

**Running Head:** Growth in a freshwater top-predator

**Title:** “*Individual heterogeneity and early life conditions shape growth in a freshwater top-predator*”

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## **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-year 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 advocated environmental drivers like temperature and water flow did not explain much of this trend, and overall persistent among-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, 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 modelling 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 and 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 modelling 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 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 modelling 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 non-random measurement error resulting from the use of year rings on fish scales, and apply it to a unique dataset of large-sized brown trout *Salmo trutta* spanning over 30 years. We underline the importance of individual variation over the whole life cycle, highlight the relevance of quantifying measurement error and structure therein, 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 a growth model for a population of brown trout (hereafter: trout) inhabiting the lake Mjøsa and its main inlet river Gudbrandsdalslågen in eastern Norway. These trout, commonly referred to as “Hunder trout” (Aass et al. 1989), are famous for their large body size (up to 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 to 5 years, 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 to 4 years 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 in 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.

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*

Modelling the growth process requires a model that accurately represents the trout's life history and incorporates growth variation among years and individuals. 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 modelled 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. We assumed that the river growth rate  $h_{i,t}$  is subject to random individual and random year variation. Since a preliminary analysis of this model indicated a linear trend in estimated random year effects (and, consequently, an inflated estimate for random year variation), we additionally included a linear 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 further included a log-linear effect of spawning status on  $k_{i,t}$ . The general and hierarchical structures of the model are described in detail in Appendix S3.

## State-space formulation and implementation

We formulated the model in a state-space framework, in which a stochastic version of the above growth model represents the process model, and the observation model accounts for measurement error in the data. We assumed that the data  $L_{i,t}$  (lengths inferred from scale year ring measurements, Appendix S2) were normally distributed with mean  $\mu_{i,t}$  and measurement error standard deviation  $\sigma_{i,t}$ . Based on a priori knowledge regarding factors affecting accuracy of length estimates based on scale samples (Appendix S2), we allowed  $\sigma_{i,t}$  to differ between the river and the lake period of growth. As measurement error  $\sigma_{i,t}$  and random process error are not separately estimable, we integrated two sets of auxiliary data on the former into our model: (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 (see Appendix S3 for details).

We tested the general model structure on simulated data first in order to assess model performance (Appendix S5). We then fitted all models 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. As sex was not known for all individuals, we pooled data for males and females and assumed that growth parameters were independent of sex. 249 fish were missing data for the river period of growth (replacement scales not present in early life) and we therefore modelled lake growth for those under the assumption that length at smolting was distributed normally with the mean and standard deviation observed 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 (RCore Team 2017). We ran 3 chains with an adaptation period of 50000, followed by 300000 iterations, of which the first 200000 were discarded as burn-in. BUGS code for the model is available in Appendix S3.

### *Biphasic growth model including environmental covariates*

When random year variation and time trends contribute to changes in growth, the question arises as to what components of the environment are responsible for this change. Two common candidates in fish growth are temperature and water flow. The former directly affects body temperature and therefore metabolic rate and growth potential in fish (Forseth et al. 2009, Wootton 2012), while both covariates can affect trout growth indirectly through availability of habitat and food, ease of forage and stress levels related to intraspecific interaction (Aass et al. 1989). Appendix S4 describes an extension of the model where growth rates are functions of average river/lake temperature and river discharge during the growing season (May to October).

## **Results**

### *Model fit*

Based on residual analysis (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 (means of posterior distributions of estimated lengths using 1000 MCMC samples) 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 otherwise gave little indication of systematic bias, and neither process error nor residual variation showed strong signs of temporal autocorrelation.

