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

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Abstract: ~280

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**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**

Body growth is a fundamental process that links different levels of biological organization. It 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 2018a). Therefore, understanding of how growth rates are affected by global warming is of key importance for making predictions about future ecosystem.

We only have a limited understanding of the mechanistic basis of fish growth bioenergetics, and this impairs our ability to predict changes in growth due to climate change (Rosenfeld *et al.* 2015; Lefevre *et al.* 2017; Audzijonyte *et al.* 2018; Barneche & Allen 2018a; Marshall & White 2018). What we do know and where both theoretical models “of Pütter-type”, such as the Ontogenetic Growth Model (OGM) (West *et al.* 2001) or the von Bertalanffy Growth Equation (VBGE) (von Bertalanffy 1957), and empirical studies e.g. (Björnsson *et al.* 2007) agree is that specific growth rates decrease with body size and increase with temperature until an optimum temperature is reached (Pauly 1979; Jobling 1997; Morita *et al.* 2010). At temperatures below optimum, growth, being a biological process, has been suggested to scale with temperature as metabolic rate, i.e. as , where is Boltzmann’s constant () and is the activation energy or the coefficient to in a log-log regression (Sibly *et al.* 2015). In an attempt to mechanistically explain the temperature-dependence of growth, Sibly *et al.* 2015 used the metabolic theory of ecology-framework to show that in the VBGE is proportional to growth rate at 1/2. They found the slope to be , which is slightly lower than activation energy of metabolic rate (Clarke & Johnston 1999; Downs *et al.* 2008), and also that growth scales differently with asymptotic mass across and between species, which challenges current growth models. An important point however is that is not a growth rate per se as it is in unit time-1 (FishR), and is only proportional to growth rate at 1/2 under the assumption that anabolism and catabolism in the VBGE scale as 2/3 and 1, respectively (Sibly *et al.* 2015). This assumption has recently been questioned on physiological and evolutionary grounds (Lefevre *et al.* 2017, 2018a; Marshall & White 2018, 2019a). In addition, is in this case one of three parameters describing ontogenetic growth rates in the VBGE and is therefore not independent from estimates of with asymptotic size, (Pauly 1979). This warrants more research on characterizing growth rates over ontogeny rather than single growth parameters when possible.

Moreover, the effect of temperature on growth (e.g. or any other parameter related to growth performance) is often inferred from measurements across gradients of environmental temperatures. The response to warming over time of a single population is assumed to follow the same pattern as that found along the thermal gradient over a snapshot in time. The benefit of this assumption is that one can use the large amounts of data available on databases such as Fishbase. Using this approach, (Barneche & Allen 2018a) showed that the cost of growth – the energy needed to produce one unit of biomass – could increase with warming, with potential consequences for energy transfer efficiency across trophic levels (Barneche & Allen 2018). Increasing costs of growth with warming was later also found in an detailed experimental study tracking growth over ontogeny (Barneche *et al.* 2019). However, in general, it is still unknown how well spatial temperature-patterns match responses to warming over time. The main difference between the two effects of temperature is that average habitat temperatures rarely exceed optimum temperatures and the response along a spatial gradient is rarely unimodal. Therefore, average field growth rates across populations of a species is not necessarily the same as the average growth rates within a population experiencing warming over time, as the inferred thermal performance curves may have different shapes. The latter might however be more relevant in the context of global warming. Better exemplify unknown about T\_opt being size dep (cite morita) and exponent being constant in this section.

Another potential issue that limits our understanding of how body growth rates scale is that the effects of temperature and body mass are commonly assumed to be independent (Zuo *et al.* 2012; Sibly *et al.* 2015). This could lead to biases when normalizing rates to a specific body mass or temperature if the effect of body size is not identical at different temperatures. In fact, interactions between temperature and mass are fairly common in the literature. For instance, temperature-dependent mass-scaling exponents and the related finding of declines in optimum growth temperature with mass have been found in experiments of fish (Fonds *et al.* 1991; Björnsson *et al.* 2007; García García *et al.* 2011) and also in other taxa e.g. molluscs and arthropods (Wyban *et al.* 1995; Heasman *et al.* 1996; Steinarsson & Imsland 2003). However, the generality of temperature-size interactions has also been questioned (Elliott & Hurley 1995), and the size-scaling exponents of specific growth rates are also often found to be constant at different temperatures (Brett & Shelbourn 1975). Understanding the effects of body mass for growth rates at different temperatures is important, as decreasing mass-scaling exponents with warming implies lower optimum-temperatures for growth as individuals grow in size (Björnsson *et al.* 2007; García García *et al.* 2011), and climate change may change may push species’ to experience thermal limits (Pörtner & Knust 2007).

