


## Individual heterogeneity and early life conditions shape growth in a freshwater top predator

CHLOÉ R. NATER <sup>1,5</sup>, ATLE RUSTADBAKKEN,<sup>2</sup> TORBJØRN ERGON,<sup>1</sup> ØYSTEIN LANGANGEN,<sup>1</sup>  
S. JANNICKE MOE,<sup>3</sup> YNGVILD VINDEENES,<sup>1</sup> LEIF ASBJØRN VØLLESTAD,<sup>1</sup> AND PER AASS<sup>4</sup>

<sup>1</sup>Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology, University of Oslo, P. O. Box 1066 Blindern, N-0316 Oslo, Norway

<sup>2</sup>The Freshwater Fish Administration, County Governor of Hedmark, P. O. Box 4034, N-2306 Hamar, Norway

<sup>3</sup>Norwegian Institute for Water Research (NIVA), Gaustadalléen 21, N-0349 Oslo, Norway

<sup>4</sup>Zoological Museum, The Natural History Museums and Botanical Garden, University of Oslo, Sars Gate 1, N-0562 Oslo, Norway

**Abstract.** Body size can have profound impacts on survival, movement, and reproductive schedules shaping individual fitness, making growth a central process in ecological and evolutionary dynamics. Realized growth is the result of a complex interplay between life history schedules, individual variation, and environmental influences. Integrating all of these aspects into growth models is methodologically difficult, depends on the availability of repeated measurements of identifiable individuals, and consequently represents a major challenge in particular for natural populations. Using a unique 30-yr time series of individual length measurements inferred from scale year rings of wild brown trout, we develop a Bayesian hierarchical model to estimate individual growth trajectories in temporally and spatially varying environments. We reveal a gradual decrease in average juvenile growth, which has carried over to adult life and contributed to decreasing sizes observed at the population level. Commonly studied environmental drivers like temperature and water flow did not explain much of this trend and overall persistent and among-year individual variation dwarfed temporal variation in growth patterns. Our model and results are relevant to a wide range of questions in ecology and evolution requiring a detailed understanding of growth patterns, including conservation and management of many size-structured populations.

**Key words:** biphasic growth model; brown trout; early life; environment; environmental covariate; growth; individual heterogeneity; measurement error; ontogeny; size decrease.

### INTRODUCTION

Body size is an important component of life history in many species and often has profound impacts on demographic variables related to survival, reproduction, and migration (Peters 1986). The process of growth, and accurate modeling thereof, is thus of central importance to questions in life history theory, population ecology, and eco-evolutionary dynamics (Berner and Blanckenhorn 2007, Ozgul et al. 2009, de Valpine et al. 2014).

Realized growth is the result of a complex interplay of many factors. Growth patterns may differ considerably between life-history stages and exhibit pronounced ontogenetic shifts, for example when organisms start providing for themselves (English et al. 2012), change their habitat or diet (de Roos and Persson 2013), or mature and begin allocating resources to reproduction (Minte-Vera et al. 2016). Within this pre-set trajectory given by life history, individual growth will vary further depending on innate differences in growth potential arising from variation in metabolic rates (Metcalf

et al. 1995), behavioral traits (Vøllestad and Quinn 2003), and their interaction with the sequence of environmental conditions an individual experiences during its life (Pfister and Stevens 2003, Shelton and Mangel 2012). Not accounting for individual variability in growth leads to bias in growth model parameters (Pilling et al. 2002, Hart and Chute 2009), and this bias can propagate into predictions of population- and eco-evolutionary dynamics (Pfister and Stevens 2003, Vindenes and Langangen 2015). Nonetheless, approaches to growth modeling that account for ontogeny, individual variation, and their interaction with environmental conditions are rare owing to two major methodological issues: difficulty of implementing non-linear hierarchical models and the requirement of longitudinal data with multiple captures per individual (English et al. 2012, Vincenzi et al. 2014).

