*Intraspecific scaling of individual growth, consumption and metabolism with temperature and body mass across fishes*

Max Lindmarka,1, Jan Ohlbergerb, Anna Gårdmarkc

a Swedish University of Agricultural Sciences, Department of Aquatic Resources, Institute of Coastal Research, Skolgatan 6, Öregrund 742 42, Sweden

b School of Aquatic and Fishery Sciences (SAFS), University of Washington, Box 355020, Seattle, WA 98195-5020, USA

c Swedish University of Agricultural Sciences, Department of Aquatic Resources, Skolgatan 6, SE-742 42 Öregrund, Sweden

1 Author to whom correspondence should be addressed. Current address:

Max Lindmark, Swedish University of Agricultural Sciences, Department of Aquatic Resources, Institute of Coastal Research, Skolgatan 6, Öregrund 742 42, Sweden, Tel.: +46(0)104784137, email: [max.lindmark@slu.se](mailto:max.lindmark@slu.se)

**KEY WORDS**:

**WORD COUNT**:

Abstract: ~280

Introduction: ~1256

Methods: ~1860

Results: ~737

Discussion: ~1400 (missing one section currently)

Total: ~ 3900

**Abstract**

1. Understanding how temperature affects processes such as body growth, metabolism and consumption rates in ectotherms is important for predicting physiological and ecological processes in future climates.
2. Warming of aquatic communities is generally predicted to increase growth rates and reduce asymptotic body sizes. However, we lack a mechanistic understanding the causes, and empirical data on changes in growth-related traits are limited to either field data on exploited species or limited to few specific studies.
3. To estimate the effect of body size and temperature on growth, and to examine the link between growth and metabolic- and maximum consumption rates, we performed a systematic review and collated experimental data on growth, metabolism and consumption. We used only studies with a factorial body mass-temperature set up and fit hierarchical models to explore how these rates scale with mass and temperature within species, while accounting for variation between species. The mass- and temperature scaling was evaluated in relation to metabolic scaling theory and mechanistic growth models.
4. We find clear support for a declining optimum growth temperature as individuals grow in body size, and a positive effect of warming on growth rates that declines with increased body mass. Moreover, we find mass-dependent effects of temperature on metabolism at sub-optimum temperatures but not for consumption, and the scaling of these rates cannot predict the observed growth dynamics.
5. Our findings suggest that small individuals within a species will likely be able to increase their growth rates with initial warming, while larger individuals may gain little or nothing in terms of growth. Size-dependent changes in growth dynamics due to climate warming may have implications for the structure and functioning of future aquatic ecosystems.

**Introduction**

**General**

Individual body growth is a fundamental process that affects individuals’ fitness and life history traits such as maturation size, population growth rates (Savage *et al.* 2004) and ultimately energy transfer across trophic levels (Andersen *et al.* 2009a; Barneche & Allen 2018). Therefore, understanding not only how body growth scales with body size and temperature but also the underlying processes affecting growth rates, is important for predicting the impacts of global warming on the structure and functioning of ecosystems.

The temperature size-rule suggest that warmer rearing temperatures lead to faster developmental times (and larger initial size-at-age or size-at-life-stage), but smaller adult body sizes (Atkinson 1994). This relationship is found in numerous experimental studies (Atkinson 1994; Forster *et al.* 2012a), as well as latitudinal gradient studies of insects (Horne *et al.* 2015), and is stronger in aquatic than terrestrial environments. The underlying mechanisms are not well understood, but are likely results of interplay between ecology and physiology (Ohlberger 2013a; Audzijonyte *et al.* 2018; Neubauer & Andersen 2019). However, despite the debated mechanisms, the empirical examples identifying climate signals on growth trajectories are increasing. For instance, reconstructed growth histories of individual fish through ageing based on bony structures (otoliths) often show positive correlations between growth rates and warming (Thresher *et al.* 2007; Neuheimer *et al.* 2011; Baudron *et al.* 2014; Huss *et al.* 2019). This increased growth can also be predicted from numerous experimental studies showing that at intermediate temperatures, growth increases with temperature until a peak is reached, after which additional warming is deleterious (Brett *et al.* 1969; Elliott & Hurley 1995; Jobling 1997; Morita *et al.* 2010; García García *et al.* 2011). Less clear however is the negative effect of warming on the growth or body size of large fish. Time series of asymptotic or maximum body mass have shown negatively correlations with temperature (Baudron *et al.* 2014; van Rijn *et al.* 2017). However, a contributing factor could be that these examples stem from commercially exploited species and fishing disproportionally targets large fish. In a large scale semi-natural heating experiment, only small fish of a non-exploited species increased their specific growth rates with warming and the growth of larger fish was comparable to the non-heated control area. This lack of relationship between asymptotic or large fish size and temperature was also found in an experiment of ontogenetic growth (Barneche *et al.* 2019). Predictions about declines in asymptotic body mass have also been made from theoretical growth models (Pauly & Cheung 2018). However, the physiological mechanisms in these models (e.g. oxygen-limitation) have been questioned, both as a mean of causing asymptotic growth curves in the first place (Marshall & White 2019a) and also for causing smaller asymptotic sizes as temperatures rise (Lefevre *et al.* 2017). This leads to the question about whether or not large individuals within a population are more exposed to deleterious effects of warming on growth or not from a physiological perspective. To increase the understanding of the effect of body size and temperature on growth, it is important to quantify the intraspecific scaling of growth and other rates affecting it from controlled experiments.

