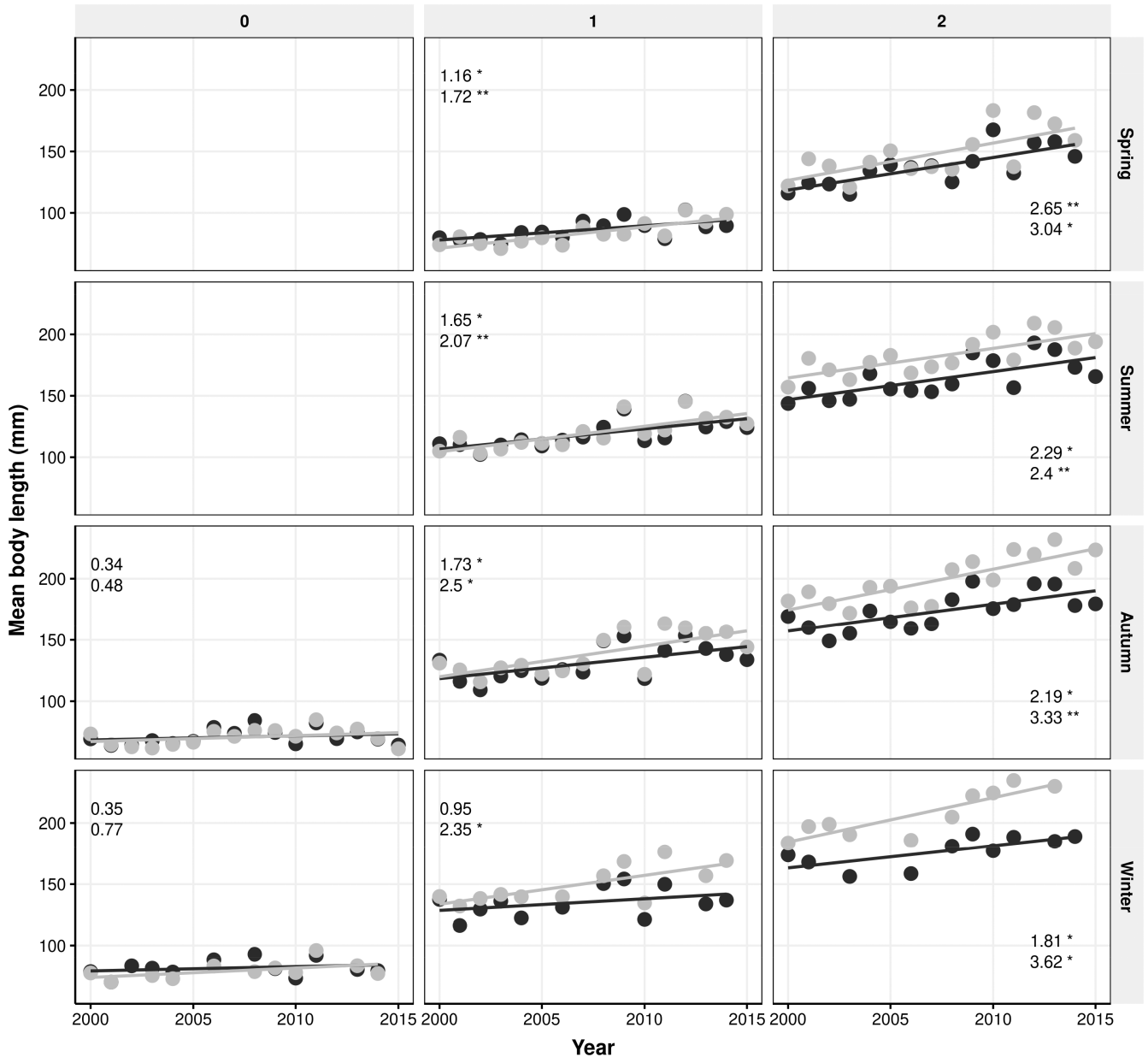

FIGURE 5 Mean body length (mm) across years for each growth year (columns), season (rows) and species (brook trout = black, brown trout = grey). Numbers in the panels represent slopes of linear regressions of length over time (brook trout, top; brown trout, bottom) and the number of stars next to slopes indicated significance at $p < 0.05$ (*) or $p < 0.001$ (**). Age-0 means in the autumn include untagged fish <60 mm to represent the full size range of observed fish.

growth year 0/1 brook trout, temperature explained the most growth rate variation (52%), while Atlantic salmon abundance explained the most variation in growth year 0/1 brown trout growth (46%). Subdividing sensitivities more finely (by age and season) identified seasonal effects of flow for older fish (Figure A8). For both species, flow accounted for >90% of growth rate variation in the summer and autumn.

Simulating growth trajectories at low and high values (−1.5 SD, +1.5 SD) of stream temperature, flow and Atlantic salmon abundance revealed that temperature range alone could explain the observed size range in brook trout and that Atlantic salmon range alone could explain the observed size range in brown trout (Figure 10). Low flows generated unrealistically small body sizes, suggesting the range of stream flows cannot explain the increasing trend of observed size trajectories.

4 | DISCUSSION

Our 15-year, intensive study of a small stream network revealed changes over time in both abiotic and biotic aspects of the system. The major abiotic change was detectable increases in stream temperature in spring and summer. The primary biotic change was a decrease in abundance and eventual loss of juvenile Atlantic