Recent advances using hierarchical state-space frameworks have seen the successful inclusion of random individual variation into standard growth models (English et al. 2012, Shelton and Mangel 2012, Vincenzi et al. 2014). The dependence on long-term individual-based data, however, remains a vexing problem for the majority of study systems. A large number of individuals need to be captured and measured repeatedly over a sufficiently long period in order to fit

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<sup>5</sup>E-mail: c.r.nater@ibv.uio.no

growth models including variation among individuals and over time, an objective that is costly and often impossible for natural populations. An alternative offers itself for organisms that form structures reflecting their growth history, for instance year rings in trees or fish scales. When such structures can be utilized to reconstruct an individual's growth history, a single sample from one individual provides data for several years, making recapture unnecessary. Estimates of body size based on proxies like year rings, however, are likely to be subject to considerable and likely systematic, non-random error arising from measurement and interpolation (Panfili et al. 2002, Dietrich and Cunjak 2007). Thus, while size estimates inferred from year rings can be very valuable for modeling growth, they require investigation of and accounting for measurement error and structure therein.

Here, we develop a biphasic growth model that accounts for ontogeny, individual variation, and temporal changes in the presence of structured measurement error resulting from the use of year rings on fish scales and apply it to a unique data set of large-sized brown trout *Salmo trutta* spanning over 30 yr. We underline the importance of individual variation over the whole life cycle, highlight the relevance of quantifying measurement error, and show how a model for individual growth trajectories can be used to disentangle mechanisms underlying a trend of decreasing size observed at the population level.

## METHODS

### Model system and data collection

We developed growth models for a population of brown trout (hereafter: trout) inhabiting the lake Mjøsa and its main inlet river Gudbrandsdalslågen in eastern Norway. These trout, referred to as “Hunder trout” (Aass et al. 1989), are famous for their large body size (over 100 cm). The life history is characterized by a juvenile period exclusively constrained to the river and an adult period in the lake including biennial spawning migrations to the river (Fig. 1). The juvenile period typically lasts for 3–5 yr, after which young fish undergo smolting and migrate downstream into the lake at an average length of 250 mm (Appendix S1: Fig. S1, Table S1). After another 2–4 yr in the lake, the trout reach sexual maturity and start their first spawning migration upriver at an average length of 625 mm (Appendix S1: Fig. S1, Table S1). Upriver spawning migrations can begin anytime between late June and early October, but the majority of fish migrate upriver in late August and early September (Aass et al. 1989). Eggs are deposited in the river, where they hatch the following spring. Spawning trout return to the lake after the reproductive season is over and usually take a resting year before spawning again (Aass et al. 1989).

The Hunderfossen waterfalls in the lower part of the river were dammed for hydroelectric power production in 1961, resulting in large changes in hydrological conditions in the river and causing a drastic reduction of suitable spawning and recruitment area for the trout (Aass et al. 1989). Two measures were introduced in 1966 to mediate this: (1) stocking program with annual releases of recognizable, hatchery-reared smolt and (2) construction of a fish ladder to partially restore connectivity to the upriver spawning areas.

