*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 body 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 models of body growth as well as food web dynamics.
2. To estimate the effect of body size and temperature on body growth, and to examine the link between growth rate and rates of metabolism and consumption, we collected experimental data through a systematic literature review. We used only studies combining body mass and temperature treatments. We fit hierarchical models to evaluate how these three rates scale jointly with mass and temperature within species, while accounting for variation between species.
3. We find clear support for that optimum growth temperature declines with body mass within species, and growth rates increase with temperature. We find mass-dependent effects of temperature on metabolism at sub-optimum temperatures but not so 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. Larger individuals will be the first to experience negative effects of warming on growth. Size-dependent changes in growth dynamics due to climate warming 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 how growth scales with body size and temperature as well as 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). Empirical evidence of climate signals in time series of individual growth rate is accumulating. For instance, reconstructed growth histories of individual fish through ageing based on bony structures (otoliths) often show positive correlations between growth rates and increasing temperatures (Thresher *et al.* 2007; Neuheimer *et al.* 2011; Baudron *et al.* 2014; Huss *et al.* 2019). This increased growth rate can also be predicted from numerous experimental studies showing 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 of large fish within populations. Time series of asymptotic or maximum body mass have shown negative correlations with temperature (Baudron *et al.* 2014; van Rijn *et al.* 2017), but a contributing factor could be the history of commercial exploitation of the studied 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 (Huss et al. 2019). 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 by which 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 populations is limited by warming from purely physiological constraints. More accurate predictions of the effect of body size and temperature on growth from controlled experimental studies can aid both the development of theoretical growth models and providing predictions about the effect of temperature on growth.

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 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. Assessing these dependencies should ideally be done at the intraspecific, rather than interspecific, level to better represent the individual-level processes, as variation within and between species 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 processes in individuals. 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 effects 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 cases when 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)), within-species thermal response curves are generally unimodal (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 of rates with mass and temperature is less understood than interspecific scaling relationships. Contributing factors could be the logistical challenges of replicating experiments for ranges of body masses and temperature (Jerde *et al.* 2019) and a lack of comprehensive data (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 based on single, 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 their intraspecific scaling with mass and temperature is highly warranted.

In this study, we performed a systematic literature review by searching the 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 predictions on how the rates depend on temperature and body mass, 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 patterns of mass- and temperature-dependence of rates that 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 as a proxy for metabolic rate (Nelson 2016). We used 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 the five 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 size or temperature treatments), it allows us to fit multivariate models and estimate the effects of mass and temperature jointly, and to evaluate the probability of interactive mass- and temperature effects within species. We compiled in total 154, 2790 and 626 data points from published articles on growth rates (with an optimum shape), metabolic rate and maximum consumption rate, from 13, 35 and 18 species, respectively, representing a diverse range of taxonomic groups, habitats and lifestyles (Appendix S1). Data were extracted from published tables, or figures using Web Plot Digitizer (Rohatgi 2012).

We excluded larval studies as they can have different mass-scaling and represent a small fraction of the ontogeny of most fish. Studies were included if (i) a unique experimental temperature was recorded for each trial (), (ii) fish were provided food at *ad libitum* for consumption and growth data, fish were unfed for measurements of resting or routine metabolic rate , (iii) fish exhibited normal behavior. We used only one study per species to ensure 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, as well as in their experimental temperature (in absolute values and relative to their mean environmental temperature) (Fig S2, S6-S7). Therefore, we standardized our predictor variables, in some cases by species. This was done by expressing temperature as the difference between the experimental temperatures used and the median environmental temperature for each species. 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 mass relative to maximum mass as a predictor (based on literature estimates taken from FishBase between 2019.06.01-2019.12.01), as we were interested in examining relationships within species while accounting for variation in relative body masses between experiments. 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 *i*th observation of the rescaled optimum temperature of the growth rate in 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 the ratio between body mass and the maximum body mass within species (all mass measured in ), defined as . In Eq. 3, the subscript refers 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 a mass-coefficient not varying by species (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 at temperatures 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 Arrhenius fractal supply model (Gillooly *et al.* 2001; Brown *et al.* 2004). Mass and temperature dependence was not assumed a priori but estimated jointly to evaluate the effects of temperature and body mass simultaneously. This approach is more appropriate if the mass-scaling exponent is not exactly 3/4 (Downs *et al.* 2008), as suggested by empirical data (Sibly *et al.* 2015; Jerde *et al.* 2019), and 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) scales 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 (the mass-scaling exponent and activation energy, respectively) and their interaction (i.e. the term in the mass-scaling exponent) using hierarchical Bayesian 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 expressed as unit , consumption rates as unit and metabolic rates as 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) to represent metabolic rate (Beamish 1964). Routine and resting metabolism constitute 55% of the data used and standard metabolism 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 included 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 including beyond optimum temperatures*