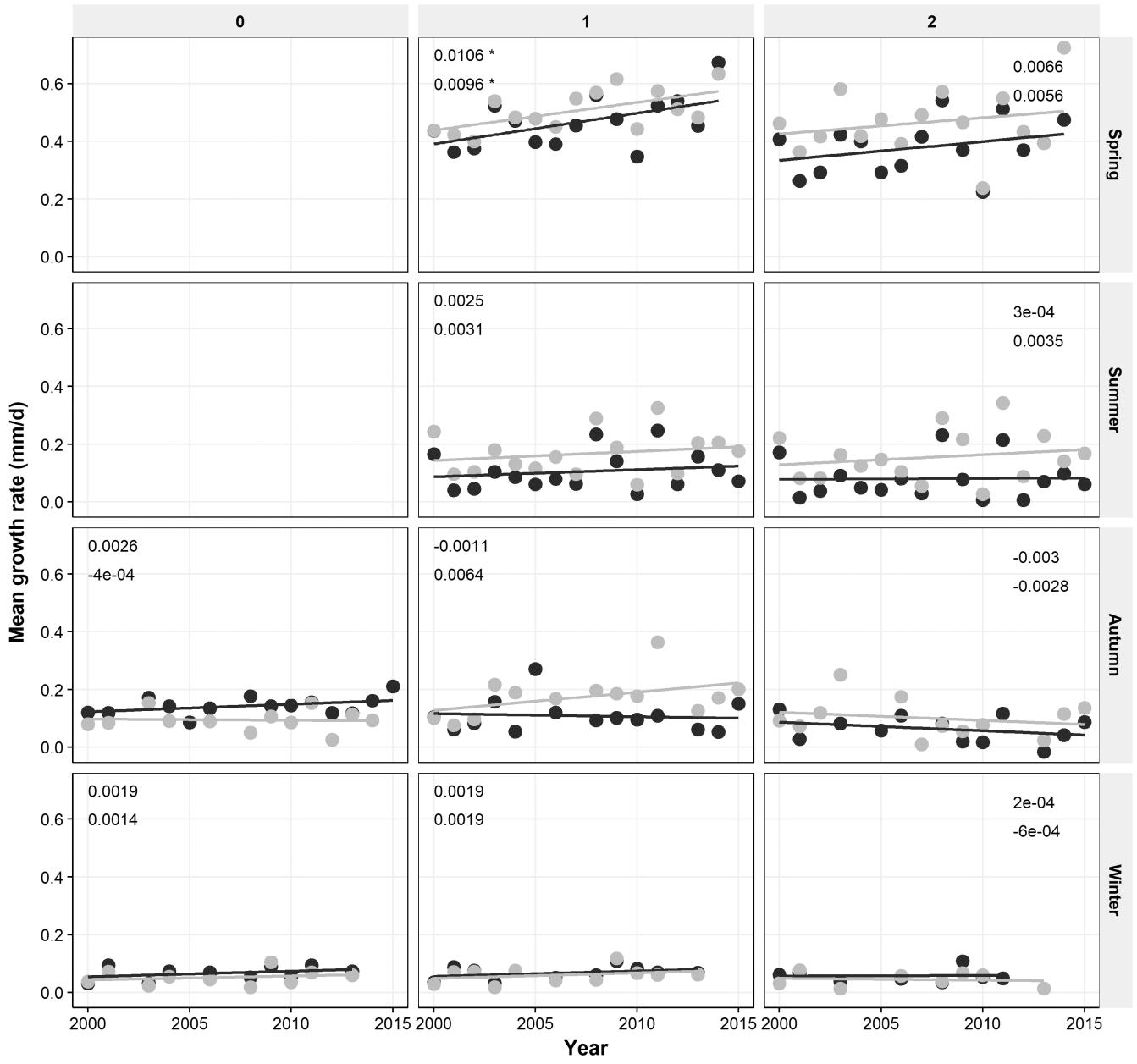

FIGURE 6 Mean growth rates (mm/day) across years for each growth year (columns), season (rows) and species (brook trout = black, brown trout = grey). Numbers in the panels represent slopes of linear regressions of length over time (brook trout, top; brown trout, bottom) and the number of stars next to slopes indicated significance at $p < 0.05$ (*).

salmon. Over the same time period, individual body size of both brook trout and brown trout increased over the course of the study. As observed size-selective gains and losses would have resulted in smaller body sizes and size at first tagging did not change substantially over time, observed increases in body size were best explained by higher individual growth rates. For brook trout, increasing water temperatures during the spring season, when both species accomplish most of their total annual growth, was the primary decadal-scale driver of somatic growth rate for juvenile fish and the environmental factor most related to increases in mean body size over time. For brown trout, by contrast, increased juvenile growth and body size were explained primarily by reduction in and subsequent elimination of juvenile Atlantic salmon *Salmo salar* midway through the study period. In addition to these major drivers, a considerable amount of interannual variation in growth and size was also explained by other abiotic (stream flow) and biotic (population density) factors with the direction and magnitude of these effects differing by season and age-class. For example, variation in stream flow explained most of the interannual growth rate variation for adult fish, but there was no consistent trend in stream flow over time. Our work supports the general contention that for high-latitude ectotherms, increasing spring temperatures associated with a warming climate can result in increased growth and individual body size (Bacon et al., 2005), but also illustrates

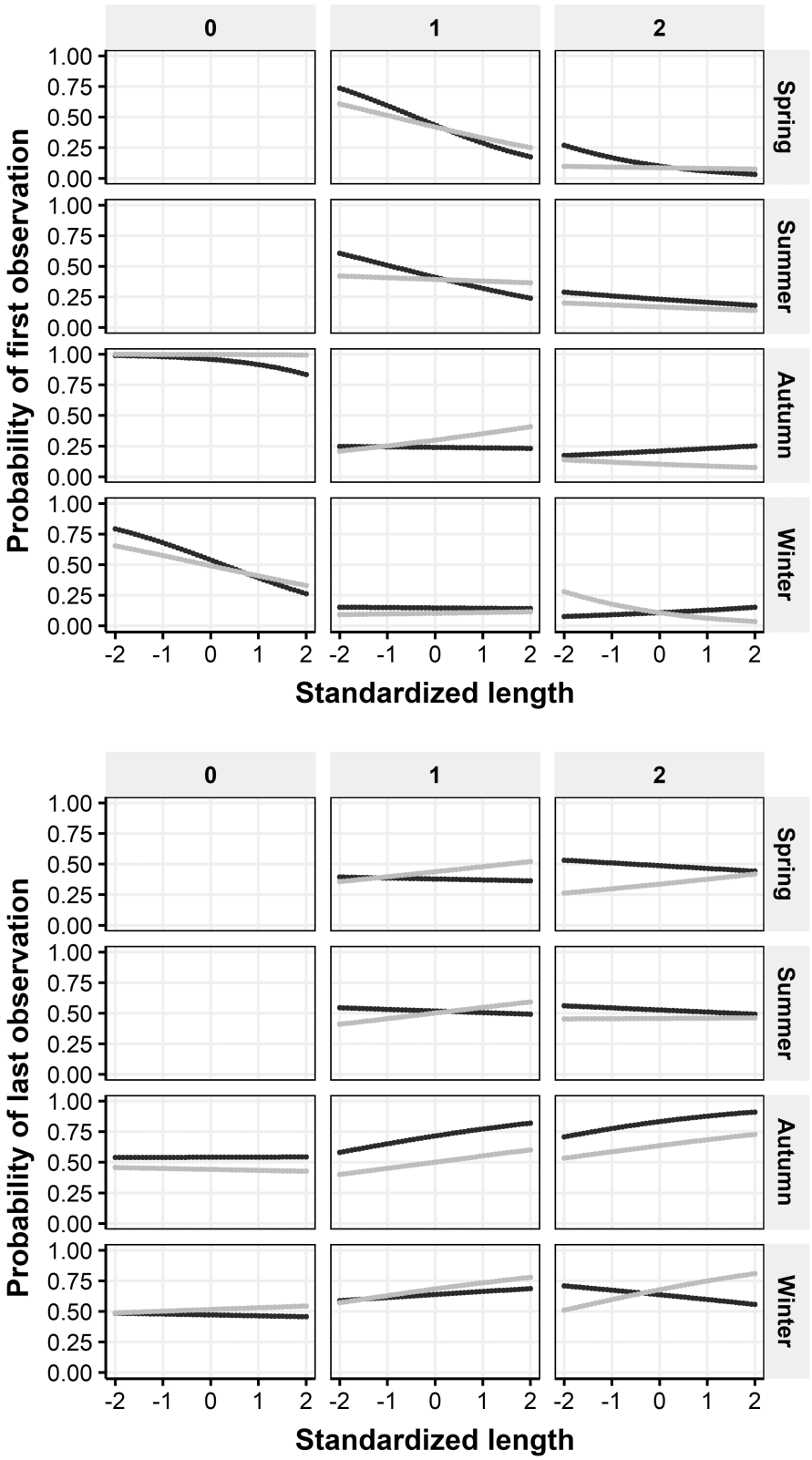

FIGURE 7 Strength of size dependence for the probability of entering (gain, above) or the probability of leaving (loss, below) the trout population across body size for tagged brook trout (black) and brown trout (grey) for different ages (columns) and seasons (rows). Lines represent predictions for the middle cohort from the study.

the way that multiple sources of change can complicate interpretation and understanding of causal links. Furthermore, we contribute an example to the expanding literature of long-term, intensive population studies testing hypotheses about the effects of multiple biotic and abiotic factors in the context of a changing climate (e.g. Ozgul et al., 2009).