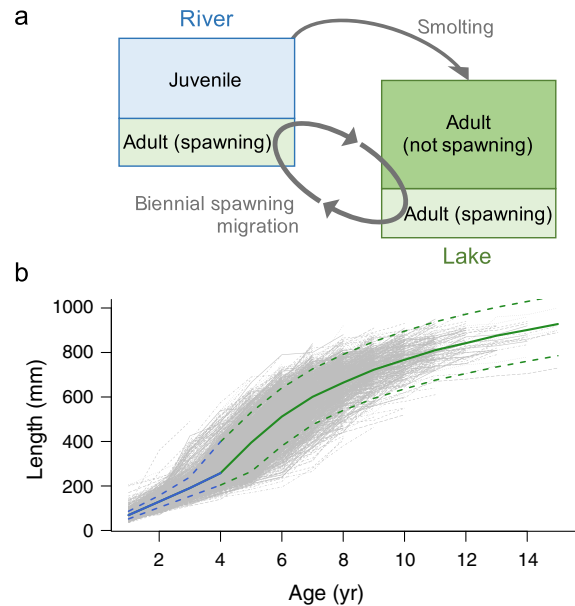


FIG. 1. (a) Overview of the life history of the Hunder trout. Juveniles in the river (blue box) grow linearly with age until smolting and migration to the lake. Fish in the lake have non-linear growth that is much reduced in years of spawning (migration to the river and back, green boxes). (b) Fit of the general biphasic growth model to length-at-age data from 1969 trout (gray). The solid colored line represents the mean predicted growth trajectory; dashed colored lines mark the 95% quantiles under consideration of individual, year, and measurement error variation.

With the fish ladder established, a mark–recapture protocol for migrating trout was implemented. Between 1966 and 2015, all trout passing the fish ladder were captured, individually marked, measured, sexed, and allowed to migrate upstream. Additionally, many fish had a scale sample taken in order to reconstruct individual growth trajectories and life history schedules. Individual growth data is thus conditional on survival until at least the first spawning run and on passage of the fish ladder (Appendix S2: Fig. S4). Data collection and scale analysis protocols are described in detail in Appendix S2, and in Aass et al. (2017).

### General biphasic growth model

Modeling the growth process requires a model that accurately represents the trout's life history and incorporates growth variation among individuals and years. The use of biphasic growth models has been advocated for capturing shifts in resource allocation across life history transitions and provides better descriptions of lifetime growth patterns (Quince et al. 2008, English et al. 2012, Minte-Vera et al. 2016). The original biphasic growth model for fish proposed by Quince et al. (2008) assumes that growth changes from being linear to following a von Bertalanffy growth curve when individuals reach sexual maturity and start investing energy into reproduction. In our study population, however, the most substantial change in growth happens at smolting, when young fish migrate from the river to the lake and shift to a piscivorous diet (Aass et al. 1989), providing nutrients and energy for initially faster growth (Appendix S1: Fig. S3). We therefore assumed linear growth for the river period up to the

year of smolting (identified using scales, Appendix S2) and asymptotic growth following a von Bertalanffy curve to approximate non-linear growth in the lake period afterwards (Fig. 1).

We formulated the general process model for linear growth during the river period as:  $\mu_{i,t+1} = \mu_{i,t} + h_{i,t}$ , where  $\mu_{i,t}$  is the true length and  $h_{i,t}$  the linear growth rate of individual  $i$  in year  $t$ . The length at hatching ( $\mu_0$ ) was estimated as an additional constant parameter. Since a preliminary analysis of this model indicated a linear decline in river growth rates over time, we also included a fixed effect of year on  $h_{i,t}$ . For lake growth, we used the length-dependent form of the von Bertalanffy function (Fabens 1965), allowing carry-over effects of earlier growth as well as utilization of data from individuals for which the year of birth and total age are unknown (due to partially unreadable scales):  $\mu_{i,t+1} = \mu_{i,t} + (\mu_{i,\infty} - \mu_{i,t}) (1 - e^{-k_{i,t}})$ , where  $\mu_{i,\infty}$  represents the individual asymptotic size and  $k_{i,t}$  the individual- and year-specific growth capacity (hereafter lake growth rate). As yearly growth increments of mature fish differ between spawning and non-spawning years due to costs of reproduction (Appendix S1: Fig. S4), we included a log-linear effect of spawning status on  $k_{i,t}$ . In an extension of this general model we also accounted for the effects of commonly studied environmental covariates during the growing period (May–October): water temperature, which directly affects body temperature and therefore metabolic rate and growth potential in fish (Forseth et al. 2009, Wootton 2012), and water flow, which can affect growth indirectly through availability of habitat and food, ease of forage and stress levels related to intraspecific interaction (Aass et al. 1989).