### *Parameter estimates from the general model*

Posterior summaries from the model with period-dependent measurement error standard deviation (river vs. lake) are presented in Appendix S1: Table S2. Trout were estimated to grow on average between 64.4 mm/year (year=1971) and 56.4 mm/year (year=2002) in the river. Average growth thus decreased by 0.26 mm year<sup>-1</sup> (Fig. 2a). Individual variation was



considerable (SD = 6.9 mm) and larger than random year variation (SD = 2.3 mm, Figure 3a, b). Growth rate in the lake (parameter  $k_{i,t}$  in the von Bertalanffy equation) 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, individual variation in the growth rate was larger than random year variation (SD on the log-scale = 0.12 and 0.09 respectively, Figure 3a, c). 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 = 90.2 mm). Measurement / process error standard deviations were estimated at 7.6 / 11.4 mm and 21.5 / 16.0 mm for the river and lake periods respectively.

#### *Influence of environmental covariates*

Effects of all tested environmental covariates were weak, with river temperature, lake temperature and river discharge 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 discharge, and positive for river and lake temperature, but posterior distributions of 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 is explained by changes in juvenile growth in the river, and that a large proportion of growth heterogeneity can be attributed to persistent among-individual variation.

Hierarchical modelling allows teasing apart different sources of variation, and in our case revealed an overwhelming importance of among-individual variation - relative to among-year environmental variation - in shaping trout growth trajectories (Appendix S1, Table S2). This was the case particularly in the river period of life and 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) indicating that the majority of individual growth variation in this population is due to differences inherent to each individual, and not due to cohort effects. Individuals that grew faster during early life in the river also seemed to grow faster in the lake, reached a larger asymptotic size, and smolted and matured earlier and at larger sizes (Appendix S1, Figure S5 & Table S4), indicating that the large observed individual variation represents differences in individual quality. This quality variation could be a consequence of persistent intrinsic differences in metabolic and behavioural traits (Metcalf et al. 1995, Vøllestad and Quinn 2003) conveyed via genetic or maternal effects. Alternatively, individual quality differences in salmonids such as brown trout may also 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). Once this large individual heterogeneity was accounted for, temporal patterns in growth became evident. Despite being smaller than individual variation, considerable among-year variation in average growth rate was evident in both the river and the lake period (Fig. 2). Surprisingly, we found that very little of this variation could be attributed to average summer water temperature and river discharge (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 (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 discharge interact with other drivers such as food availability and population density, and thus affect growth only indirectly (Jonsson and Jonsson 2009, 2014, Bærum et al. 2013).

Contrary to the weak effects of temperature and river discharge, a linearly decreasing time trend explained more than 40% of among-year variation in river growth (Appendix S3, 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) may be 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 the case also for potential impacts of hatchery propagation on growth patterns. 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 role of individual heterogeneity in mediating it.

249 Roles and relative strengths of environmental conditions and individual traits can differ  
250 markedly across life-history phases, and growth parameters estimates can be sensitive to  
251 ontogenetic transitions to the point that fitting models ignoring them may be impossible (such  
252 as fitting a simple mono-phasic von Bertalanffy model to our data, Appendix S3). Accounting  
253 for life-history is thus crucial when modelling growth, and here we have shown how a  
254 hierarchical biphasic growth model can be used to quantify individual and among-year  
255 variation, as well as time-dependent effects on growth across the entire life cycle. While we  
256 have primarily focused on time trends and variance components in growth here, the model is  
257 versatile and can easily be extended to study a wide range of questions regarding, for  
258 example, sex differences, stocking effects and life-history trade-offs including the  
259 relationships between individual growth and smolting, maturation and survival.

260 Applying models like the one presented here to natural populations is a major challenge due  
261 to high data demands (Shelton et al. 2013). Here we have demonstrated how this problem can  
262 be alleviated by using size measurements inferred from scales, and thus making repeated  
263 captures of the same individual unnecessary. Size measurements inferred from proxies such  
264 as year ring radii, however, are likely to be subject to considerable and possibly systematic  
265 error and failing to account for this can have large impacts on the estimation of model  
266 parameters (Dennis et al. 2006, Brooks et al. 2017). In our case, the model only converged  
267 when we made an assumption of different measurement error for the river and lake periods of  
268 life, highlighting the importance of accounting for structure in measurement error (Appendix  
269 S3). Furthermore, when we ran the model without distinguishing between measurement and  
270 process error, estimates of individual variation were inflated (Appendix S3). We therefore  
271 advise to collect data on measurement error whenever possible, and to carefully consider the  
272 possibility and nature of systematic error whenever size estimates are inferred from a proxy

(year rings, hindfoot length, wing span etc.), particularly when the goal of growth modelling is to disentangle different components of variation.