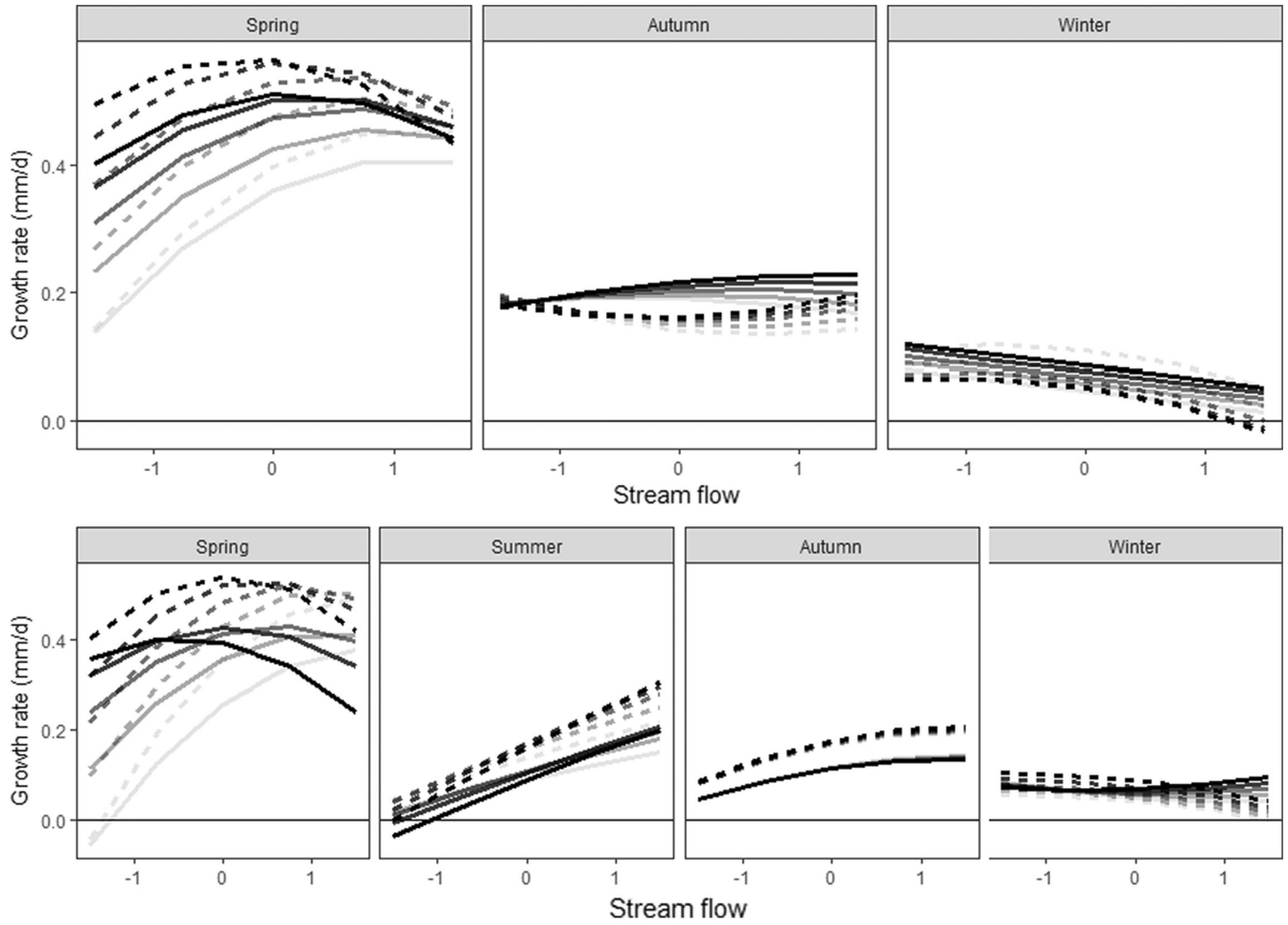

FIGURE 8 Stream flow, temperature interaction effect on growth rate for brook trout (solid line) and brown trout (dashed line). Temperature is indicated by opacity, warmer = darker where light to dark ranges from −1.5 to 1.5 standard deviation units. Growth year 0/1 fish are in the first row and growth year 1+ fish are in the second row.

The positive effect of increasing springtime water temperatures on growth and size in north and north-temperate freshwater fishes was suggested by some of the earliest assessments of potential climate change impacts (Hill & Magnuson, 1990) and has subsequently been supported by several studies (Bacon et al., 2005; Elliott & Elliott, 2010). These findings appear to run counter to the MTE and other general predictions of smaller body sizes as environments warm (Killen et al., 2010; Pauly & Cheung, 2018) as well as several empirical examples (Baudron et al., 2014; Huang et al., 2021). Consideration of the environmental context of fish growth and size in high-latitude freshwater ecosystems suggests some likely explanations. The spring season is generally characterized by high availability of aquatic invertebrate prey in both lotic (Angermeier, 1982) and lentic (Mittelback, 1981) habitats so that the increased metabolic demands of warmer temperatures may be less of a factor than in other seasons. Furthermore, under the moderate (<20°C) water temperatures encountered during the northern and north temperate spring seasons, fish foraging and prey capture success have been shown to increase with increasing temperatures, particularly for juvenile salmonids such as brook trout and brown trout feeding on drifting invertebrate prey (Hill & Grossman, 1993; Hughes & Dill, 1990; Nislow et al., 1999). Our observation of growth requiring more flow at cooler temperatures is consistent with the need for higher flux rates of drifting invertebrate prey when temperature-dependent capture success is low. Additionally, observed mean spring temperatures (9–12°C) were below the annual thermal optimum for brook trout (12°C) and brown trout (13°C) growth in the West Brook (Childress & Letcher, 2017), suggesting scope for increasing growth with warming spring temperatures. Given the generality of these considerations, in the absence of strong negative trends in prey availability, we expect that an increase in growth rate and body size may be frequently observed in many northern and north temperate freshwater fish populations.

More generally, these findings underscore the importance of seasonality in both individual growth and in the direction and magnitude of environmental change in estimating the impacts of a changing climate. While temperatures warmed in all four seasons during the course of our study, these increases had positive effects on growth during the spring where characteristic temperature ranges were generally below thermal optima for brook trout growth, but