In both models, we decomposed the process variance in river and lake growth rates into persistent individual differences and among-year variation shared by all individuals, and also explicitly accounted for residual process variation in growth increments (within-individual among-year variation). We used a state-space framework to separate these process variance components from measurement error arising when lengths are inferred from scale year rings, which we knew a priori to differ between the river and lake periods of life (Appendix S2). This we achieved by integrating two sets of auxiliary data into our growth models: (1) lengths estimated from scales paired with length measures from fish captured alive and (2) pairs of length estimates from different scales of the same individual. Model structure, variance decomposition, and integration of auxiliary data are described in detail in Appendices S3 and S4 (including BUGS code).

After assessing the performance of the models on simulated data (Appendix S5), we fitted them to data from scales of 2217 wild-born trout from the study population that began either the river or the lake period of their lives between 1972 and 2002. Sex was not known for all individuals and as initial modeling of separate sexes did not indicate large differences in growth patterns, we pooled data for males and females. For the river period of growth data was missing for 249 fish and we therefore modeled lake growth for these under the assumption that length at smolting was normally distributed with mean and standard deviation equal to the observed values for all other individuals (Appendix S1: Table S1). We fitted our model using JAGS

4.2.0 (Plummer 2003) and the package dclone (Solymos 2010) for parallel MCMC computation in R 3.3.0 (R Core Team 2017). We ran three chains with an adaptation period of 50,000, followed by 300,000 iterations, of which the first 200,000 were discarded as burn-in.

## RESULTS

### *Fit of the general model*

Based on analyses of model fit and residuals (detailed in Appendix S3), we concluded that the biphasic growth model fit the data well. The correlations between observed individual growth trajectories (data) and those predicted by the model (posterior means of predicted lengths) were high for both the river (0.991; 95% CI [0.991, 0.992]) and the lake period (0.990; 95% CI [0.990, 0.991]). Residual analysis revealed a slight tendency for the river model to overestimate lengths of larger individuals, but this did not affect the main conclusions drawn from the model. Otherwise there was little indication of systematic bias and neither process nor residual variation showed signs of strong temporal autocorrelation.

### *Parameter estimates from the general model*

Posterior summaries from the model without environmental covariates are presented in Appendix S1: Table S2. Trout were estimated to grow on average between 64.4 mm/yr (year = 1971) and 56.4 mm/yr (year = 2002) in the river. Average growth thus decreased by 0.26 mm/yr (Fig. 2a). Persistent individual (SD = 6.9 mm) and residual process (SD = 11.9 mm) variations were considerable and larger than random year variation (SD = 2.3 mm, Fig. 3a). Growth rate in the lake (parameter  $k_{i,t}$ ) was estimated at an average of 0.177 for non-spawning and 0.046 for spawning individuals, meaning the former realized on average 16.2% of their remaining growth per year (95% CI [15.6, 16.7]) while the latter only achieved around 4.5% (95% CI [4.1, 5.0]). Again, persistent individual variation in the growth rate was larger than random year variation (SD on the log-scale = 0.12 and 0.09, respectively) and had a similar impact on variation in growth increments as residual process variation (SD = 16.9 mm, Fig. 3b). In contrast to river growth rate, we found no evidence for a time trend in lake growth rate (Fig. 2b). Size at hatching and asymptotic size were predicted with posterior means of 8.1 mm and of 1145.8 mm, respectively. The latter was subject to considerable individual variation (SD = 89.9 mm). Measurement error standard deviations were estimated at 7.6 and 21.9 mm for the river and lake periods, respectively.