The specific growth rate of a non-reproducing individual can be represented as the difference between energy acquisition and expenditure (von Bertalanffy 1938; Kitchell *et al.* 1977; Jobling 1997). Energy acquisition or assimilation is typically the amount of food consumed multiplied with a coefficient describing the available nutrients in the food. Expenditure is defined as fasting, activity and feeding metabolism. These different metabolic processes are in turn usually assumed to be proportional to resting metabolism, measured as the oxygen consumption of unfed fish at rest (Jobling 1997). These components of the biomass dynamics of growth are found in simple mechanistic Pütter-type growth models, such as the von Bertalanffy Growth Model (VBGM), or the Ontogenetic Growth Model –(OGM) (Pütter 1920; von Bertalanffy 1938; Ursin 1967; West *et al.* 2001), as well as more complex models dynamic energy budget models (Kooijman 1993; Kearney 2019) including multispecies dynamics models such as physiologically structured population models (PSPMs) (Roos & Persson 2001) and size-spectrum models (Hartvig *et al.* 2011; Maury & Poggiale 2013; Blanchard *et al.* 2017). In order to understand growth dynamics in changing environments and to evaluate the physiological basis of growth models of varying complexity, it is therefore important to understand how metabolism and consumption rates on average scale with body size and temperature at the intraspecific level rather than interspecific level. This could contribute to better understanding of this fundamental process through mechanistic models (Marshall & White 2019b).

start this para with intraspecific!

Metabolically driven rates vary predictable with body mass and temperature (Kleiber, 1934), and many approaches exist to statistically describe these relationships (Downs et al 2004). Because of its mechanistic basis, the metabolic theory of ecology (MTE) (Brown *et al.* 2004a) is a popular framework for linking individual metabolism to ecological processes in a bio-energetic framework (Vasseur & McCann 2005; O’Connor 2009; Brose *et al.* 2012; Gilbert *et al.* 2014; Sentis *et al.* 2017). The MTE predicts metabolism to scale in proportion to , where is body mass and is the activation energy, is Boltzmann’s constant and is absolute temperature in , based on the assumption that metabolism is limited by resource uptake and distribution (West *et al.* 1999), and that organisms typically inhabit thermal environments where rates scale with temperature exponentially. However, it the universality of these scaling relationship for metabolically driven rates are often questioned, as experimental data frequently show deviations in both the mass- and temperature coefficients, and their independence (Bokma 2004; Clarke 2004; Dell *et al.* 2011; Englund *et al.* 2011; Ohlberger *et al.* 2012; Jerde *et al.* 2019). This is especially true for intraspecific scaling, where rates in addition are typically asymmetrically unimodal over a large enough temperature range (Dell *et al.* 2011; Englund *et al.* 2011). Despite that processes such as growth, metabolism and consumption are individual-level processes, and individual-level processes shape ecological dynamics and structure (Andersen *et al.* 2009b; De Roos & Persson 2013), there is a knowledge gap about general intraspecific scaling of these processes. This could be due to the logistical challenges of replicating experiments for ranges of body masses and temperatures in a factorial setting (Jerde *et al.* 2019) or due to the lack of comprehensive data bases (Dell *et al.* 2011). One approach to estimate average intraspecific scaling, and potentially reduce the observed variation found across single experiments (Englund *et al.* 2011), is to apply hierarchical (mixed-effects) models on data from multiple experiments, which can account for variation between experiments or species and also provide predictions based on partial pooling of data across species to minimize the influence of extreme values. Something about mass and temp here fore covariation… and about the difficulty of standardizing from detailed experiments (detaild for that species maybe but generalizing?)