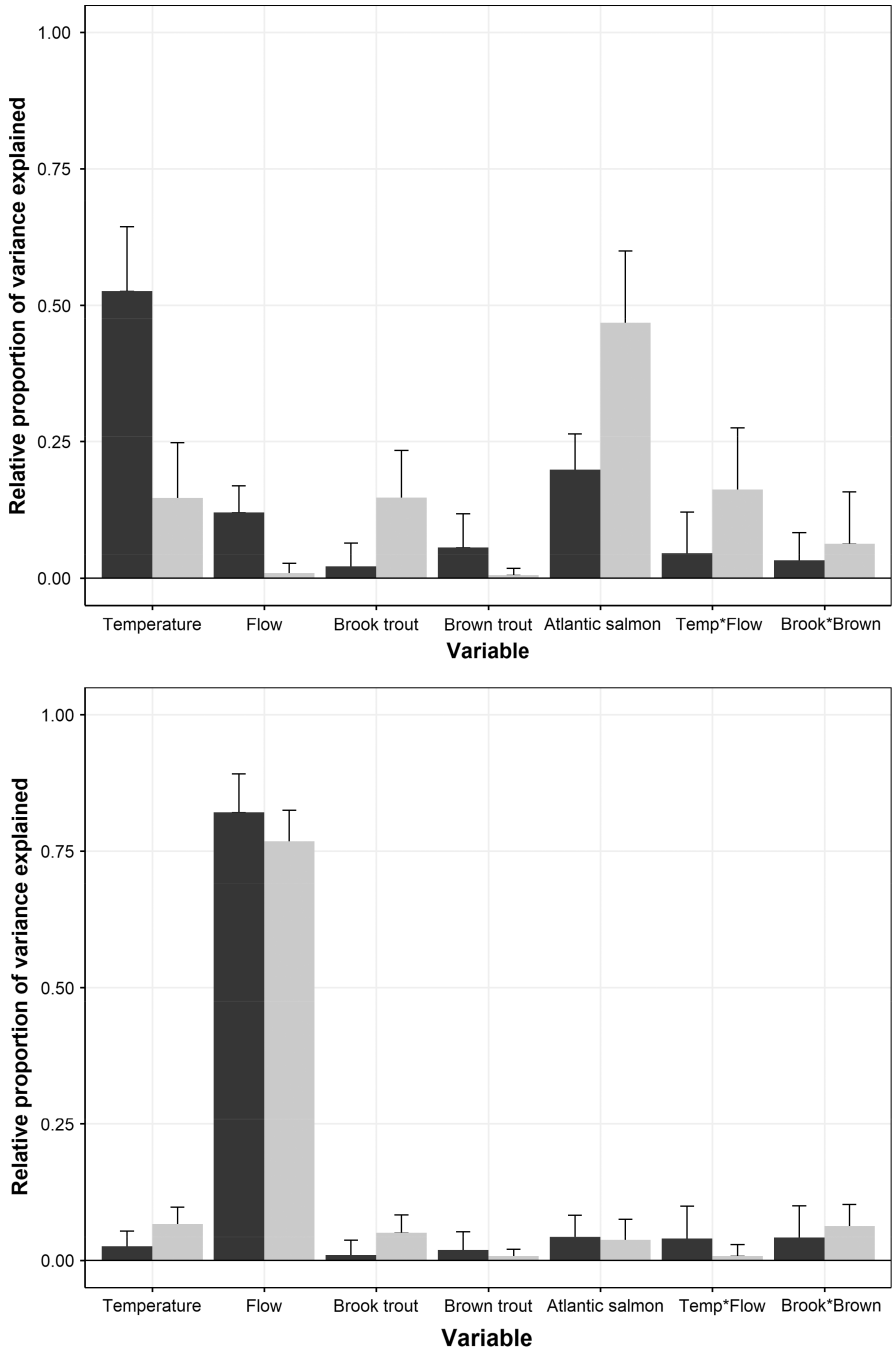

FIGURE 9 Relative proportion of variance in simulated growth rates explained by variables from the growth model for growth year 0/1 fish (above) and growth year 1+ (below) (mean ± 95% C.I. across Markov chain Monte Carlo [MCMC] interactions). Black bars = brook trout, grey bars = brown trout.

negative effects during the summer, where ranges were already above optimal values (see Huss et al., 2019; Rogers et al., 2011 for similar responses in marine fish). It is possible then that at some point increasing temperatures would have less of a positive effect during spring that could be outweighed by negative effects in the rest of the growing season, but because of the large proportion of growth accomplished during spring this would have to be a major shift in the temperature regime, to the point where other ecological factors would likely come in to play. Elliott and Elliott (2010) observed a very similar pattern in migratory brown trout in their study stream in England and estimated that it would take three times the currently observed level of warming before growth and size would decline. In our study, another climate-driven environmental factor, stream flow, unlike stream temperature, did not exhibit a trend over time in any season. However, like stream temperature, the effect of stream flow on growth was season specific, with high flows decreasing growth in winter, increasing growth in summer, and having a strong interactive effect with temperature in spring. Without the seasonal resolution provided by our study, these pathways and effects would likely be obscured.

As observed for brook trout, individual body size and juvenile growth rates of co-occurring brown trout increased over time, and warmer spring temperatures positively influenced growth and size. Previously, we had reported (Letcher et al., 2022) that body size and cohort strength in the West Brook covaried for the two species over time and space, suggesting that these resident populations were

