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

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**Abstract**

1. Warming of aquatic communities is generally predicted to increase growth rates and reduce asymptotic body sizes of ectotherms. However, we lack a comprehensive overview of average intraspecific scaling of growth with body mass and temperature from controlled experiments, and mechanistic growth models are usually not informed by empirical estimates of intraspecific scaling of key processes such as metabolism and consumption. This limits our ability to link experimental data to empirical patterns of growth as well as developing growth models.
2. 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 these rates. We used only studies with body mass and temperature treatments and fit hierarchical models to evaluate how these rates scale with jointly with mass and temperature within species, while accounting for variation between species.
3. We find clear support for a declining optimum growth temperature with body mass within species, and a positive effect of warming on growth rates. We find mass-dependent effects of temperature on metabolism at sub-optimum temperatures but not for consumption, and that activation energies at sub-optimum temperature generally conform to theoretical predictions while mass-scaling does not.
4. Thus, small individuals within a species will likely be able to increase their growth rates with initial warming and that larger individuals will first experience deleterious effects of warming on growth. Size-dependent changes in growth dynamics due to climate warming may have implications for the structure and functioning of future aquatic ecosystems.

**Introduction**

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.

Global warming is predicted to lead to declines in the body size of organisms (Daufresne *et al.* 2009; Gardner *et al.* 2011). The temperature size-rule predicts 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.* 2012), 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 2013; Audzijonyte *et al.* 2018; Neubauer & Andersen 2019). However, the empirical examples identifying climate signals in time series of growth trajectories are accumulating. 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.* 2010a; 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. The lack of clear 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 2018b). However, the physiological mechanisms in these models (e.g. oxygen-limitation) have been questioned, both for the cause of asymptotic growth curves in the first place (resource limitation) (Marshall & White 2019a) and the mechanism for why warming leads to smaller asymptotic sizes (Lefevre *et al.* 2017). As empirical findings differ and theoretical predictions are questioned, is still remains unclear to which extent the growth of large fish within a population is limited by warming from purely physiological constraints (e.g. when accounting for other factors such as food availability. More accurate predictions about the effect of body size and temperature on growth from controlled experimental studies can aid both the development of theoretical growth models as well as providing predictions about the effect of temperature on growth. This includes also the scaling og key processes affecting growth, such as metabolic- and consumption rates.

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. This scaling should ideally be at the intraspecific level rather than interspecific level to better represent the individual-level processes, as these can differ (Jerde *et al.* 2019).

However, the average scaling of individual growth, metabolism and consumption with body mass and temperature is often inferred from interspecific data even when representing individual processes. In addition, the temperature- and mass dependence of metabolism and other related rates are also often assumed to follow the mass-scaling model by (West *et al.* 1999) coupled with the Boltzmann-Arrhenius model (Gillooly *et al.* 2001), in the metabolic theory of ecology (Brown *et al.* 2004). This model, henceforth referred to as the Arrhenius fractal supply model (AFS), provides predictions from first principles and is therefore often empirically evaluated (Gillooly *et al.* 2001; Downs *et al.* 2008). The AFS assumes that metabolically-driven rates () (individual growth, metabolism and consumption), to scale as: , where is the activation energy, is Boltzmann’s constant and is temperature in Kelvin. Importantly, the model assumes mass-scaling of ¾ when estimating temperature effects, as well as independent effect of mass and temperature (Downs *et al.* 2008). There is however numerous examples of deviations from this mass-scaling exponent (Clarke & Johnston 1999; Bokma 2004; Jerde *et al.* 2019), and body mass and temperature can have interactive effects (Xie & Sun 1990; García García *et al.* 2011; Ohlberger *et al.* 2012; Lindmark *et al.* 2018). Moreover, while the AFS does tend to provide good statistical fits to interspecific data (Clarke 2004), and could also fit intraspecific data depending on the temperature range (Brown *et al.* 2004; Clarke 2004) (but see (Englund *et al.* 2011)), thermal response curves are generally unimodal in intraspecific data (Dell *et al.* 2011; Englund *et al.* 2011; Rall *et al.* 2012). These assumption-violations, and model misspecifications, could affect the estimates of temperature-dependencies. Instead of mass-correcting according to the AFS, it could be more appropriate to fit multivariate models where coefficients are estimated jointly (Downs *et al.* 2008), or define models that can capture the negative rate-temperature relationships at higher temperatures (Dell *et al.* 2011; Englund *et al.* 2011). Overall, average intraspecific scaling is less understood, and contributing factors could be the logistical challenges of replicating experiments for ranges of body masses and temperatures in a factorial setting (Jerde *et al.* 2019) and due to the lack of comprehensive data bases (Dell *et al.* 2011). This appears to be especially true for consumption and growth rates (Englund *et al.* 2011; Barrios‐O’Neill *et al.* 2019). Inference about scaling parameters are therefore often limited to few detailed experiments, which makes inference about average intraspecific scaling across species difficult. However, individual-level processes shape ecological dynamics and structure (Andersen *et al.* 2009b; De Roos & Persson 2013), and therefore overcoming the knowledge gap about intraspecific scaling is highly warranted.