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 extending 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 avoid the risk of removing true effects in data, at the cost of losing 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 species-specific mean body mass in ). The species predictions and data are plotted together in Fig. S21 to illustrate the spread in optimum temperature measured as distance to environmental median. Due to general data limitation we did not fit an interaction term that alters the optimum temperature by mass, however this has been identified in data-rich single-species 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 10000 iterations for 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 *‘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 regressions  for growth, consumption and metabolism (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  for consumption  (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 (Fig. 1). The optimum temperature declines with per unit increase in the natural log of relative body mass (Fig. 1), and the general relationship is given by: . We find strong model support that optimum temperature declines with mass, because 99% of the posterior density of the slope estimate () is below 0. We selected the model containing a species-level effect on the intercept () and a common slope across species () (model M1, Table 2), based on parsimony. This model has a lower WAIC but the standard errors of the WAIC from the two models are large.

We find that the average intraspecific mass- and temperature dependence of specific body growth at below optimum temperatures across species can be described by the equation: . The model with best fit to data contains a body mass-temperature interaction (model M1 in 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 to a large extent overlapping (, . We therefore find limited support for a mass-temperature interactions 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 [] (brackets indicate 95% Bayesian credible intervals). We estimate the activation energy, , (coefficient to the relative Arrhenius temperature, ) of growth to be [], which is lower, ,than what is typically found for metabolic rate (Downs *et al.* 2008) and for body 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 for each species) increases growth rates by 86%.

We find that the average intraspecific scaling of whole-organism metabolic rate can be described by the equation , and consumption rate at temperatures below optimum as (see Fig. 3 for a general intraspecific prediction for a given mass and two temperatures). Some notable differences exist in the mass- and temperature-dependences 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 mass-scaling exponent predicted 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 [] whereas for maximum consumption rate it is ([]). However, this difference is less clear than that of 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). Both activation energy estimates fall 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 increase faster with temperature than metabolic rates.

We find strong statistical support for a negative interaction between the effect of body mass and temperature on metabolic rate (99.7% of the posterior distribution of is above 0, Fig, 5), yet the effect size is relatively small. We estimate it to be on an Arrhenius temperature scale, which corresponds to a decline in the mass scaling exponent of metabolic rate by 0.002 . In the selected model of consumption, all coefficients vary by species whereas for the selected models of metabolism, all but the interaction coefficient vary by species (Table 2).

Over a larger temperature range, biological rates tend to be unimodal. We identified such tendencies in nine species in the consumption data set, and fit polynomial models to the consumption rate in 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 mismatch between metabolic costs and feeding gains depends on the current temperature relative to optimum temperature. 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 relative temperature at which consumption is maximized (“optimum”) (Fig. 6). These temperatures range from -2.3 to +17, in degrees Celsius difference in temperature between optimum temperature and median environment temperature, by species (i.e. ). 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 depend on mass and temperature (below optimum temperatures). M1 is the full model and is described in text (Eqns. 3-5). The column M\*T indicates whether the model for the rate includes an interactive effect of mass and temperature. The WAIC columns shows WAIC (WAIC, SE), where WAIC is the difference between each models’ WAIC and the lowest WAIC 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 the individual observation’s WAIC). Bold indicates the model with the strongest support based on WAIC (lowest value).

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| 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 across species) 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 body growth. A) Growth rate [% day-1] as a function of standardized body mass, both on natural log scale. Lines are mean marginal predictions at temperatures -0.75 and 0 in unit mean-centered Arrhenius temperature (1/kT) standardized to median environmental temperature (lines correspond approximately to 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 in Eqs. 6-8). The slope corresponds to the mass-scaling exponent. Posterior distributions of mass-scaling exponent (B) and activation energy (C) of ln(specific body growth) are shown in the bottom row. The dashed white line shows the posterior median. Data points belong to different species (n species=13).*

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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 in Eqs. 6-8) for two temperatures on Arrhenius scale (1/kT): warm (red) and cold (blue), which is approximately a deviance from the median environment temperature with +10 and +2.5 respectively. Clusters in data generally represent species (n=18 and n=35 for consumption and metabolism, respectively, see Fig. S8).*

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***Fig. 4****. Posterior medians of activation energies and mass exponent 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 an unknown species (i.e. and in Eqs. 6-8 for the mass and temperature coefficient, respectively). Shaded vertical areas correspond 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). Numbers in the 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 (and note that the mass-temperature interaction is estimated and presented on an Arrhenius temperature scale, 1/kT).*

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***Fig. 6****. Standardized maximum consumption rates (relative to mean consumption rate within species) as a function of standardized 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 species’ median environmental temperature”, and the vertical dashed and dotted lines correspond to the across-species mean optimum temperature 1 standard deviation.*

**Discussion**

Individual growth, consumption and metabolic rate represent fundamental processes in ecology, and their dependence on 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). Relationships of how biological rates scale with temperature and/or mass are commonly inferred from either meta-analysis of single-species studies or interspecific relationships. 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 not 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 how these rates depend on temperature and mass at the intraspecific level. By accounting for variation between species, we find that unimodal growth rates scale similarly 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 greater than predicted and for consumption it is smaller than predicted. This has implications for mechanistic models of individual growth, as well as population and food web dynamics.