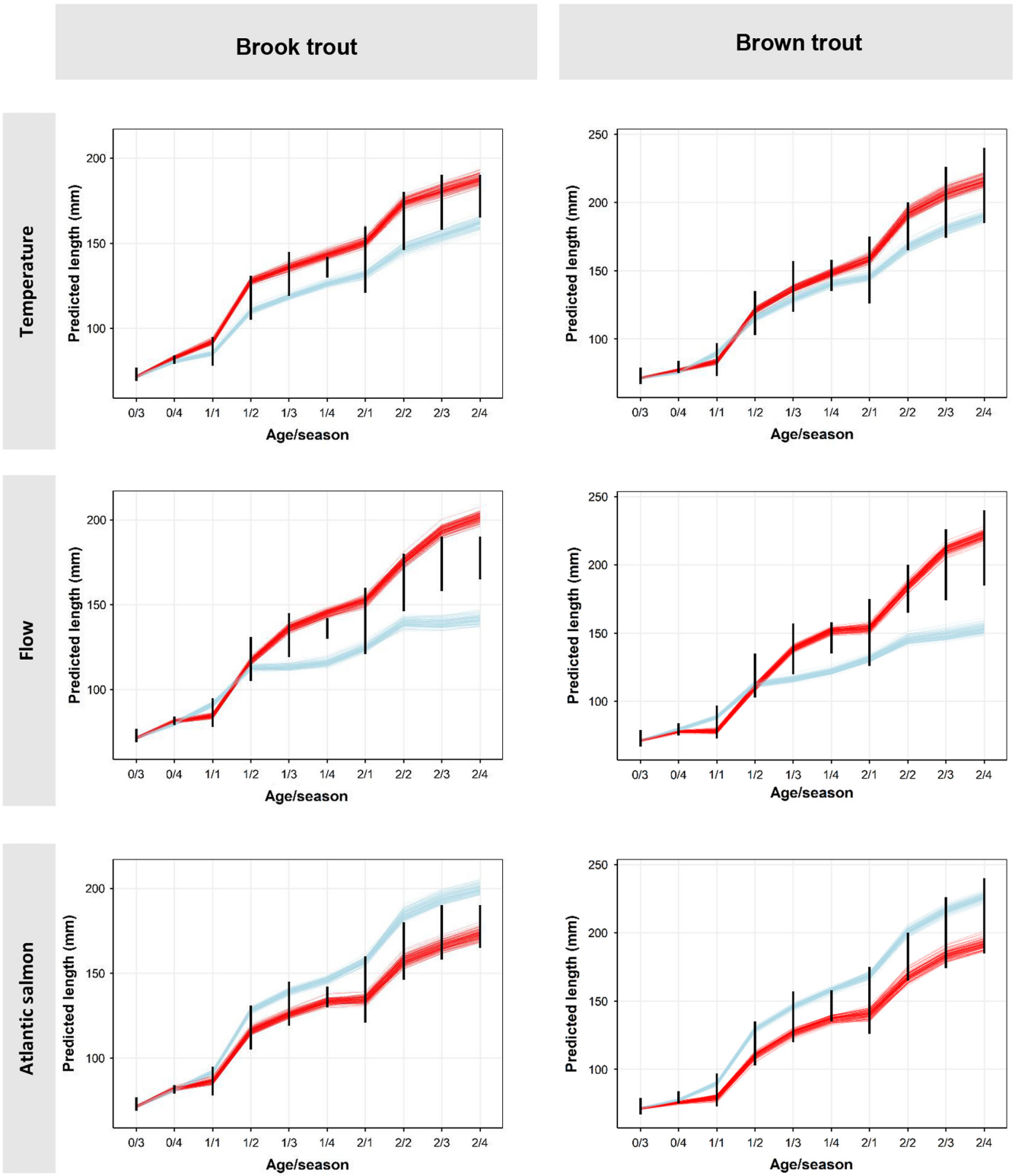

FIGURE 10 Predicted body sizes for brook trout (first column) and brown trout (second column) for changes in temperature (first row), flow (second row) and Atlantic salmon (third row) holding all other variables constant at average values. Red (upper) lines are predictions using values of +1.5 SD for each variable and blue lines are for −1.5 SD individual lines are predictions from randomly chosen Markov chain Monte Carlo [MCMC] iterations and represent the uncertainty in model predictions. Vertical black lines represent ranges of body sizes observed during the field study (Figure 5).

responding to common environmental drivers. However, in the more detailed growth model presented here, we observed that the primary driver of body size increase for brown trout was the decline and elimination of juvenile Atlantic salmon (comprising over half of the total salmonid biomass during the peak of their abundance) over the course of the study. It is not surprising that juvenile salmon

abundance had a stronger effect on brown trout than on brook trout given their distinct spatial distributions within the stream network (Letcher et al., 2022). Essentially all juvenile salmon, and >95% of the brown trout observations were in the mainstem West Brook. In contrast, a substantial proportion of the brook trout population in the West Brook uses the two small salmon-free tributaries during some part of their life cycle. Furthermore, previous studies suggest that Atlantic salmon and brown trout may have greater overlap in microhabitat preferences (Heggenes et al., 2002) than do salmon and brook trout, which would also contribute to the stronger influence of salmon on brown trout, even if brown trout tend to be competitively dominant over juvenile salmon (Armstrong et al., 2003; Burton et al., 2012) in direct interactions.

Body size increases in response to increasing temperatures may also have implications for species interactions and coexistence, an important consideration given that brown trout and brook trout are both invasive and invaded over parts of their native European and North American distributions (Korsu et al., 2007; Krueger & May, 1991). In this study, growth and body size of both species increased over time, but there was some indication that body size of brown trout, which are generally larger than brook trout in our study system, was increasing faster. Part of this difference may be due to their somewhat higher thermal optimum(13.3 vs. 11.9°C; Childress & Letcher, 2017) for growth of brown trout relative to brook trout. However, the influence of juvenile salmon on brown trout growth and size suggests that the presence of competitive species may, in some cases, interact with and modify the direct effects of a rising temperatures. It has been previously shown that for stream fishes, assemblage diversity can provide a measure of biotic resistance preventing the establishment of invasives (Gido et al., 2004). Our results bring up the intriguing possibility that maintenance of assemblage diversity can mediate interspecific interactions that may otherwise result in competitive displacement or extirpation (Rahel & Olden, 2008). More specifically, our results provide an additional mechanism explaining the importance of small, species-poor headwater streams to brook trout persistence and establishment in native and introduced settings (Letcher et al., 2007, 2022; Öhlund et al., 2008). Finally, results also underscore the need to improve understanding of interactions between juvenile anadromous and resident salmonids in the context of a changing environment in complex stream networks (Brenkman et al., 2008; Nislow et al., 2010). This is particularly relevant given that local abundance of anadromous salmonids tends to exhibit considerable interannual variation (Elliott, 1994; Glover et al., 2020) and also given large-scale declines in anadromous stocks worldwide (Limburg & Waldman, 2009).

Increased spring water temperature and the presence of juvenile salmon were primary drivers of long-term increases in body size in our system, but other factors had important influences on growth and size. The most supported statistical model included direct and indirect effects of temperature, stream flow and density, with these effects varying across seasons, species and age-classes, and in some cases dominating the effects of temperature. As one example, for adult brook and brown trout, a large proportion (>75%) of the annual variation in growth and size was due to variation in stream flow. Incorporating these multiple biotic and abiotic drivers is essential to capture the multiple dimensions of climate change across a range of environmental settings. For example, in salmonid streams in western North America, water availability is more limited than in the east and most climate projections forecast even drier future conditions (Isaak et al., 2012). Stream flow has been found to be a dominant driver of size and growth and may become even more so in the future. This is consistent with our observation of >75% of the interannual variation in adult growth during the generally low-flow summer and autumn seasons is positively associated with stream flow even under the mesic conditions of our region, and this influence may increase depending on future changes in hydrologic regimes. In addition, changes in streamflow can have effects on size and growth mediated by biotic (density dependent) mechanisms. Density-dependent negative effects on growth and body size are ubiquitous in salmonids (Grant & Imre, 2005) and have been reported previously for our study system (Bassar et al., 2016; Letcher et al., 2022). Density-dependent effects (apart from the effect of juvenile salmon on brown trout) appear to be relatively small compared to other factors in our present analysis. However, for fall-spawning salmonids (such as all three species in our study system), high flows during the winter incubation period have strongly negative impacts on recruitment and, by extension, population size and density (Bassar et al., 2016; Kanno et al., 2015). Forecasted increases in winter runoff and extreme flows in the North Atlantic region (Ning et al., 2015) via strong negative effects on cohort strength and population density may therefore exert a stronger influence on individual growth and body than currently observed.

Climate-driven impacts on growth and size have important implications for ecological roles and population dynamics. It will therefore become increasingly important to integrate these climate effects with other size-dependent processes influencing populations and species assemblages. For example, size-selective harvest (fishing) and barriers to migration can strongly impact growth, body size and size-structure (Fraser et al., 2014; Hutchings, 2005; Swain et al., 2007), sometimes in complex and unexpected ways (Czorlich et al., 2022). Given that these influences may be under policy and management control, they could have the possibility of either ameliorating or exacerbating climate-driven changes. Furthermore, in many size-structured populations, fecundity and reproductive value are size dependent and age dependent (Winemiller & Rose, 1992). Increases in growth and body size therefore have the potential to ameliorate population declines, including those associated with climate change, via either indirect (density dependence) or direct (thermal performance) mechanisms, but these dynamics are complex and have not been extensively explored. Models that integrate these effects on multiple vital rates and allow robust predictions are essential for this improved understanding.

AUTHOR CONTRIBUTIONS

Ben Letcher, Keith Nislow, Matthew O'Donnell, Andrew Whiteley, Jason Coombs and Todd Dubreuil conceived the ideas and

designed the methodology; Ben Letcher, Keith Nislow, Matthew O'Donnell, Andrew Whiteley, Jason Coombs and Todd Dubreuil collected the data, Ben Letcher and Daniel Turek analysed the data, Ben Letcher and Keith Nislow led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

We thank all the students, post-docs and volunteers that have helped with field work. We also thank Robert al-Chokhachy and two anonymous reviewers for providing comments that improved the manuscript. Funding has been provided by the US Forest Service, the US Fish and Wildlife Service and the USGS. Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

CONFLICT OF INTEREST

The authors have no conflict of interest to declare for this manuscript.

DATA AVAILABILITY STATEMENT

Data available in ScienceBase repository at https://doi.org/10.5066/P9PBW04Y (Letcher, 2022).