In this study we assess how body growth rates scale with size and temperature, including potential interactions, within species of fish. We address the knowledge gaps outlined above by fitting models of actual growth rates rather than growth parameters using a compiled dataset of fish growth experiments were temperature is a treatment across different size groups within species. We compiled our data set by first searching the literature for relevant studies that fulfilled our criteria and then extracted data points from tables and figures. The dataset contains X data points from Y species, spanning masses Z, with an average of ZZ size-classes per species. Using hierarchical models, we asked the following questions: i) How does body growth rate depend on temperature and body mass within fish species, and are the effects independent? ii) What is the effect of body size on the optimum growth temperature? We find interactions between temperature and body size, meaning that the positive effect of warming on growth is largest for small individuals, and clear support for declining optimum temperatures for growth as fish grow in size. Size-dependent effects of warming on growth and reduced performance of large fish within a population has implications for productivity and energetic efficiency of aquatic food webs under climate warming.

**From the scaling paper:**

The rate of energy acquisition and metabolic losses largely determine individual biomass production, which is a fundamental process in ecology. On the individual level, it shapes fitness and affects key life history traits such as body growth, mass and time of reproduction and maximum body mass (Barneche & Allen 2018b). At the community and food web level, it affects the strength of ecological interactions, trophic transfer, community stability and size-structure (Andersen *et al.* 2009b). To predict and understand individual-, population- and food web responses (e.g., through development of mechanistic and process-based models of individuals and food webs), it is important to understand how these rates scale with body mass and temperature at the appropriate scale.

It has long been recognized that 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 is now recognized that there is no universal temperature-scaling relationship for metabolically driven rates, but that this depends on other factors, including body mass, taxonomy and life history strategy (Englund *et al.* 2011; Ohlberger *et al.* 2012; Dell *et al.* 2014; Archer *et al.* 2019). The discrepancy with the universal scaling model is perhaps most evident in intraspecific data, both in terms of variation in parameter estimates (Norin & Gamperl 2018) and functional form (Dell *et al.* 2011; Englund *et al.* 2011), as the rate-temperature relationship is typically asymmetrically unimodal (Dell *et al.* 2011; Englund *et al.* 2011). 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). 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. This knowledge gap at the intraspecific level is likely due to the logistical challenges of replicating experiments for ranges of body masses and temperatures in a factorial setting (Jerde *et al.* 2019). Given that intra- and interspecific scaling can differ (Jerde *et al.* 2019), and that intraspecific processes and variation are important for understanding ecological dynamics (De Roos & Persson 2013), accurately describing the general intraspecific mass- and temperature dependence of biological rates is a high priority for understanding and predicting climate change impacts.

The need to understand the mechanistic basis of growth scaling is more evident now than ever, since reductions in average adult body sizes of ectotherms have been proposed as a third universal response to warming (Daufresne *et al.* 2009). Yet we know little about the mechanisms underpinning the empirical observations of temperature-size responses (Ohlberger 2013a; Audzijonyte *et al.* 2018; Lefevre *et al.* 2018b; Pauly & Cheung 2018). Metabolism and maximum consumption rate are key processes describing the dynamics of individual-level biomass production or body growth. This is captured in numerous models based on simple dynamic energy budget theory, including individual-level models such as Wisconsin-type bioenergetic growth models (Kitchell *et al.* 1977), to Pütter-type growth models (Ursin 1967; Essington *et al.* 2001; Marshall & White 2019b) and population and food web models, such as physiologically structured population models (PSPMs) (De Roos & Persson 2001) and size-spectrum models (Blanchard *et al.* 2017). As these are examples of mechanistic models of growth – an ontogenetic process – it is important that scaling assumptions are validated on intraspecific rather than interspecific data. More accurate estimates of scaling relationships at the individual level could contribute to better understanding of this fundamental process through mechanistic models (Marshall & White 2019b).