In this study, we performed a systematic literature review using search Web of Science core search to compile a dataset on individual growth rates, consumption and metabolic rates of fish from experiments in which the effect of fish body mass is replicated across multiple temperatures within species. We fit hierarchical Bayesian models to share information across species and account for replication within species when estimating general- and species-varying scaling parameters, both at sub-optimum and full temperature-ranges. We find support for declining optimum growth temperatures, that body size affects the temperature scaling of metabolic rate (albeit the effect size is small), and the relationship between consumption rates and temperature are unimodal, with large variation between species in the optimum temperature. These scaling patterns deviate from typical across-species patterns and scaling theory.

**Methods**

**Data acquisition**

We searched the literature for experimental studies measuring the temperature and mass dependence of individual growth rate, maximum consumption rate (feeding rate at unlimited food supply, *ad libitum*) and resting/standard/routine oxygen consumption rate (proxy for metabolic rate (Nelson 2016)), using three different searches on the Web of Science Core Collection. From the growth rate data search, we also compiled a data set containing the optimum growth rate temperature for each combination of body mass group and species. We selected studies with a. factorial body mass-temperature setup in order to estimate how these rates depend on body size and temperature within species. While this reduces the number of data points available in the literature (as most experimental studies only use a size- or temperature treatment), it allows us to fit multivariate models and evaluate interactive effects within species, rather than normalizing data assuming a specific scaling with one of the predictors separately. We found in total X, Y and Z data points from published articles on growth rate, maximum consumption and metabolic rate, for X, Y and Z species representing a diverse taxonomic, habitat and lifestyle range. We asked authors for these data in most cases, but given the age of most studies found, we also extracted the data from figures using Web Plot Digitizer (Rohatgi 2012) or from tables.

We excluded larvae-only studies to ensure that parameter estimates were representative over ontogeny. Studies were selected if (i) the original study could be found, (ii) a unique experimental temperature was recorded for each trial (), (iii) fish were provided food at *ad libitum* for consumption and growth data, no food for resting or routine metabolic rate for metabolism, (iv) fish exhibited normal behaviour. We used only one study per species. While this reduces the number of data points, it ensures that all data within a given species are comparable as measurements of these rates can vary between studies due to e.g. measurement bias or differences in experimental protocols (Armstrong & Hawkins 2008; Jerde *et al.* 2019). In cases where we found more than one study for a species, we selected the study we found most suitable, based on how well it fit with our pre-defined criteria. A more detailed description of the search protocol, criteria to selected data, data acquisition procedure, quality control, collation of auxiliary information and standardizing rates to common units can be found in Appendix S1 in the Supporting Information.

In order to estimate general intraspecific parameters with hierarchical models, we pool data across species. However, species differ in their body masses (both in absolute values and relative to their maximum body size), and in their experimental temperature (both in absolute values and relative to their mean environmental temperature) (Fig SX – add also distribution of relative mass by species). Therefore, we standardize our predictor variables by species. This was done by expressing temperature as the difference between the experimental temperature and the median environmental temperature. We used the median temperature in the environments of the respective species distribution using information available in FishBase (Froese & Pauly 2016) (<https://fishbase.org/>). When this information was missing, we used other comparable metrics (e.g. median preferred temperature or temperature of spawning habitat). For the model of optimum growth temperature, as the difference between optimum temperature for each size-class and the mean optimum temperature across all body size classes of that species. We standardized all body-mass data by dividing it with the maximum body mass by species, based on literature estimates, also taken from FishBase. More detailed definitions of standardized variables are given below each model as they differ between models and rates.