ORCID

Benjamin H. Letcher https://orcid.org/0000-0003-0191-5678
Keith H. Nislow https://orcid.org/0000-0001-8051-5765
Matthew J. O'Donnell https://orcid.org/0000-0002-9089-2377
Andrew R. Whiteley https://orcid.org/0000-0002-8159-6381
Jason A. Coombs https://orcid.org/0000-0001-6099-3954
Todd L. Dubreuil https://orcid.org/0000-0003-0189-4336
Daniel B. Turek https://orcid.org/0000-0002-1453-1908

REFERENCES

Angermeier, P. L. (1982). Resource seasonality and fish diets in an Illinois stream. *Environmental Biology of Fishes*, *7*(3), 251–264. https://doi.org/10.1007/BF00002500

Armstrong, J. D., Kemp, P. S., Kennedy, G. J. A., Ladle, M., & Milner, N. J. (2003). Habitat requirements of Atlantic salmon and brown trout in rivers and streams. *Fisheries Research*, *62*(2), 143–170. https://doi.org/10.1016/S0165-7836(02)00160-1

Bacon, P. J., Gurney, W. S. C., Jones, W., Mclaren, I. S., & Youngson, A. F. (2005). Seasonal growth patterns of wild juvenile fish: Partitioning variation among explanatory variables, based on individual growth trajectories of Atlantic salmon (*Salmo salar*) parr. *Journal of Animal Ecology*, *74*, 1–11.

Bassar, R. D., Letcher, B. H., Nislow, K. H., & Whiteley, A. R. (2016). Changes in seasonal climate outpace compensatory density-dependence in eastern brook trout. *Global Change Biology*, *22*, 577–593. https://doi.org/10.1111/gcb.13135

Baudron, A. R., Needle, C. L., Rijnsdorp, A. D., & Tara Marshall, C. (2014). Warming temperatures and smaller body sizes: Synchronous changes in growth of North Sea fishes. *Global Change Biology*, *20*(4), 1023–1031. https://doi.org/10.1111/gcb.12514

Brenkman, S. J., Pess, G. R., Torgersen, C. E., Kloehn, K. K., Duda, J. J., & Corbett, S. C. (2008). Predicting recolonization patterns and interactions between potamodromous and anadromous salmonids in response to dam removal in the Elwha River, Washington State, USA. *Northwest Science*, *82*(sp1), 91–106. https://doi.org/10.3955/0029-344X-82.S.I.91

Brooks, S., & Gelman, A. (1998). General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics*, *7*(4), 434–455. https://doi.org/10.1080/10618600.1998.10474787

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, *85*(7), 1771–1789. https://doi.org/10.1890/03-9000

Burkhead, N. M. (2012). Extinction rates in north American freshwater fishes, 1900–2010. *BioScience*, *62*(9), 798–808. https://doi.org/10.1525/bio.2012.62.9.5

Burton, T., McKelvey, S., Stewart, D. C., Armstrong, J. D., & Metcalfe, N. B. (2012). Offspring investment in wild Atlantic salmon (*Salmo salar*): Relationships with smolt age and spawning condition. *Ecology of Freshwater Fish*, *22*, 317–321. https://doi.org/10.1111/eff.12019

Chevan, A., & Sutherland, M. (1991). Hierarchical partitioning. *The American Statistician*, *45*, 90–96.

Childress, E. S., & Letcher, B. H. (2017). Estimating thermal performance curves from repeated field observations. *Ecology*, *98*(5), 1377–1387. https://doi.org/10.1002/ecy.1801

Czorlich, Y., Aykanat, T., Erkinaro, J., Orell, P., & Primmer, C. R. (2022). Rapid evolution in salmon life history induced by direct and indirect effects of fishing. *Science*, *376*(6591), 420–423. https://doi.org/10.1126/science.abg5980

de Valpine, P., Turek, D., Paciorek, C. J., Anderson-Bergman, C., Lang, D. T., & Bodik, R. (2017). Programming with models: Writing statistical algorithms for general model structures with NIMBLE. *Journal of Computational and Graphical Statistics*, *26*(2), 403–413. https://doi.org/10.1080/10618600.2016.1172487

Dell, A. I., Pawar, S., & Savage, V. M. (2011). Systematic variation in the temperature dependence of physiological and ecological traits. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(26), 10591–10596. https://doi.org/10.1073/pnas.1015178108

Elliott, J. (1994). *Quantitative ecology and the brown trout*. Oxford University Press.

Elliott, J., & Elliott, J. (2010). Temperature requirements of Atlantic salmon *Salmo salar*, brown trout *Salmo trutta* and Arctic charr *Salvelinus alpinus*: Predicting the effects of climate change. *Journal of Fish Biology*, *44*, 1–25. https://doi.org/10.1111/j.1095-8649.2010.02762.x

Forster, J., Hirst, A. G., & Atkinson, D. (2012). Warming-induced reductions in body size are greater in aquatic than terrestrial species. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(47), 19310–19314. https://doi.org/10.1073/pnas.1210460109

Fraser, D., Debes, P. V., Bernatchez, L., & Hutchings, J. a. (2014). Population size, habitat fragmentation, and the nature of adaptive variation in a stream fish. *Proceedings of the Royal Society B: Biological Sciences*, *281*(July), 20140370.

Gelman, A. (2003). A Bayesian formulation of exploratory data analysis and goodness-of-fit testing*. *International Statistical Review*, *71*, 369–382. https://doi.org/10.1111/j.1751-5823.2003.tb00203.x/full

Gelman, A., Carlin, J. B., Stern, H. S., & Rubin, D. (2004). *Bayesian data analysis* (2nd ed.). Chapman and Hall/CRC.

Gido, K. B., Schaefer, J. F., & Pigg, J. (2004). Patterns of fish invasions in the Great Plains of North America. *Biological Conservation*, *118*(2), 121–131. https://doi.org/10.1016/j.biocon.2003.07.015

Gillooly, J. F., Brown, J. H., West, G. B., Savage, V. M., & Charnov, E. L. (2001). Effects of size and temperature on metabolic rate. *Science*, *293*(5538), 2248–2251. https://doi.org/10.1126/science.1061967

Glover, R. S., Soulsby, C., Fryer, R. J., Birkel, C., & Malcolm, I. A. (2020). Quantifying the relative importance of stock level, river temperature and discharge on the abundance of juvenile Atlantic salmon

(*Salmo salar*). *Ecohydrology*, *13*(6), 1–16. https://doi.org/10.1002/eco.2231

Grant, J. W. A., & Imre, I. (2005). Patterns of density-dependent growth in juvenile stream-dwelling salmonids. *Journal of Fish Biology*, *67*(Suppl. B), 100–110. https://doi.org/10.1111/j.0022-1112.2005.00916.x

Gries, G., & Letcher, B. H. (2002). Tag retention and survival of Age-0 Atlantic Salmon following surgical implantation with passive integrated transponder tags. *North American Journal of Fisheries Management*, *22*(1), 219–222. https://doi.org/10.1577/1548-8675(2002)022<0219:TRASOA>2.0.CO;2

Heggenes, J., Saltveit, S. J., Bird, D., & Grew, R. (2002). Static habitat partitioning and dynamic selection by sympatric young Atlantic salmon and brown trout in south-West England streams. *Journal of Fish Biology*, *60*(1), 72–86. https://doi.org/10.1006/jfbi.2001.1811

Hill, J., & Grossman, G. H. (1993). An energetic model of microhabitat use for rainbow trout and rosyside dace. *Ecology*, *74*, 685–698.