### *Influence of environmental covariates*

Effects of the environmental covariates were weak, with river temperature, lake temperature, and river flow explaining 6.1%, 6.8%, and 15.0% of among-year variation in growth rates, respectively. Posterior mean estimates for environmental effects were negative for river flow, and positive for river and lake temperature, but posterior distributions of

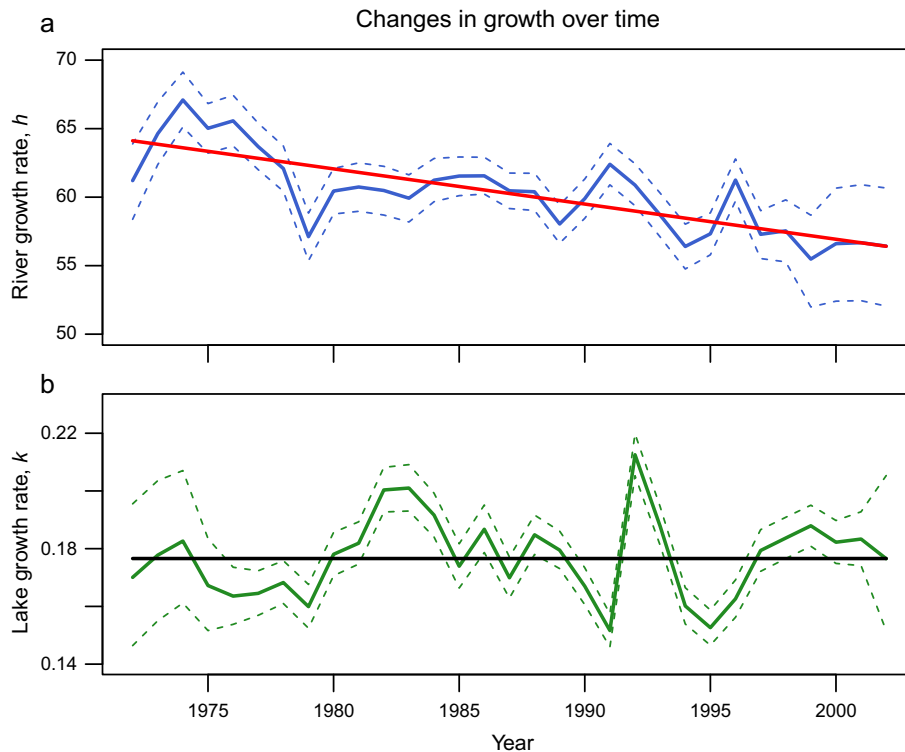


FIG. 2. Retrospective model predictions of (a) river and (b) lake growth rate for the average individual over time. Solid blue/green lines represent posterior means, dashed blue/green lines mark the 95% credible intervals. Red and black lines mark the predicted time trends based on posterior means of baseline river growth rate and the slope for the time trend.

the latter two had large overlaps with 0. For detailed results, see Appendix S4.

#### DISCUSSION

By applying a Bayesian biphasic growth model to long-term data from a natural brown trout population, we have identified several important aspects of growth in a freshwater top predator. We found that a decrease in average adult body size over time observed at the population level can be explained by changes in juvenile growth in the river and that a large proportion of growth heterogeneity is due to persistent and among-year individual variation.

Persistent individual heterogeneity played an important role in shaping trout growth trajectories, particularly during early life in the river (Appendix S1: Table S2). This is consistent with similar findings on closely related species such as marble trout (*Salmo marmoratus*; Vincenzi et al. 2014) and rainbow trout (*Oncorhynchus mykiss*; Shelton et al. 2013). Post-hoc analyses revealed that within-cohort individual variation was much larger than among-cohort variation (Appendix S1: Table S3) and that the majority of persistent individual variation in growth in this population thus arises from differences inherent to each individual and not due to cohort effects. Furthermore, individuals that grew faster during early life in the river also tended to grow faster in the lake, reach a larger asymptotic size, and smolt and mature earlier and at larger sizes (Appendix S1: Fig. S5 and Table S4), indicating that persistent individual variation in this population represents differences in individual quality. Such differences