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. To acquire both general and species-specific scaling, we fit hierarchical Bayesian models to account for variation between experiments or species and also to acquire general intraspecific scaling predictions based on partial pooling of data across species to minimize the influence of extreme observations. For maximum consumption rates, we also fit quadratic models to a subset of the data to characterize the unimodal temperature dependence. We find 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 fit the effects of mass and temeprature jointly rather than fixing one effect, as well as evaluate the probability if interactive effects within species. 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. Data from were extracted from tables, or figures using Web Plot Digitizer (Rohatgi 2012).

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, extracted between 2019.06.01-2019.12.01 (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. For the analysis of mass-dependence of optimum growth temperature within species, we use relative mass as a predictor, as we are interested in examining relationships within species while accounting for variation in relative body masses between experiments. Relative mass is here body-mass data by dividing it with the maximum body mass by species, based on literature estimates, also taken from FishBase (extracted between 2019.06.01-2019.12.01). More detailed definitions of standardized variables are given below each model in the following sections.

**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.* 2004), 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 the mean-centered natural log of body mass in unit by species (), 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 natural log of the 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 (Dell *et al.* 2011; 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 across 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 to facilitate convergence depending on how well known the parameter is based on previous literature (<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 and by ensuring (Appendix S1), which ensures 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. 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: . The model with best fit to data contains a body size-temperature interaction (Table 2). However, the predicted value of the interaction is close to 0 (only 55% of the posterior density is above 0), and the 95% intervals around the WAIC value (assuming a z-score of 1.96) are largely overlapping (, . We therefore find that mass-temperature interactions are not evident in data and only slightly improves fit, and thus exemplify the growth scaling predictions from model M5, which assumes independent but species-varying mass- and temperature coefficients. We estimate the (relative) mass-scaling exponent of growth, i.e. the mass-coefficient on log-log scale, to be to be [] (brackets indicate 95% Bayesian credible intervals). 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 86% for a fish of with a mass of 30g (corresponding to the overall mean mass in data).

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 (indicated in square brackets) (Fig. 4). This difference implies that metabolic processes increase faster with body mass than maximum consumption rates, and that both differ from the predicted mass-scaling exponent from the metabolic theory of ecology. 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 we estimate it to: ([]). However, this difference is less clear than the mass-exponents, as can be inferred from the overlapping credible intervals, partly due to the larger uncertainty of the temperature sensitivity of consumption (Fig. 4). In addition, both fall within within the prediction from the MTE (0.6-0.7 eV) (Brown *et al.* 2004). 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 (99.7% 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 0.002. In the selected model for consumption all coefficients vary by species whereas for the models of metabolism, all but the interaction coefficient varies by 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 unimodal temperature-dependence implies that even if maximum consumption rates increase faster than metabolic rates with temperature at sub-optimum temperatures (due to larger activation energy), eventually consumption rates decline relative to metabolism with further warming. 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 find 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 comparison 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). The WAIC columns shows dWAIC (WAIC, SE), where dWAIC is the difference between each models’ WAIC and the lowest AIC across models, and SE is the standard error of the WAIC (calculated as the square root of the product number of observations and the variance of individual observation’s WAIC). Bold indicates best fitting model (lowest WAIC).

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Model | M\*T | Species-varying parameter(s) | WAIC consumption | WAIC  metabolism | WAIC growth |
| M1 | Yes |  | 2.9 (530.9, 103.3) | 0.7 (289.5, 120.4) | **0 (35.5, 31.5)** |
| M2 |  | 0.9 (528.6, 102.3) | **0 (288.8, 120.5)** | 3.9 (39.4, 32.1) |
| M3a |  | 132.3 (674.7, 101.7) | 298 (586.9, 118) | 35.3 (70.8, 31.4) |
| M3b |  | 60.5 (588.2, 88.8) | 392.4 (681.2, 110.3) | 43.8 (79.3, 31.3) |
| M4 |  | 168 (710.5, 91) | 646.3 (935.2, 109.2) | 65.9 (101.2, 31.9) |
| M5 | No |  | **0 (527.6, 102.6)** | 6.1 (294.9, 121.1) | 0.9 (36.3, 32.3) |
| M6 |  | 185 (712.1, 93.5) | 682.2 (971.1, 109.7) | 63.1 (98.6, 31.7) |
| M7 |  | 598.6 (1931.9, 59.1) | 4002.7 (4291.6, 143.2) | 171.5 (206.9, 25) |
| M8 |  | 822.4 (2094.1, 48.2) | 10662.5 (10951.3, 111.4) | 187.9 (223.4, 19) |