Hill, D. K., & Magnuson, J. J. (1990). Potential effects of global climate warming on the growth and prey consumption of Great Lakes fish. *Transactions of the American Fisheries Society*, *119*(2), 265–275. https://doi.org/10.1577/1548-8659(1990)119<0265:peogcw>2.3.co;2

Horton, G. E., Dubreuil, T. L., & Letcher, B. H. (2007). A model for estimating passive integrated transponder (PIT) tag antenna efficiencies for interval-specific emigration rates. *Transactions of the American Fisheries Society*, *136*(5), 1165–1176. https://doi.org/10.1577/T06-053.1

Horton, G. E., & Letcher, B. H. (2008). Movement patterns and study area boundaries: Influences on survival estimation in capture-mark-recapture studies. *Oikos*, *117*, 1131–1142.

Huang, M., Ding, L., Wang, J., Ding, C., & Tao, J. (2021). The impacts of climate change on fish growth: A summary of conducted studies and current knowledge. *Ecological Indicators*, *121*, 106976. https://doi.org/10.1016/j.ecolind.2020.106976

Hughes, N. F., & Dill, L. M. (1990). Position choice by drift-feeding salmonids: Model and test for Arctic grayling (*Thymallus arcticus*) in subarctic mountain streams, interior Alaska. *Canadian Journal of Fisheries and Aquatic Sciences*, *47*, 2039–2048.

Huss, M., Lindmark, M., Jacobson, P., van Dorst, R. M., & Gårdmark, A. (2019). Experimental evidence of gradual size-dependent shifts in body size and growth of fish in response to warming. *Global Change Biology*, *25*(7), 2285–2295. https://doi.org/10.1111/gcb.14637

Hutchings, J. A. (2005). Life history consequences of overexploitation to population recovery in Northwest Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, *62*(4), 824–832. https://doi.org/10.1139/f05-081

Isaak, D. J., Wollrab, S., Horan, D., & Chandler, G. (2012). Climate change effects on stream and river temperatures across the northwest U.S. from 1980–2009 and implications for salmonid fishes. *Climatic Change*, *113*(2), 499–524. https://doi.org/10.1007/s10584-011-0326-z

Kanno, Y., Letcher, B. H., Hitt, N. P., Boughton, D. a., Wofford, J. E. B., & Zipkin, E. F. (2015). Seasonal weather patterns drive population vital rates and persistence in a stream fish. *Global Change Biology*, *21*(5), 1856–1870. https://doi.org/10.1111/gcb.12837

Kery, M., & Schaub, M. (2011). *Bayesian population analysis using WinBUGS—A hierarchical perspective*. Academic Press.

Killen, S. S., Atkinson, D., & Glazier, D. S. (2010). The intraspecific scaling of metabolic rate with body mass in fishes depends on lifestyle and temperature. *Ecology Letters*, *13*(2), 184–193. https://doi.org/10.1111/j.1461-0248.2009.01415.x

Korsu, K., Huusko, A., & Muotka, T. (2007). Niche characteristics explain the reciprocal invasion success of stream salmonids in different continents. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(23), 9725–9729. https://doi.org/10.1073/pnas.0610719104

Krueger, C. C., & May, B. (1991). Ecological and genetic effects of salmonid introductions. *Canadian Journal of Fisheries and Aquatic Sciences*, *48*(Suppl. 1), 66–77.

Leprieur, F., Beauchard, O., Blanchet, S., Oberdorff, T., & Brosse, S. (2008). Fish invasions in the World's river systems: When natural processes are blurred by human activities. *PLoS Biology*, *6*(2), e28. https://doi.org/10.1371/journal.pbio.0060028

Letcher, B. H. (2022). *West brook trout data*. U.S. Geological Survey data release. https://doi.org/10.5066/P9PBW04Y

Letcher, B. H., Nislow, K. H., Coombs, J., O'Donnell, M. J., & Dubreuil, T. L. (2007). Population response to habitat fragmentation in a stream-dwelling brook trout population. *PLoS ONE*, *2*(11), e1139. https://doi.org/10.1371/journal.pone.0001139

Letcher, B. H., Nislow, K. H., O'Donnell, M. J., Whiteley, A. R., Coombs, J. A., & Dubreuil, T. L. (2022). Cohort strength and body size in co-occurring salmonids in a small stream network: Variation in space and time. *Canadian Journal of Fisheries and Aquatic Sciences*, *79*(1), 133–147. https://doi.org/10.1139/cjfas-2020-0418

Letcher, B. H., Schueller, P., Bassar, R. D., Nislow, K. H., Coombs, J. A., Sakrejda, K., Morrissey, M., Sigourney, D. B., Whiteley, A. R., O'Donnell, M. J., & Dubreuil, T. L. (2015). Robust estimates of environmental effects on population vital rates: An integrated capture-recapture model of seasonal brook trout growth, survival and movement in a stream network. *Journal of Animal Ecology*, *84*(2), 337–352. https://doi.org/10.1111/1365-2656.12308

Limburg, K. E., & Waldman, J. R. (2009). Dramatic declines in North Atlantic diadromous fishes. *BioScience*, *59*(11), 955–965. https://doi.org/10.1525/bio.2009.59.11.7

Lindmark, M., Huss, M., Ohlberger, J., & Gårdmark, A. (2018). Temperature-dependent body size effects determine population responses to climate warming. *Ecology Letters*, *21*(2), 181–189. https://doi.org/10.1111/ele.12880

Mačić, V., Albano, P. G., Almpanidou, V., Claudet, J., Corrales, X., Essl, F., Evagelopoulos, A., Giovos, I., Jimenez, C., Kark, S., Marković, O., Mazaris, A. D., Ólafsdóttir, G. Á., Panayotova, M., Petović, S., Rabitsch, W., Ramdani, M., Rilov, G., Tricarico, E., … Katsanevakis, S. (2018). Biological invasions in conservation planning: A global systematic review. *Frontiers in Marine Science*, *5*, 1–13. https://doi.org/10.3389/fmars.2018.00178

Mittelback, G. (1981). Foraging efficiency and body size: A study of optimal diet and habitat use by bluegills. *Ecology*, *62*(5), 1370–1386.

Nielsen, J. P. (1999). *Record extension and streamflow statistics for the Pleasant River, Maine*. US Department of the Interior, US Geological Survey Information Services. Http://Me.Water.Usgs.Gov/Reports/Finalreport.Pdf

Ning, L., Riddle, E. E., & Bradley, R. S. (2015). Projected changes in climate extremes over the northeastern United States. *Journal of Climate*, *28*(8), 3289–3310. https://doi.org/10.1175/JCLI-D-14-00150.1

Nislow, K. H., Armstrong, J. D., & Grant, J. W. A. (2010). The role of competition in the ecology of juvenile Atlantic Salmon. In *Atlantic Salmon ecology* (pp. 171–197). Wiley-Blackwell. https://doi.org/10.1002/9781444327755.ch7

Nislow, K. H., Folt, C. L., & Parrish, D. L. (1999). Favorable foraging locations for young Atlantic salmon: Application to habitat and population restoration. *Ecological Applications*, *9*(3), 1085–1099. https://doi.org/10.1890/1051-0761(1999)009[1085:FFLFYA]2.0.CO;2

Ohlberger, J. (2013). Climate warming and ectotherm body size—From individual physiology to community ecology. *Functional Ecology*, *27*(4), 991–1001. https://doi.org/10.1111/1365-2435.12098