**Model fitting**

*Mass-dependence of optimum growth temperature*

To evaluate how the average optimum temperature in Celsius () for individual growth depends on body mass (), we fit the following hierarchical model to account for variation in both intercept and slope with respect to species:

(1)

, (2)

, (3)

Here is the rescaled optimum temperature within species : to account for variation in the actual optimum growth temperature between species. is the natural log of body mass divided by the maximum body mass within species, in , defined as . In Eq. 3, the subscript referes to parameter (0 for intercept and 1 for slope). All predictor variables are in addition mean-centered, such that 0 corresponds to the overall mean (not by species). We also fit a model with non-varying mass-coefficient (i.e. , not indexed by ), and selected the best model based on predictive out-of-sample accuracy using the Widely Applicable Information Criterion (WAIC) (Vehtari *et al.* 2017).

*Scaling of growth, metabolism and consumption with temperature below optimum*

Below optimum temperatures (i.e., a subset of the data sets including only data points for a given size-group that were below the temperature at which the rate was maximized), we assumed individual growth, metabolic rate and maximum consumption rate to scale with size using a generalized version of the core equation in the metabolic theory of ecology (Gillooly *et al.* 2001; Brown *et al.* 2004b), in which neither the mass- or temperature dependence is assumed and corrected for. This allowed us to evaluate the effects of temperature and body mass simultaneously, which is more appropriate if the mass-scaling exponent is not exactly 3/4 (Downs *et al.* 2008), which it not always is (Sibly *et al.* 2015; Jerde *et al.* 2019) and also to evaluate interactive effects of size and temperature (Ohlberger *et al.* 2012; Lindmark *et al.* 2018). We thus assumed rate (growth, metabolism or maximum consumption) scale with mass and temperature as:

, (4)

which on normal scale becomes:

, (5)

where is the intercept, is the mass-scaling exponent when , is the interaction coefficient, is the activation energy, and is Boltzmann’s constant in ().

We estimate body mass and temperature coefficients (representing the mass-scaling exponent and activation energy, respectively) using hierarchical models with different combinations of group (species)-varying coefficients and select the final model using WAIC. The full model with uncorrelated species-varying intercepts, mass-, temperature- and interaction- coefficients, can be written as:

(6)

, (7)

, (8)

where is the th observation of the natural log of the rate (growth, metabolism or consumption), and indexes regression coefficient (. In Eq. 7, is defined as , where is mass in , and is standardized temperature on Arrhenius scale, defined as ), where Arrhenius temperature is defined as in Kelvin. For the analysis of growth rates, refers to geometric mean of the initial mass and final mass of the growth experiment, unless stated otherwise (Appendix S1). All predictor variables are in addition mean-centered, such that 0 corresponds to the overall mean (not by species). We select our final model using WAIC.

*Scaling of consumption rates with temperatures including optimum*

As biological rates are unimodal over a large enough temperature range, we fit polynomial models to a subset of the maximum consumption data containing only species with data points beyond the temperature at which the rate is maximized, by species (Englund *et al.* 2011). No clear optimum curves were indicated in the metabolic rate data. The models were fit by species and then aggregated, i.e. without any hierarchical structure accounting for species variation. This was due to the difficulty of standardizing optimum-data to a common scale, as species have different consumptions rates at optimum temperature, different widths of the thermal performance curves and different optimum temperatures. By fitting models by species, we thus remove the risk of removing true effects in data, at the cost of benefits of the hierarchical model for inferring general intraspecific scaling. The model of is for the full data set defined as:

(9)

(10)

where in Eq. 9 refers to consumption rates divided by the mean rate value by species (), in Eq. 10 is mean-centered natural log of body mass in unit by species (, i.e. not normalized to maximum body mass as we fit this model by species) and is mean-centered standardized temperature by species, where the standardized temperature is defined as ().

For illustrations of model fits, we predict over the temperature range of the data for species while keeping body mass at 0 (corresponding to the mean mass within each species in ) (Fig. SX). The species predictions and data are plotted together in Fig. X, to illustrate the spread in optimum temperature measured as distance to environmental median. We also illustrate model fits by rescaling both data and predictions to the maximum predicted rate within species and subtract the optimum temperature from each temperature and add the overall mean optimum temperature, as in (Englund *et al.* 2011) (Fig. SX). Due to general data limitation we did not fit an interaction term which alters the optimum temperature by mass, however this has been identified in data-rich experiments (García García *et al.* 2011).

