*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 general species 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 and food web 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 collated experimental data from a systematic literature review. 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 evidence of 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), but a contributing factor could be the history of commercial exploitation of these species as fishing disproportionally targets large fish. For example, 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), and across temperature gradients (van Denderen *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 vary and theoretical predictions are questioned, it remains unclear to which extent the growth of large fish within a population is limited by warming from purely physiological constraints. 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 of 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 energy available in consumed food and expenditure is defined as fasting, activity and feeding metabolism. Metabolic processes are in turn usually assumed to be related to resting metabolism, often 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 in general 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 applied to represent individual processes. In addition, the temperature- and mass dependence of metabolism and other related rates are also often assumed to follow Arrhenius fractal supply model (AFS) in the metabolic theory of ecology (Gillooly *et al.* 2001; Brown *et al.* 2004; 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 tends 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 temperature (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). Scaling parameters are therefore often limited to 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 Collection 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 account for variation between species and to acquire general intraspecific scaling predictions based on partial pooling of data across species to minimize the influence of extreme observations for general scaling relationships. 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, routine and standard (see ‘*model fitting’*) oxygen consumption rate, which is a 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 temperature jointly rather than fixing one effect, as well as evaluate the probability of interactive effects within species. We compiled in total 154, 2790 and 626 data points from published articles on optimum-shaped growth rates, metabolic rate and maximum consumption rate, from 13, 35 and 18 species, respectively, representing a diverse taxonomic, habitat and lifestyle range (Appendix S1). Data from were extracted from tables, or figures using Web Plot Digitizer (Rohatgi 2012).

We excluded larvae studies as they can have different mass-scaling and represent a small fraction of the ontogeny of most fish. Studies were selected if (i) a unique experimental temperature was recorded for each trial (), (ii) fish were provided food at *ad libitum* for consumption and growth data, no food for resting or routine metabolic rate for metabolism, (iii) fish exhibited normal behavior. 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 (Appendix S1). 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 complied data individuals differed in their body masses non randomly (i.e. by species and study), 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 standardized our predictor variables, in some cases 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, we standardized temperature by subtracting the mean optimum growth temperature by species. For the analysis of mass-dependence of optimum growth temperature within species, we used relative mass as a predictor, as we were interested in examining relationships within species while accounting for variation in relative body masses between experiments. This relative mass is calculated by 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. The values are for most species derived from quadratic models in the original papers (), but in some cases taken to be temperature where growth is maximized from a unimodal curve (). 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 in standardized body mass (not by species). We also fit a model with non-varying mass-coefficient (i.e. , not indexed by ), and selected the best fitting 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 below the temperature at which the rate was maximized, by size group), we assumed individual growth, metabolic rate and maximum consumption rate to scale as a generalized version of the AFS model (Gillooly *et al.* 2001; Brown *et al.* 2004), in which neither the mass- or temperature dependence is assumed and corrected for but estimate jointly. 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 the natural log of 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 (sthe mass-scaling exponent and activation energy, respectively) using hierarchical models with different combinations of group (species)-varying coefficients and compare models using WAIC and support for coefficients. 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). Growth rates were recalculated to unit , consumption rates to recalculated to unit and metabolic rates to unit (Appendix S1). We use resting or routine metabolism (mean oxygen uptake of a resting unfed fish only showing some spontaneous activity) and standard metabolism (resting unfed and no activity, usually inferred from extrapolation or from low quantiles of routine metabolism) (Beamish 1964). Routine and resting constitute 55% of data and standard 45%. Because the definitions of these different estimates differ between studies, we did not attempt to rescale them to a single unit assuming a fixed relation, but instead account for variation between these through the random species effects, since we also use only one experiment per species. All predictor variables are in addition mean-centered, such that 0 corresponds to the overall mean (not by species). We select best fitting models using WAIC.

*Scaling of consumption rates with temperatures including optimum*

As maximum consumption is unimodal over a large enough temperature range, we fit polynomial models to a subset of these data containing only species with data points beyond the temperature at which the rate is maximized (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 the 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 ( 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), and the full general relationship is given by: . This decline in optimum temperature with mass is clear, as 99% of the posterior density of the slope estimate () is below 0. We select the model containing a species-level effect on the intercept () and a common slope across species (), based on parsimony. This model has a lower WAIC but the standard errors of the WAIC from the two models are large.

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 ). Colors indicate species (n=13) (see Appendix S1) and point size corresponds to mass in unit .*

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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. Data points belong to different species (n species = 13, Fig. SX)*

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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. Clusters in data generally represent species (n=18 and n=35 for consumption and metabolism, respectively, see Fig. SX).*

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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, and the their scaling with body 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, activation energies of these rates 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.