Öhlund, G., Nordwall, F., Degerman, E., & Eriksson, T. (2008). Life history and large-scale habitat use of brown trout (*Salmo trutta*) and brook trout (*Salvelinus fontinalis*)—Implications for species replacement patterns. *Canadian Journal of Fisheries and Aquatic Sciences*, *65*(4), 633–644. https://doi.org/10.1139/F08-003

Ozgul, A., Tuljapurkar, S., Benton, T. G., Pemberton, J. M., Clutton-Brock, T. H., & Coulson, T. (2009). The dynamics of phenotypic change and the shrinking sheep of St. Kilda. *Science*, *325*(5939), 464–467. https://doi.org/10.1126/science.1173668

Pauly, D., & Cheung, W. W. L. (2018). Sound physiological knowledge and principles in modeling shrinking of fishes under climate change. *Global Change Biology*, *24*(1), e15–e26. https://doi.org/10.1111/gcb.13831

Payne, N. L., Smith, J. A., van der Meulen, D. E., Taylor, M. D., Watanabe, Y. Y., Takahashi, A., Marzullo, T. A., Gray, C. A., Cadiou, G., & Suthers, I. M. (2016). Temperature dependence of fish performance in the wild: Links with species biogeography and physiological thermal tolerance. *Functional Ecology*, *30*(6), 903–912. https://doi.org/10.1111/1365-2435.12618

Peralta-Maraver, I., & Rezende, E. L. (2020). Heat tolerance in ectotherms scales predictably with body size. *Nature Climate Change*, *11*(January), 58–63. https://doi.org/10.1038/s41558-020-00938-y

Plummer, M., Nest, N., Cowles, K., & Vines, K. (2006). CODA: Convergence diagnosis and output analysis for MCMC. *R News*, *6*, 7–11.

Rahel, F. J., & Olden, J. D. (2008). Assessing the effects of climate change on aquatic invasive species. *Conservation Biology*, *22*(3), 521–533. https://doi.org/10.1111/j.1523-1739.2008.00950.x

Reuman, D. C., Holt, R. D., & Yvon-Durocher, G. (2014). A metabolic perspective on competition and body size reductions with warming. *Journal of Animal Ecology*, *83*(1), 59–69. https://doi.org/10.1111/1365-2656.12064

Rogers, L. A., Stige, L. C., Olsen, E. M., Knutsen, H., Chan, K. S., & Stenseth, N. C. (2011). Climate and population density drive changes in cod body size throughout a century on the Norwegian coast. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(5), 1961–1966. https://doi.org/10.1073/pnas.1010314108

Royle, J. A. (2008). Modeling individual effects in the Cormack-jolly-Seber model: A state-space formulation. *Biometrics*, *64*(2), 364–370. https://doi.org/10.1111/j.1541-0420.2007.00891.x

Rubin, D. (1984). Bayesianly justifiable and relevant frequency calculations for the applied statistician. *The Annals of Statistics*, *12*(4), 1151–1172.

Sheridan, J. A., & Bickford, D. (2011). Shrinking body size as an ecological response to climate change. *Nature Climate Change*, *1*(8), 401–406. https://doi.org/10.1038/nclimate1259

Siddique, R., Karmalkar, A., Sun, F., & Palmer, R. (2020). Hydrological extremes across the Commonwealth of Massachusetts in a changing climate. *Journal of Hydrology: Regional Studies*, *32*(September 2020), 100733. https://doi.org/10.1016/j.ejrh.2020.100733

Sigourney, D. B., Horton, G. E., Dubreuil, T. L., Varaday, A. M., & Letcher, B. H. (2005). Electroshocking and PIT tagging of juvenile Atlantic Salmon: Are there interactive effects on growth and survival? *North American Journal of Fisheries Management*, *25*(3), 1016–1021. https://doi.org/10.1577/M04-075.1

Singh, J. S. (2002). The biodiversity crisis: A multifaceted review. *Current Science*, *82*(6), 638–647.

Smoliński, S., Deplanque-Lasserre, J., Hjörleifsson, E., Geffen, A. J., Godiksen, J. A., & Campana, S. E. (2020). Century-long cod otolith biochronology reveals individual growth plasticity in response to temperature. *Scientific Reports*, *10*(1), 1–13. https://doi.org/10.1038/s41598-020-73652-6

Stocker, T. F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S. K., Boschung, J., Nauels, A., Xia, Y., Bex, V., & Midgley, P. M. (Eds.). (2013). *IPCC, 2013: Climate change 2013: The physical science basis. Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change*. Cambridge University Press.

Stoffels, R. J., Weatherman, K. E., Bond, N. R., Morrongiello, J. R., Thiem, J. D., Butler, G., Koster, W., Kopf, R. K., McCasker, N., Ye, Q., Zampatti, B., & Broadhurst, B. (2020). Stage-dependent effects of river flow and temperature regimes on the growth dynamics of an apex predator. *Global Change Biology*, *26*(12), 6880–6894. https://doi.org/10.1111/gcb.15363

Swain, D. P., Sinclair, A. F., & Hanson, J. M. (2007). Evolutionary response to size-selective mortality in an exploited fish population. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1613), 1015–1022. https://doi.org/10.1098/rspb.2006.0275

U.S. Geological Survey. (2018). *National Hydrography Dataset Plus High Resolution (NHDPlus HR) for 4-digit Hydrologic Unit - 0108*. https://prd-tnm.s3.amazonaws.com/StagedProducts/Hydrography/NHDPlusHR/Beta/GDB/NHDPLUS_H_0108_HU4_GDB.zip%0A%0A

U.S. Geological Survey. (2020a). *National Elevation Dataset (10M)*. https://datagateway.nrcs.usda.gov/

U.S. Geological Survey. (2020b). *National Hydrography Dataset (24K)*. https://datagateway.nrcs.usda.gov/

Walter, J. A., Sheppard, L. W., Anderson, T. L., Kastens, J. H., Bjørnstad, O. N., Liebhold, A. M., & Reuman, D. C. (2017). The geography of spatial synchrony. *Ecology Letters*, *20*(7), 801–814. https://doi.org/10.1111/ele.12782

Winemiller, K. O., & Rose, K. A. (1992). Patterns of life-history diversification in north American fishes: Implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences*, *49*(10), 2196–2218. https://doi.org/10.1139/f92-242

Xu, C. L., Letcher, B. H., & Nislow, K. H. (2010). Size-dependent survival of brook trout Salvelinus fontinalis in summer: Effects of water temperature and stream flow. *Journal of Fish Biology*, *76*(10), 2342–2369. https://doi.org/10.1111/j.1095-8649.2010.02619.x

Zydlewski, G. B., Horton, G. E., Dubreuil, T. L., Letcher, B. H., Casey, S., & Zydlewski, J. (2006). Remote monitoring of fish in small streams: A unified approach using PIT tags. *Fisheries*, *31*(10), 492–502. https://doi.org/10.1577/1548-8446(2006)31[492:RMOFIS]2.0.CO;2

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Letcher, B. H., Nislow, K. H., O'Donnell, M. J., Whiteley, A. R., Coombs, J. A., Dubreuil, T. L., & Turek, D. B. (2023). Identifying mechanisms underlying individual body size increases in a changing, highly seasonal environment: The growing trout of West brook. *Journal of Animal Ecology*, *92*, 78–96. https://doi.org/10.1111/1365-2656.13833