could be a consequence of intrinsic variation in metabolic and behavioral traits conveyed via genetic or maternal effects (Metcalf et al. 1995, Vøllestad and Quinn 2003). Alternatively, individual quality differences in salmonids such as brown trout may be related to hatching phenology, providing early hatchers with both a prior residence effect (O'Connor et al. 2000) and a longer first growing season that can give them a permanent advantage (Letcher et al. 2011). Particularly in the river, a large amount of variation in growth was also attributed to residual process variation. Although some of this could be explained by a lack of fit of the growth model, model residuals indicate that lack of fit is modest compared to the estimated residual process variances (Appendix S3). Consequently, our results suggest there also are considerable differences within individuals over time and growth thus highly flexible throughout life. Such differences might arise from temporal variation either in an individual's state (e.g., behavior, physiology, pathology), or in environmental conditions within microhabitats (e.g., local densities of food and competitors), but further studies will be required to understand the mechanistic drivers of this variation.

Despite being smaller than individual variation, general temporal variation was evident in river and lake growth rates (Fig. 2). Surprisingly, we found that very little of this variation could be attributed to average summer water temperature and river flow (Appendix S3), two environmental covariates frequently associated with growth in fish (Jonsson and Jonsson 2009). It is nonetheless possible that these covariates do have direct effects on growth of the studied trout, but that the average over the growing period

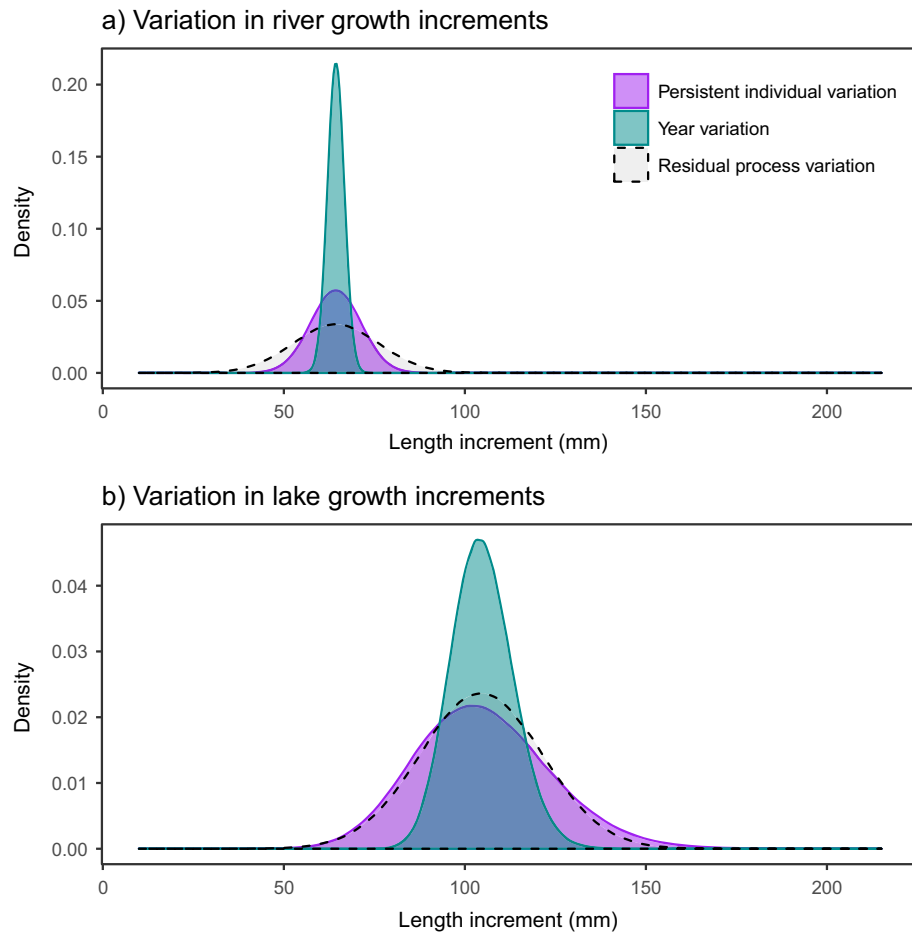


FIG. 3. Predicted variation in (a) river and (b) lake length increments originating from different variance components. Predicted increments were calculated from posterior mean estimates for average growth parameters and random effect (RE) standard deviations (1,000,000 draws from normal distributions, REs on lake growth rate and asymptotic size from multivariate normal distribution due to high within-individual correlation). For river growth, increments pertain to the first year in the study period (1971). For lake growth, increments are calculated for a non-spawning individual with a length of 500 mm.