*Parameter estimation*

We fit the models in a Bayesian framework, using R version 3.5.0 (R Core Team 2018) and JAGS (Plummer 2003) through the R-package ‘*rjags*’ (Plummer 2019). We used a mix of flat, weakly informative and non-informative priors depending on how well understood the parameter is based on previous literature to facilitate convergence (<https://github.com/stan-dev/stan/wiki/Prior-Choice-Recommendations>) (Table 1). We used 3 Markov chains with 10000 iterations each, following on 10000 iterations burn-in and 5000 for adaptation. Model convergence was assessed by visually inspecting trace plots (Appendix S1) and by ensuring , suggesting all three chains converged to a common distribution (Gelman & Rubin 1992). We relied heavily on the R packages within the *‘tidyverse’* (Wickham 2017) for data processing, as well as ‘*ggmcmc*’ (Fernández-i-Marín 2016) and ‘*bayesplot*’ (Gabry *et al.* 2019) for visualization. All data and R code (data manipulation, analyses and figures) can be downloaded from a GitHub repository (<https://github.com/maxlindmark/scaling>) and will be archived on Zenodo upon publication.

Table 1 Description of model parameters and their prior distributions

|  |  |  |  |
| --- | --- | --- | --- |
| Model | Parameter | Description | Prior distribution |
| Linear model  (Eqns. 1-3) |  | Hyperparameter (intercept) |  |
|  | Hyperparameter (mass coefficient) |  |
|  | Hyperparameter (intercept variance) |  |
|  | Hyperparameter (mass coefficient variance) |  |
|  | Variance |  |
| Log-linear regression (Eqns. 6-8) |  | Hyperparameter (intercept) |  |
|  | Hyperparameter (mass exponent) |  |
|  | Hyperparameter (activation energy) |  |
|  | Hyperparameter (interaction) |  |
|  | Hyperparameter (intercept variance) |  |
|  | Hyperparameter (mass exponent variance) |  |
|  | Hyperparameter (activation energy variance) |  |
|  | Hyperparameter (interaction variance) |  |
|  | Variance |  |
| Polynomial  (Eqns. 9-10) |  | Intercept |  |
|  | Mass coefficient |  |
|  | Temperature coefficient |  |
|  | Quadratic temperature coefficient |  |
|  | Variance |  |

**Results**

The temperature at which optimum growth is achieved declines with body size declines with per unit increase in the natural log of relative body mass (Fig. 1). This decline in optimum temperature with mass is clear, as 99% of the posterior density of the slope estimate () is below 0 (Fig. SX). The selected model contains a species-level effect on the intercept () and a common slope across species ().

At below optimum temperatures, we find that the average intraspecific size-and temperature dependence of specific growth across-species can be described by the equation: . We estimate the (relative) mass-scaling exponent of growth, i.e. the mass-coefficient on log-log scale, to be to be [] (brackets indicated 95% Bayesian credible intervals) when is held at 0 (mean). The model with best fit to data contains a body size-temperature interaction (Table 2), and the posterior median for the interaction coefficient is . This means the mass-specific scaling exponent of growth increases with an increase in relative inverse temperature, i.e. the relative mass-exponent (on normal scale) is larger in colder temperatures. Specifically, the relative mass-scaling exponent of growth decreases with approximately 0.0023 per unit change in . However, evidence for this interaction is weak and only 55% of the posterior density is above 0. We estimate the activation energy, , (coefficient to the relative Arrhenius temperature, ) to be [], which is lower than what is typically found for metabolic rate, i.e. more temperature-sensitive (Downs *et al.* 2008) and growth based on field data (Sibly *et al.* 2015). To illustrate this in terms of specific growth (normal scale), an increase in relative temperature from approximately +to (relative to median environmental temperature) increases growth rates by a factor of 83% for a fish of with a mass of 0.2% of maximum mass.

We find that the average intraspecific scaling of whole-organism metabolic rate can be described by the equation: , and consumption rate as: (See Fig. 3 a general intraspecific prediction for a given mass and two temperatures). Some notable differences exist in the scaling of these two rates. First, metabolic rate scales with a larger mass-scaling exponent ( []) than maximum consumption ( [), inferred from non-overlapping Bayesian 95% credible intervals (indicate with square brackets) (Fig. 4). This difference implies that metabolic processes increase faster with body mass than maximum consumption rates. We also find that maximum consumption rate is more temperature sensitive than metabolism when measured at temperatures below optimum. The activation energy for metabolism is estimated to be [] and ([]) for maximum consumption rate. However, this difference is less clear, as can be inferred from the overlapping credible intervals, partly due to the larger uncertainty of the temperature sensitivity of consumption (Fig. 4). This implies that at temperatures below optimum, maximum consumption rates on average faster with temperature than metabolic rates. We also found support for a negative interaction between body mass and temperature (90% of the posterior distribution of is above 0, Fig, 5). However, the effect size is relatively small. We estimate it to be on an Arrhenius temperature scale, which on a Celsius temperature scale corresponds to a decline in the mass scaling exponent of metabolic rate by 0.001. Both the metabolism and consumption model allowed for all coefficients in the respective model to vary between species (Table 2).