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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) and activation energy (C) are shown in the bottom row. The dashed white line shows the posterior median.*

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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 the 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 intraspecific mass-scaling exponents and activation energies (, and for metabolism also the non-species varying interaction coefficient ()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. 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**

Individual growth, consumption and metabolic rate represent fundamental processes in ecology. The scaling of these rates with mass and temperature is used to predict the effects of warming on individual growth, population and community dynamics using mechanistic models (Vasseur & McCann 2005; Rall *et al.* 2010; Cheung *et al.* 2013). It is common to inform scaling relationships from either meta-analysis of single-species studies or interspecific relationship. However, the former can result in large variation in intraspecific scaling parameters, and the latter relies on the assumption that rates scale identically within and between species, which is often found not to be the case (Rall *et al.* 2012; Jerde *et al.* 2019). As growth, consumption and metabolic rate represent individual-level processes, it is important to understand general scaling of these rates at the intraspecific level. By accounting for variation between species, we find that unimodal growth rates scale similar to predictions from scaling theories (e.g. the metabolic theory of ecology) at sub-optimum temperatures, and that the optimum temperature for growth declines with body size. We also find, on average, that activation energies are close to scaling predictions, but not when including optimum temperatures. However, the mass-dependence of metabolism is larger than predicted and for consumption it is smaller than predicted. This has implications not only for scaling theories but also for mechanistic models of growth-, population and food web dynamics.

Our results show that temperature increases growth rates equally for all sizes at sub-optimum temperatures, and that there is no support for interactive effects of body mass and temperature in these temperature ranges, as found in (Elliott & Hurley 1995) (but see (Wangila & Dick 1988)). We also find differences in the mass-scaling exponent from earlier studies (Wangila & Dick 1988; Elliott & Hurley 1995), which predict an exponent of . Our estimate is essentially the same from a single-species experiment in a more recent study on the ontogenetic growth of fish (Barneche *et al.* 2019). These differences from previous could be due to species effects, where our estimate is based on general intraspecific values across species. It could also be due to differences in temperature ranges included in the analyses, as we find clear signals of declining optimum growth temperatures with body mass, within species – in contrast to e.g. (Elliott & Hurley 1995). This has potentially large implications for the size-dependence of growth rates, leading to smaller individuals potentially being more likely to benefit from warming in terms of growth (as they are often found to do in natural systems, e.g. (Thresher *et al.* 2007; Baudron *et al.* 2014; Huss *et al.* 2019)) compared to larger individuals. The relatively large effect size found here (X decline in Y mass) is especially notable given the relatively small size range used in the experiments (few individuals larger than ), which could mean that largest fish in a population have even lower relative optimum growth temperatures. This prediction for natural systems however is based on the “ideal” scenarios found in the experiments, mainly unlimited food supply, no predation pressure and constant temperatures. In natural systems, growth is mediated through species-dependent and complex ecological interactions. However, the finding that large fish experience deleterious effects of warming first suggest there might be purely physiological constraints to the body growth of large fish within a species in warm environment. It is difficult however to assess to what degree this reduced thermal optima can explain observed changes in growth in natural systems, as species occupy different thermal habitats in relation to their physiological capacity (Neuheimer *et al.* 2011). This is also mirrored in our data, as we find large differences between species in their optimal growth relative to their habitat temperature. It could however explain the lack of beneficial effects of warming on the growth of older fish, as shown in Huss et al in which growth, environmental temperature data and a bioenergetics model was assessed for perch. On the other hand, 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). 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).