## Acknowledgements

This work was supported by the Research Council of Norway through the project SUSTAIN (244647/E10). We thank the Directorate for Nature Management, Oppland and Hedmark County Governors, and Eidsiva Vannkraft AS for financial and logistic support. Model fitting was performed on the Abel Cluster (University of Oslo and the Norwegian meta-centre for High Performance Computing).

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## Figure legends

### **Figure 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). b) Fit of the general biphasic growth model to length-at-age data from 1969 trout (grey). 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.

### **Figure 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% quantiles based on 30'000 posterior MCMC samples. 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.

### **Figure 3:**

a) Variation in length increments predicted with only individual random variation (purple) or year random variation (grey) on river / lake growth rates. Predictions are based on posterior mean estimates for average growth rates and random effect standard deviations. 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 400 mm. Posterior distributions based on 30'000 MCMC samples for the individual (purple) and year (grey) random effect standard deviations on b) river growth rate ( $h_0$ ) and c) log lake growth rate ( $\log(k_0)$ ).

## Figures

Figure 1

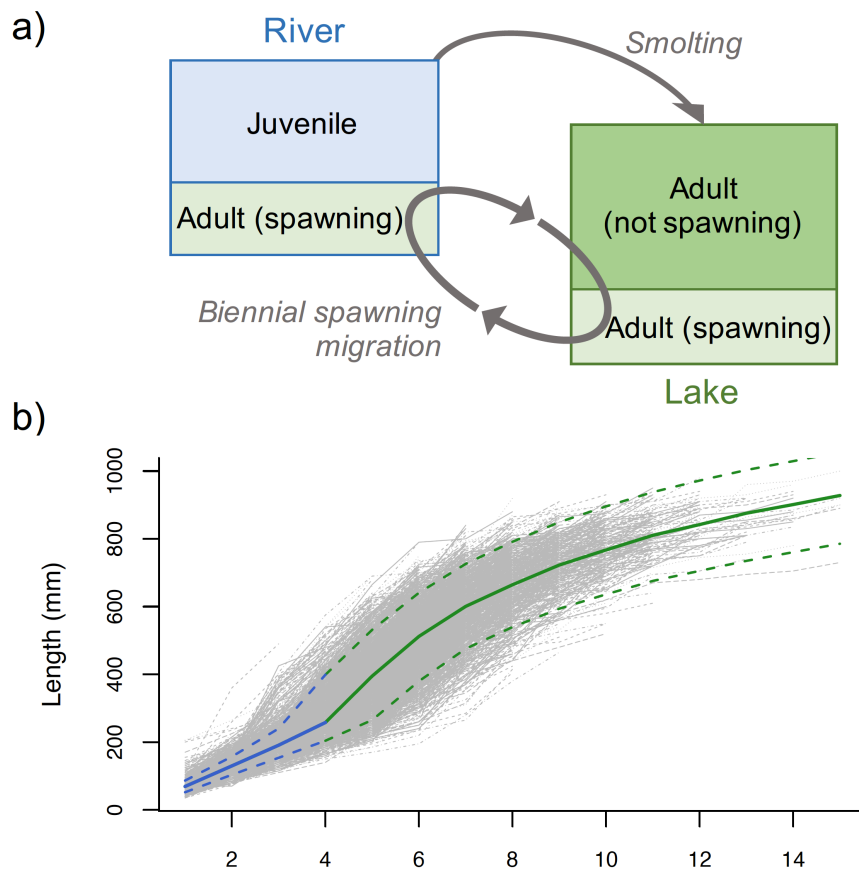


Figure 2

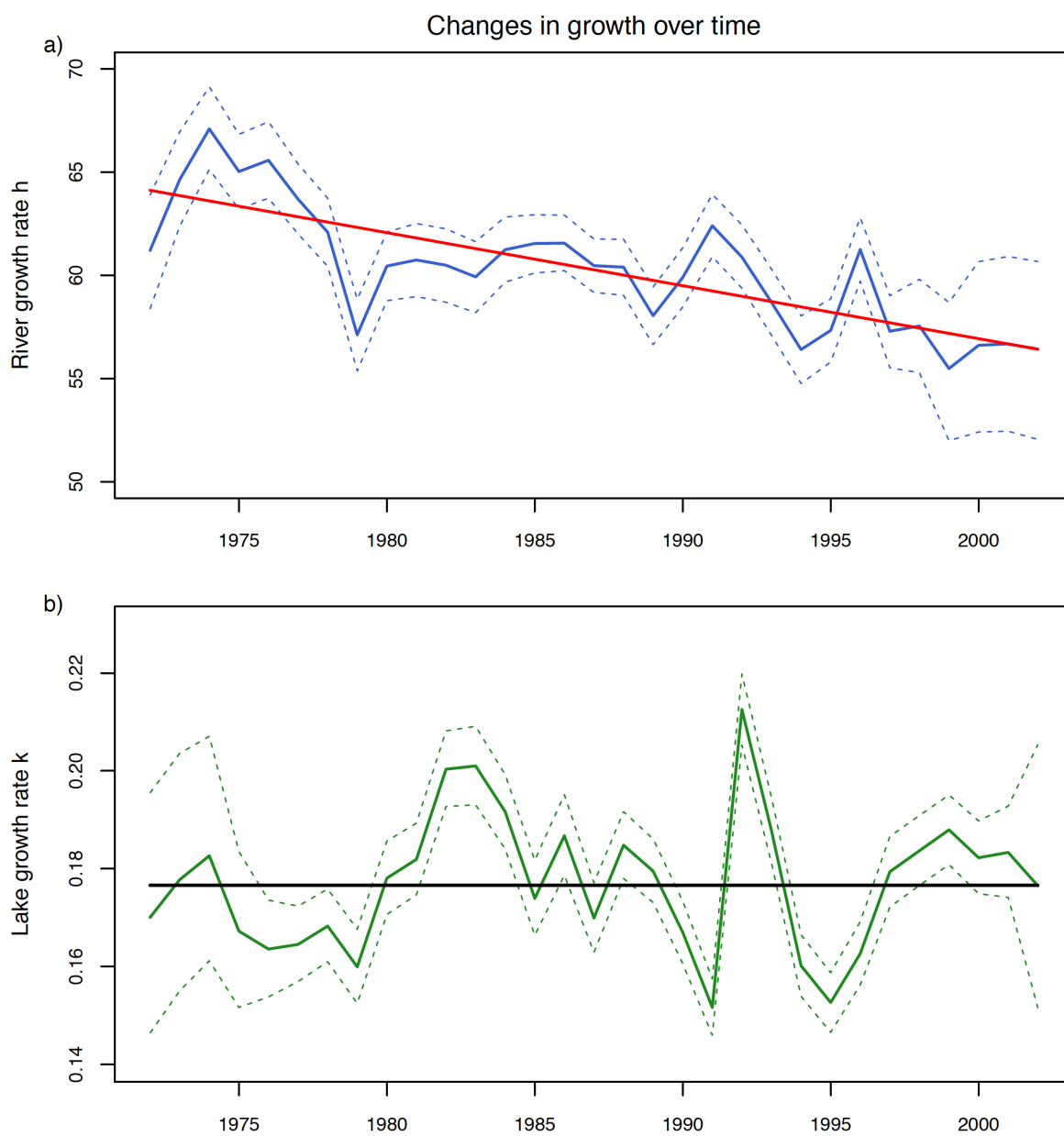


Figure 3