Over a larger temperature range, biological rates tend to be unimodal. We identified such tendencies in 9 species in the consumption data set, and fit polynomial models to those species (Fig. 6). The predictions from the model show that consumption rates are unimodal, which implies that even if maximum consumption rates increase faster than metabolic rates with temperature at sub-optimum temperatures, eventually, consumption declines with further increases. In other words, the effect of temperature on the metabolic costs-feeding gains mismatch depends on the current temperature relative to optimum. However, when standardizing the temperature data to a common unit, here relative to median temperature in the environment (to overcome that experiments are performed at different temperatures relative to the species’ preferred temperature), we large variations in the temperature at which consumption is maximized (“optimum”) (Fig. 6). These temperatures range from -2.3 to +17, in units median environment temperature subtracted from optimum temperature, by species (i.e. , in Celsius). Across species, the mean in intraspecific is 6 in the same unit (with a standard deviation of 6).

Table 2. Model selection for the log-linear regressions of how consumption, metabolism and growth scale with mass and temperature (below optimum temperature). M1 is the full model and is described in text (Eqns. 3-5). Values in bold indicated the model selected based on the Widely Applicable Information Criterion (WAIC).

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Model | M\*T | Species-varying parameter(s) | WAIC consumption | WAIC  metabolism | WAIC growth |
| M1 | Yes |  | 530.9 | **289.53** | **32.51** |
| M2 |  | 528.62 | 290.37 | 37.46 |
| M3a |  | 674.66 | 627.56 | 72.05 |
| M3b |  | 588.24 | 681.3 | 78.72 |
| M4 |  | 710.46 | 973 | 100.56 |
| M5 | No |  | **527.64** | 295.02 | 45.71 |
| M6 |  | 712.1 | 971.32 | 98.98 |
| M7 |  | 1931.92 | 7988.06 | 313.42 |
| M8 |  | 2094.1 | 9523.28 | 337.25 |

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Fig. 1. *Optimum temperature for growth (standardized to optimum temperature within species and mean-centered) as a function of natural log of standardized body mass (mass/maximum mass within species). Probability bands represent 80% and 95% credible intervals and solid line represent the median prediction from the average across-species effect ( and ).*

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Fig. 2. *Effects of temperature and body mass on growth depends A) Growth rate [% day-1] as a function of body mass, both on natural log scale. Lines are mean marginal predictions at temperatures -0.75 and 0 in unit mean-centered Arrhenius temperature standardized to median environmental temperature, which is approximately median environment temperature +10 and +5 respectively. Shaded areas correspond to 80% and 95% credible interval and the solid line is the median prediction from the average across-species effect ( and ). The slope corresponds to the mass-scaling exponent. Posterior distributions of mass-scaling exponent (B), activation energy (C) and the mass-temperature interaction coefficient (D) are shown in the bottom row. The dashed white line shows the posterior median, and in (D) the dashed red line is 0.*

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*Fig 3. Natural log of metabolic rate (A) and maximum consumption rates (B) vs. natural log of standardized mass. Shaded areas correspond to 80% and 95% credible interval and the solid line is the median prediction from the average across-species effect ( and ) for two temperatures on Arrhenius scale: warm (red) and cold (blue), which is approximately median environment temperature +10 and +2.5 respectively*

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*Fig. 4. Posterior medians of species-varying activation energies and mass-coefficients from the hierarchical model fitted to below temperature optimum data, and their 80% and 95% credible interval. Vertical dashed lines correspond to the median prediction for a general species (i.e. and for the mass and temperature coefficient, respectively). The shaded vertical area corresponds to posterior median of the posterior median.*

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*Fig. 5. Posterior distributions of the average across-species parameters () for metabolic rate (top row) and maximum consumption rate (bottom row). Text in top left corner corresponds to the posterior median. Note that the final model for maximum consumption rate did not include a mass-temperature interaction term and the scale is the same within parameters across rates for comparison.*