Size-dependence of optimum growth temperature has been reported in some studies, and not only in fish (Panov & McQueen 1998; Steinarsson & Imsland 2003; Björnsson *et al.* 2007; Handeland *et al.* 2008), but was not found for e.g. brown trout (*Salmo trutta*) (Elliott & Hurley 1995). We are able to demonstrate clear signals of optimum growth temperatures declining as fish grow in size. The effect size also appears relatively large considering the small size range used in the experiments (a decline in by 0.3 per unit increase in natural log of relative body mass). 73% of individuals are smaller 1% of their asymptotic body size (Fig. SX), and it is thus likely to assume that the largest fish in a population have even lower relative optimum growth temperatures. Moreover, the individuals in the experiment likely invest little energy to reproduction, which suggests that predicted changes in size-at-maturation from the TSR is not the only explanation to declines in growth, and by extension possibly size-at-age, of large individuals with warming. Translating these effects of experimental derived optimum growth temperature to natural systems is challenging due to the “ideal” conditions found in the experiments, mainly unlimited food supply, no predation pressure and constant temperatures, which affects both growth rates and optimum temperatures for growth (Brett *et al.* 1969). 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. However, 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). While most species occupy thermal habitats that are below optimum for specific rates such as consumption as growth (sub-optimum temperatures are in fact optimal in natural environments as the temperature varies (Bernhardt et al 2019)), the thermal margins vary between species and biogeography. Empirical evidence does indicate that warming can have negative (or lack of positive) effects on species living at the edge of their physiological tolerance in terms of growth (Neuheimer *et al.* 2011; Huss *et al.* 2019) 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.

Interestingly, declines in optimum growth temperature with mass is also predicted from the von Bertalanffy growth model (VBGM): , where is body mass and is temperature, under two conditions: (which also is a necessity for asymptotic growth) and that growth has an optimum over temperature, as shown by (Morita *et al.* 2010b). While this is one of the most applied growth models, the first condition has been debated recently. is in the classic VBGM 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 and a lack of empirical data (Ursin 1967)). From a physiological perspective, it is more common to assume 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 both assimilation and standard metabolic rate. This dichotomy can be resolved by considering the overlooked energetic investment into reproduction (mass-scaling exponent larger than 1) (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 to the intraspecific scaling of metabolic rate in relation to assimilation or consumption. Our finding that the mass-scaling exponent metabolism is larger than for maximum consumption rates implies 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. In natural systems however, realized consumption is mediated by predator-prey encounter rates and search rates, whereas maximum consumption rates largely correspond to the physiology of digestion (Ursin 1967). Regardless, changes in the maximum feeding capacity 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 affected 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). We find that when 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 largely overlap, meaning there is no clear loss or gain of energetic efficiency with warming. The larger posterior median of the activation energy for consumption compared to metabolism could therefore be due to chance. This result fits well with the finding that growth rates increase with temperature, which would be difficult to explain from a bioenergetics perspective if warming reduced net energy gains. We also find the general temperature scaling to be less uncertain than what has been reported previously (e.g. in (Downs *et al.* 2008; Englund *et al.* 2011)). A likely contributing factor is the use of hierarchal models and partial pooling to estimate higher level (across species) scaling from species-data as opposed to either aggregating all data (complete pooling) or summarizing single-species estimates (no pooling). 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). This was however not found in a recent intraspecific study of metabolic rate in fishes (Jerde *et al.* 2019), possibly due to differences in modelling temperature, where we followed the AFS. The effect size of the interaction is relatively small and the ecological implications could therefore also be, although larger estimates have been reported in single species studies and the small general 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 over essentially all temperatures. 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), and opens up for the question about the relevance of optimum thermal response curves in natural systems. As previously discussed, there are indications that it is important to account for unimodal thermal responses of growth rates in some cases. To what degree this is due to metabolic mismatch due to unimodal consumption vs exponential metabolism, as is often argued from a conceptual point of view (Jobling 1997), remains uncertain. This is perhaps best evaluated on a species level, given the large variation between species in their optimum temperature relative to their natural temperature (Fig. 6).

As the aim of our study was to evaluate the joint effect of body mass and temperature, we collated data only from studies that included both these treatments. This constitutes logistical challenges for the experimentalists. Therefore, the number of studies that were selected from the initial searches constitutes a small fraction of the available data that includes single-temperature or single-size experiments (Appendix S1), and that the size replicates within each temperature treatment or vice versa are relatively small. The relatively small amount of data is especially evident for the consumption experiments, which show larger variation both within and between species. This is likely due to the more manual estimations in feeding experiments (e.g. weighing added food and subtracting uneaten food) compared to respirometry or growth trials. The appetite of individual fish can also vary across food items and depending on the experimental set up, including number of conspecifics in trials. There are also likely additional sources of uncertainty in our data sets simply from the fact that our studies span decades of experimental research, and research practices and publications have evolved during this time. In a recent study focusing on estimating the mass-exponent of metabolism, the literature search was selective than here and only recent studies from a detailed selection of metabolism-experiments where used (Jerde *et al.* 2019). This dataset allows for more data per experiment and thus the potential for more complex random effects structure. Their estimate is slightly larger than ours (0.89 vs 0.8), although our credible interval overlaps with their uncertainty interval and difference in implementing temperature could contribute to this. However, as it is important to jointly estimate the effects of mass- and temperature when scaling coefficients differ from general predictions (Downs *et al.* 2008), we argue that our wide-spanning literature search is warranted. Hierarchical models and use of literature-informed priors can aid in acquiring relatively certain general scaling relationships by pooling information across species and by facilitating convergence.

Understanding the scaling of rates such as growth, metabolism and consumption is fundamental for linking individual processes to population and food web dynamics. We argue that one contributing factor to mismatch between mechanistic models, scaling theory and empirical scaling is due to lack of synthesis of data at the intraspecific level. Systematic data-analysis of accumulated experimental data combined with models accounting for uncertainty at species and general relationships constitutes an approach that can guide process-based predictions of climate change impacts on individuals and food webs.

**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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