Declines in optimum growth temperature with mass is interestingly also predicted from the von Bertalanffy growth model (VBGE), defined as , where is body mass and is temperature, under two conditions: (which also is a necessity for asymptotic growth) and growth has an optimum over temperature, as shown by (Morita *et al.* 2010b). While this constitutes likely is the most common growth model for asymptotic growth curves, the first condition has been debated recently. Specifically, while not necessary for the condition itself, is in the classic VBGE assumed proportional to body mass. This originates from the argument that maintenance should be proportional to mass, as spontaneous denaturation occurs in every cell (von Bertalanffy 1957; Pauly & Cheung 2018a) (and likely also from mathematical convenience (Ursin 1967)). From a physiological perspective, it appears more common to assume that maintenance costs are proportional to standard metabolic rate (oxygen consumption of a resting and fasting organism) (Ursin 1967; Jobling 1997; Lefevre *et al.* 2017). In this case supply and demand models, such as the VBGM or OGM, either fail to represent the physiological processes they aim to or fail to exhibit asymptotic growth. This is especially true if assuming universal mass scaling exponents of 3/4 for the scaling of assimilation and standard metabolic rate. This dichotomy can be resolved by considering energetic investments into reproduction (mass-scaling exponent larger than 1), which in these models have overlooked (Marshall & White 2019b), or by applying more complex energy pathways in dynamic energy budget models (Kearney 2019). However, these recent debates about scaling coefficients has called for an investigation in the intraspecific scaling of metabolic rate in relation to assimilation or consumptions. Our results on the smaller mass-scaling exponent of maximum consumption rates compared to metabolism suggests that “costs” for maintenance increase faster than energy assimilation with body mass – assuming no other processes such as assimilation efficiency scale in ways to counteract this. This could result in reduced growth efficiency over ontogeny and bioenergetics models may need to account for this difference in scaling, which is in contrast to universal mass-scaling predictions.

In addition to the scaling of net energy efficiency (e.g. difference between energy assimilation and costs) with body mass, it is important to understand how this balance is modified by temperature. The match- or mismatch between the temperature dependence of feeding vs metabolic rates is a central question in experiments, meta-analyses and food web models (Vasseur & McCann 2005; Lemoine & Burkepile 2012; Fussmann *et al.* 2014; Lindmark *et al.* 2019). Using strictly sub-optimum temperatures, the general (average intraspecific) predictions about the activation energy of growth, metabolism and consumption vary but the 95% credible intervals large overlap, which means there is no clear loss or gain the net energetic efficiency with increasing temperature – as long as they are sub-optimum. The larger posterior median of the activation energy for consumption compared to metabolism could therefore be due to chance. We also find that the general (average intraspecific across species) temperature scaling, to be less uncertain than what has been reported previously (e.g. in Englund), and a likely contributing factor is the use of hierarchal models to estimate higher level (across species) scaling from species-data. However, in contrast to scaling theory, we also find that body mass can affect the temperature scaling on physiological rates, which previously has been reported for single species studies (Beamish 1964; Xie & Sun 1990; Ohlberger *et al.* 2012; Fossen *et al.* 2019) and between species (Killen *et al.* 2010). However, this was not found in a recent intraspecific study of metabolic rate in fishes (Jerde *et al.* 2019). The effect size is however relatively small and the ecological implications could therefore also be, although large estimates have been reported and the small effect size could be due to the known variation between species in this effect (Ohlberger *et al.* 2012; Lindmark *et al.* 2018).

While we find no clear evidence of temperature induced metabolic mismatch at sub-optimum temperatures, we do find clear mismatches at higher temperatures due to consumption rates being unimodally related to temperature whereas metabolic rates increase exponentially in essentially all temperatures investigate in the studies here. This qualitative result is in line with numerous previous studies (Dell *et al.* 2011; Englund *et al.* 2011; García García *et al.* 2011; Rall *et al.* 2012). This opens up for the question about the relevance of optimum curves in natural systems. Most species are assumed to occupy thermal habitats that are below optimum for specific rates such as consumption as growth. In fact, sub-optimum temperatures are in fact optimal in natural environments as the temperature varies (Bernhardt et al 2019). However, the thermal margins of species (current habitat temperature vs tolerance limits) vary between species and biogeography. Empirical evidence however show that that warming can have negative effects on species living at the edge of their geographical distributions in terms of growth (Neuheimer *et al.* 2011) or even survival (Pörtner & Knust 2007). This implies that assumptions about species occupying thermal habitats corresponding to increasing part of unimodal thermal responses is a simplification that may not always be warranted in a climate change context.

**So what are the main limitations in data and models?** \*Add section here about limitations in experiments and all uncertainties from that\*, including pros and cons with standardization… size variation.

**Final touch:** 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 limit our understanding of important aspects beyond individual body size, including energy transfer & efficiency of food webs and ecosystems. Progress towards unification of theory and empirical findings can be made through systematic data-analysis, which can guide process-based predictions of climate change impacts on growth and body size of ectotherms.

**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.

**References**

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