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*Fig. 6. Standardized maximum consumption rates (relative to mean within species) as a function of temperature from the data subset containing only species with data points at temperatures higher than where the rate is maximized (“optimum”). Points show data and lines are predictions from the polynomial model where the centered body mass is held at 0 (corresponding to mean mass within species), by species (indicated by color). The shaded areas show 80% credible interval for the median prediction. Arrows depict the optimum temperature for each species, in units “difference from median environmental temperature”, and the vertical dashed and dotted lines correspond to the mean optimum temperature 1 standard deviation.*

**Discussion**

While suboptimum temperatures likely reflect average conditions for ecological processes (Brown *et al.* 2004a), and thus in general would fit the MTE equation (Dell *et al.* 2014), there are potentially important exceptions. First, even below optimum, thermal performance curves (TPCs) may not always be log-linear, which the Arrhenius-equation assumes (Englund, 2011). Second, it has been shown that sub-optimum temperatures are in fact optimal in varying environments, which makes it challenging to define the ascending part of a thermal response curve (Bernhardt et al 2019). Lastly, climate change is already causing populations at the edge of their distributions to experience lethal heat waves (Pörtner & Knust, 2007).

This estimate is very similar to the estimated in (Barneche *et al.* 2019).

Rall, Dell Englund and Ecology paper – what do they say about scaling? What do I say that differs? What does it mean for growth?

Another observed deviation from scaling theories (including the MTE) is that body mass can affect the temperature scaling on physiological rates, both within (Beamish 1964; Xie & Sun 1990; Ohlberger *et al.* 2012; Fossen *et al.* 2019) and between species (Killen *et al.* 2010). This could lead to size-dependent thermal performance curves (e.g. body growth), with important effects on individuals and populations.

We have shown that temperature affects body growth rates of fishes differently depending on their body mass, through 1) small changes in the mass-scaling exponent 2) clear declines in optimum growth temperatures with body size. These results mean that smaller individuals within a population may benefit more in terms of faster growth rates with, but this potential to capitalize on warming declines with body size.

The empirical observation that higher temperatures lead to faster development and smaller adult body sizes within species (“temperature-size rule”, TSR) (Atkinson 1994; Daufresne *et al.* 2009), has fueled research into climate-driven changes in growth trajectories of also fish - especially since TSR-effects are predicted to be stronger in aquatic systems (Forster *et al.* 2012b; Horne *et al.* 2015). Studies on changes in individual growth trajectories typically utilize time series of age-at-length or catch data (Thresher *et al.* 2007; Baudron *et al.* 2014; van Rijn *et al.* 2017; Huss *et al.* 2019). In most cases such data are only available species with a long history of commercial exploitation and time-varying population abundances and food productivity, which could confound or dilute any climate change signals in individual growth data. Therefore, it is important to compare field studies with controlled environments. Our finding that growth rates increase with temperature is similar to finding positive correlations between and temperature, as was many have found also in field data.

While our data do not contain individuals that are close to their predicted asymptotic body sizes, we do see weak evidence of the positive effects of warming on growth leveling off over ontogeny. This would be analogous to declines in maximum body size, or in time series (Baudron *et al.* 2014; van Rijn *et al.* 2017). However, we estimate a relative small interaction-effect, meaning notable impacts on growth only manifest over large temperature and body mass ranges (see Fig. 3) (but we also note that this estimate is almost an order of magnitude lower than what has been reported for some single species studies, e.g. Björnsson *et al*. (2007)). On the contrary, we find clear effects of body mass on optimal growth temperatures. Assuming that fish exhibit similar temperatures in the environment over ontogeny, this would lead to warming lowering growth performance of the largest fish in a population first (we estimate roughly a 4 change in optimum over ontogeny). However, this may not always be the case, as for instance Heincke’s law states that individuals move to deeper habitats over ontogeny (Heincke 1913; Audzijonyte & Pecl 2018), and other type of ontogenetic habitat shifts are well documented, e.g. (Werner & Hall 1988). For inferences about impacts of climate change, the change in optimum growth temperature that we report here should be viewed in relation to size-dependent habitat temperatures if those change over ontogeny. That said, there are already empirical evidence of the largest individuals being the first to suffer negative impacts of warming from e.g. heatwaves (Pörtner & Knust 2007). Taken together, while temperature has a clear positive effect on growth at for small fish in a population, in line with empirical findings, the effect of temperature on the large fish within a species is still not properly understood. This was also mirrored in a recent experimental study by Barneche *et al*. (2019), where a negative relationship between asymptotic body size and temperature was evident only at high temperatures. The inability to capture clear temperature-effects on asymptotic size over a realistic temperature-range experimentally could mean other factors are involved in time series of field-sampled fish, e.g. life history evolution in response to intensive fishing. However, we are not really able to make that conclusion since large individuals are generally not covered in experimental studies, including those compiled in this study, and large fish may still find direct negative impacts of warming on body growth.