(May–October) is not a representative metric (English et al. 2012, van de Pol et al. 2016). However, it is more likely that temperature and river flow interact with other drivers such as food availability and population density and thus affect growth only indirectly and possibly with a time delay (Jonsson and Jonsson 2009, 2014).

Contrary to the weak effects of temperature and river flow, a linearly decreasing time trend explained more than 40% of among-year variation in river growth (Appendix S4: Fig. S4), indicating that fish in the river have been growing more and more slowly in recent years. This finding is consistent with an observation of decreasing length but unchanged age at smolting in this population (Appendix S1: Fig. S2, Haugen et al. 2008). At the same time, we find no evidence for trends in lake growth rate (despite directional environmental changes in lake Mjøsa; Hobæk et al. 2012), suggesting that observed decreases in length-at-age in the lake (Haugen et al. 2008) represent carry-over effects from reduced early growth in the river. Haugen et al. (2008) proposed directional selection imposed by the fish ladder as the cause of size declines, but this remains a hypothesis in the absence of genetic studies. This is also the case for potential effects of hatchery propagation. Alternatively, the decrease in

river growth may be a direct plastic response of juvenile fish to changes in population density or unknown environmental drivers in the river or an indirect plastic response mediated by parental effects imposed by adult fish experiencing directional changes in temperature, nutrient, and potentially prey availability in either the river or the lake (Løvik and Kjellberg 2003, Hobæk et al. 2012). Given the great interest of anglers and conservationists in maintaining the uniquely large body size of the Hunder trout, and the fish's role as a top predator in this river–lake ecosystem, efforts should be directed at uncovering the mechanism responsible for the decline in river growth and the roles of persistent and among-year individual heterogeneity in mediating it.

Accounting for life-history is crucial when modeling growth, and here we have shown how a hierarchical biphasic growth model can be used to quantify individual and among-year variation, as well as time-dependent effects on growth across the entire life cycle. Indeed, the relative strengths of factors affecting growth can differ markedly across life-history phases, to the point that fitting models ignoring them may be impossible (such as fitting a simple mono-phasic von Bertalanffy model to our data, Appendix S3). While we have primarily focused on time trends and variance components

here, our model is versatile and can easily be extended to study a wide range of questions regarding, for example, sex differences, stocking effects and life-history trade-offs involving growth, smolting, maturation, and survival.

Applying models like the one presented here to natural populations can be challenging due to high data demands (Shelton et al. 2013). We have demonstrated how this problem can be alleviated by using size measurements inferred from scales, and thus making repeated captures of the same individual unnecessary. Size measurements inferred from proxies such as year ring radii, however, are likely to be subject to considerable and possibly systematic error and failing to account for this can have large impacts on the estimation of model parameters (e.g. Brooks et al. 2017). In our case, including different measurement error for the river and lake periods of life was prerequisite to model convergence (Appendix S3), highlighting the importance of accounting for structure in measurement error. Furthermore, when we fitted the model without distinguishing between measurement error and residual process variation, estimates of persistent individual variation were inflated (Appendix S3). As this distinction was only possible when using auxiliary information on measurement error, we advise to collect data on the latter whenever possible (c.f. Ives et al. 2003) and to carefully consider the possibility and nature of systematic error whenever size estimates are inferred from a proxy (year rings, tarsus length, wing span *etc.*), particularly when the goal of growth modeling is to disentangle different components of variation.

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