In this study, we search Web of Science to compile a dataset on 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 clear temperature-size interactions for metabolic rates at sub-optimum temperature, and that the optimum temperature for both metabolism and consumption declines with a mass. These scaling patterns deviate from typical across-species patterns and scaling theory. Based on simple bioenergetic principles, the observed scaling of consumption and metabolism could contribute to altered growth dynamics and reduced growth potential with warming, with implications for ecological interactions and potentially trophic transfer efficiency.

**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 . 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 rates 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 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. 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 rates with temperature: 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). 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.

**Growth model**

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.

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**

*99.1% of the posterior density of the slope estimate ()*

The temperature at which optimum growth is achieved declines with body size declines with per order of magnitude increase in relative body size (Fig. 4).

We find that the size-and temperature dependence of growth can be described by the equation: . We estimate the mass-scaling exponent of growth (the mass-coefficient on log-log scale) to be to be (95% Bayesian credible intervals:) when equals the median environmental temperature (Fig. 2b). This estimate is very similar to other studies using another data set or experiments (Sibly *et al.* 2015; Barneche *et al.* 2019). We find some support for a temperature-size interaction. The mean of the posterior for the interaction coefficient is , meaning the mass-specific scaling exponent of growth increases with an increase in inverse temperature, i.e. the mass-exponent (on normal scale) is larger in colder temperatures. Specifically, the mass-scaling exponent of growth decreases with approximately 0.004 per unit change in . However, the interactions is less statistically clear than the mass-scaling exponent as the 80% Bayesian credible intervals just overlap zero (95% CI: ) (Fig. 1C). We estimate the activation energy, , (coefficient to the relative Arrhenius temperature, ) to be (95% CI: ), which is lower than what is typically found for metabolic rate (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 to increases growth rates by a factor of 1.4 for a fish of mass but a factor of 1.2 for a fish of mass , respectively (Fig. 3).

+ Add scaling results including

+ Add model selection for T\_opt here in text

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 |

Table 3 Model selection for the polynomial model of how consumption and metabolism depend on mass and temperature (including 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 | WAIC  consumption | WAIC  metabolism |
| M1 | No |  | **942.63** | **901.4305** |
| M2 |  | 1363.59 | 4779.198 |
| M3 | , | 1258.1 | 5951.29 |
| M4 | Yes |  | 945.6 | 903.1162 |
| M5 |  | 1366.11 | 4781.286 |
| M6 | , | 1253.43 | 5942.267 |
| M7 |  | 1371.52 | 6184.961 |

A close up of a map

Description automatically generated

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 ).*

A close up of a map

Description automatically generated

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 -1 and 1 (in unit mean-centered Arrhenius temperature standardized to median environmental temperature), shaded areas correspond to 80% and 95% credible interval. 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.*

A picture containing text

Description automatically generated

Fig 3. Natural log of metabolic rate (A) and maximum consumption rates (B) vs. natural log of standardized mass. Lines correspond to predicted average scaling relationships from the hierarchical model for two temperatures: warm (red) and cold (blue). Shaded areas correspond to 80% and 95% credible interval.

**A screenshot of a cell phone

Description automatically generated**

Fig. 4. Posterior medians of species-varying activation energies and mass-scaling exponents from the hierarchical model (triangles) 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 and the shaded area correspond to the 95% credible interval of the mean prediction.

A picture containing boat, text, map

Description automatically generated

Figure 5. Posterior distributions of the grand mean parameters for how metabolic rate (top row) and maximum consumption rate (bottom row) scale with mass and temperature when fitted to below optimum temperature data. Text in top left corner corresponds to the median. Note that the final model for maximum consumption rate did not include a mass-temperature interaction term.

*A close up of a map

Description automatically generated*

Figure 6. Growth as a function of body mass from the Pütter

**Discussion**

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.* 2012; 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\*

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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