We still lack mechanistic understanding and theoretical models for the causes of TSR (Marshall & White 2019a; Pauly 2019). This is likely because it appears to be a response to several co-varying mechanisms at different levels of biological organization (Ohlberger 2013b; Audzijonyte *et al.* 2018). We are also still discussing what drives the asymptotic body size of fish, so perhaps it is not strange we cannot explain the causes of directional changes in asymptotic mass. One of the reasons could be to general lack of experimental data of ontogenetic growth rates. This is most likely an artefact of the logistical challenges of performing growth rate experiments in the factorial design (size x temperature) needed. Moreover, body growth is an ontogenetic process, and there is only so much interspecific comparisons can ultimately say about ontogenetic growth. In a step to overcome this, we have systematically compiled growth data for different size-classes at different temperatures in order to get as close as possible to the ontogenetic scaling of growth without limiting ourselves to “truly” ontogenetic data (in which case our data set would have been smaller). We argue that this approach to systematic review of already existing literature can be fruitful in combination with hierarchical models and variable-standardization, as this can address the general aspects of ontogenetic growth that are shared across species, which single species studies will struggle with. One example is the size-dependence of optimum growth temperatures, which we find clear signals of even when analyzing data from a diverse set of species on a common scale. In doing so, our study adds a new take on aspects of intra-specific growth scaling for a “general” fish, adds data to the literature and highlights the lack of representation of large individuals in growth experiments.

\*Add section here about limitations in experiments and all uncertainties from that\*, including pros and cons with standardization…

Do as in Englund and discuss effects on population and community dynamics?

See notes about the scaling, important to do intraspecific aspect!

To illustrate the effects of the intraspecific mass- and temperature-dependence of metabolic and consumption rates estimated from the experimental studies, we apply a generic Pütter-type growth model (Pütter 1920) of the form: , where is body mass. von Bertalanffy assumed, based on theoretical arguments and mathematical convenience, that and represent anabolism and catabolism and scale with exponents (based on the scaling of surfaces to volumes) and (von Bertalanffy 1938). However, the mechanistic interpretation of these two terms varies (Marshall & White 2019b), and are often defined as energy assimilation and expenditure, respectively (Ursin 1967; Essington *et al.* 2001). With this definition, the model constitutes a simple mass-balance equation that resembles bioenergetic models (Ursin 1967; Kitchell *et al.* 1977; Essington *et al.* 2001). It can further be assumed that assimilation and expenditure are proportional to consumption rates (at constant food levels) and oxygen consumption rates (Ursin 1967). In this case, the temperature dependence of and can be approximated by Eq. 5 for temperatures below optimum. The growth model and assumptions are great simplifications of the factors influencing growth dynamics over size and temperature, omitting for example specific dynamic action, food dependence of respiration and energetic investment into reproduction (Ursin 1967; Kitchell *et al.* 1977; Marshall & White 2019b). However, it can illustrate an example of the ability of simple bioenergetic models to capture the size-and temperature dependence of ontogenetic growth, and the assumptions can also be relaxed by applying the allometric functions into more complex bioenergetic models.

In the context of climate change impacts on ecosystem functioning and productivity, it is important to acknowledge the now widespread finding in field and experimental studies that warming has the potential to increase growth rates – at least in the smaller end of the species’ size-spectrum. This poses a challenge to general theoretical growth models that feed into climate projections. Body growth is a fundamental process, and not being able to characterize it properly may limits our understanding of important aspects beyond individual body size, including energy transfer & efficiency of food webs and ecosystems.

**Author contributions**

ML, JO, AG designed research; ML conceived the study; ML performed research; ML analyzed data; ML, JO, AG wrote the paper and contributed to revisions of the manuscript.

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