That optimum growth temperature vary with body size has been reported in some studies, including but not limited to 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). Here, we find strong support that optimum growth temperatures decline as fish grow in size (mass). The effect size also appears relatively large considering the small range of body sizes used in the experiments (a decline in by 0.3 per unit increase in natural log of the ratio of body mass to the species’ maximum body mass). Because 73% of individuals in the experiments assembled for this study are < 1% of their asymptotic body size (Fig. SX), the largest fish in a population may experience even lower relative optimum growth temperatures than what our model predicts. Moreover, the individuals in the experiments likely invest little energy in reproduction. This suggests that predicted changes in size-at-maturation from the temperature-size-rule is not the only explanation to declines in growth, and by extension possibly also to size-at-age, of large individuals with warming. Translating effects of empirically derived optimum growth temperatures to natural systems is challenging because experimental conditions such as unlimited food supply, lack of predation, and constant temperatures do not reflect natural condition, yet these variable affect growth rates and optimum temperatures for growth (Brett *et al.* 1969). In natural systems, growth is mediated through species- and trait-dependent complex ecological interactions. Nevertheless, the finding that large fish would be the first in a population to experience negative effects of warming suggests there might be purely physiological constraints to body growth of large fish within a species in warm environments. 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), which indicate/could counteract… 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 their optimum for 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 indicates that warming can have negative (or lack of positive) effects on populations 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 the increasing part of unimodal thermal responses is a simplification that may not always be warranted in a climate change context.

Interestingly, a decline in optimum growth temperature with mass is also predicted by the von Bertalanffy growth model (VBGM) , where is body mass and is temperature), under two conditions: (which also is a necessity for growth to be asymptotic) and that growth has an optimum over temperature, as shown by (Morita *et al.* 2010b). While this is one of the most commonly applied growth models, the first condition has been debated recently. in the classic VBGM is assumed to be 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 of body growth, such as the VBGM or OGM, either fail to represent the physiological processes they aim to capture, or fail to exhibit asymptotic growth. This is especially true if assuming a ‘universal’ mass scaling exponents of 3/4 for both assimilation and standard metabolic rate. This dichotomy can be resolved by considering the overlooked energetic investment into reproduction (and its hyper-allometric mass-scaling, i.e. exponent larger than 1) (Marshall & White 2019b), or by applying more complex energy pathways in dynamic energy budget models (Kearney 2019). This recent debate about scaling coefficients call for an investigation of the intraspecific scaling of metabolic rate in relation to assimilation or consumption. Our finding that the mass-scaling exponent of metabolism is larger than that for maximum consumption implies that “costs” for maintenance increase faster with body mass than energy assimilation – 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 the mass-scaling of metabolism and consumption, which is in contrast to universal mass-scaling predictions.

In addition to resolving 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 metabolism and consumption vary, but the 95% credible intervals largely overlap, meaning there is no clear loss or gain of energetic efficiency with warming. 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 always reduced net energy gains.

We also find the general temperature scaling of metabolism, maximum consumption and specific growth rate 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 our 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 only 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, however, relatively small. The ecological implications could therefore also be small, although larger estimates have been reported in single species studies and the small predicted effect size could be due to the known variation between species, which includes positive and negative effects (Ohlberger *et al.* 2012; Lindmark *et al.* 2018).

While we find no clear evidence of mismatch between metabolic demands and maximum consumption induced by temperature at sub-optimum temperatures, we do find clear mismatches at higher temperatures. These are due to consumption rates being unimodally related to temperature, whereas metabolic rates increase exponentially 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 caused by the unimodal temperature-dependence of consumption vs the exponential one of 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 among species in their optimum temperature relative to their preferred temperature (Fig. 6).

As the aim of our study was to evaluate the joint effect of body mass and temperature on rates of body growth, metabolism and consumption, we collected data only from studies that included both these treatments. Such a factorial treatment constitutes logistical challenges for 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). It also resulted in 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 oxygen depletion rates (metabolism) measured in 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 more selective than herein 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 of the mass exponent of metabolic rate 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 to facilitate 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 the 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 existing experimental data combined with models that account 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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