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

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**Abstract**

Warming of aquatic ecosystems is generally predicted to increase individual growth rates and reduce asymptotic body sizes of ectotherms. However, we lack a comprehensive understanding of average intraspecific scaling of growth and the key processes affecting it (e.g., metabolism and consumption) with body mass and temperature. This limits our ability to inform mechanistic growth models, to link experimental data to observed patterns of growth, and to advance mechanistic food web models. To estimate the effect of body size and temperature on growth, and to examine the link between growth rate and rates of metabolism and consumption, we collated experimental data through a systematic literature review. We used only studies combining body mass and temperature treatments (in a factorial set-up), and fit hierarchical models to evaluate how growth, metabolism and maximum consumption rate scale jointly with mass and temperature within species, while accounting for variation between species. Mass-scaling exponents of maximum consumption are smaller than both the predicted ¾ and metabolism-exponents and are unimodal over the full temperature range. This contributes to unimodal thermal responses of growth. These are characterized by declining optimum temperatures for body growth to temperature. Accordingly, our analysis of growth data demonstrates that optimum growth temperatures declines as a function of body size within species. Thus, small individuals within a species will likely be able to increase their growth rates with initial warming and larger individuals could be the first to experience negative effects of warming on growth. We argue that syntheses of existing experimental data on intra-specific scaling of key physiological rates, accounting for uncertainty at the species-level, can help overcome the mismatch between mechanistic growth and food webs models, general scaling theory, and observations.

**Introduction**

Individual body growth is a fundamental process powered by metabolism, and thus depends on body size and temperature (Brown *et al.* 2004). It affects individuals’ fitness and life history traits, such as maturation size, population growth rates (Savage *et al.* 2004) and ultimately energy transfer across trophic levels (Andersen *et al.* 2009; Barneche & Allen 2018). Therefore, uunderstanding how it scales with body size and temperature 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), as well as latitudinal gradient studies of insects (Horne *et al.* 2015), and is stronger in aquatic than terrestrial environments (Forster *et al.* 2012; Horne *et al.* 2015). The underlying mechanisms are not well understood, but likely results from an 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.* 2010; García García *et al.* 2011). Less clear, however, is the negative effect of warming on the growth of large fish within populations, as would be predicted form the temperature size-rule. Some studies have found negative correlations between maximum or asymptotic body size and temperatures in commercially exploited fish species (Baudron *et al.* 2014; van Rijn *et al.* 2017), whereas others, including large scale experiments, controlled experiments and latitudinal studies, have failed to find this relationship between maximum size and temperature (Barneche *et al.* 2019; Huss *et al.* 2019; van Denderen *et al.* 2019; van Dorst *et al.* 2019). Predictions about declines in asymptotic body mass, and declines in optimum temperature for growth, have also been made from theoretical growth models, such as the von Bertalanffy growth model (VBGM) which is a special case of a Pütter model (Pütter 1920; von Bertalanffy 1938; Morita *et al.* 2010; Pauly & Cheung 2018b). However, the physiological basis of these models has been questioned for multiple reasons, including unrealistically large effects of temperature on asymptotic size and mass scaling exponents not matching empirical observations (Lefevre *et al.* 2017; Marshall & White 2019a, b). 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 temperature.

The specific somatic growth rate of an individual can be represented as the difference between energy acquisition and expenditure (von Bertalanffy 1938; Kitchell *et al.* 1977; Jobling 1997). In mature individuals, the remaining excess energy is partitioned between somatic growth and gonads. Energy acquisition, or assimilation, is typically the amount of energy extracted from 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 growth-energetics 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 (Kitchell *et al.* 1977; Kooijman 1993; Kearney 2019) including physiologically structured population models (PSPMs) (de 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 level, rather than the interspecific level, to better represent the individual-level processes, and because allometric and temperature relationships within and between species can differ (Glazier 2005; Rall *et al.* 2012; 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 the Arrhenius fractal supply model (AFS), as 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 () (e.g. metabolism and consumption) scale as: , where is the activation energy, is Boltzmann’s constant and is temperature in Kelvin. Importantly, the model assumes mass-scaling of 3/4 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; Glazier 2005; García García *et al.* 2011; Ohlberger *et al.* 2012; Lindmark *et al.* 2018) (but see Jerde *et al*. (2019)). Moreover, while the AFS tends to provide good statistical fits to interspecific data (Clarke 2004), and intraspecific data with a restricted temperature range (Brown *et al.* 2004; Clarke 2004; Rall *et al.* 2012) (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; Uiterwaal & DeLong 2020). These simplifications could affect the estimates of temperature dependencies (Downs *et al.* 2008). Instead of mass- or temperature-correcting rates according to the AFS (Brown *et al.* 2004), it could be more appropriate to fit multiple regression models where regression coefficients for mass and temperature are estimated jointly (Downs *et al.* 2008), as well as fit non-linear models that can capture the de-activation of biological rates at higher temperatures (Schoolfield *et al.* 1981; 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 experiments, which makes generalization across species difficult. However, it is important to understand both general tendencies and variability of intraspecific body mass- and temperature-scaling across species, given the importance of intraspecific trait variation as a driver of ecological dynamics, and that body size is as much a trait of an individual as it a characteristic of species (Bolnick *et al.* 2011; Miller & Rudolf 2011; Persson & De Roos 2013; Brose *et al.* 2017). Therefore, overcoming the knowledge gap about intraspecific scaling with mass and temperature is important for advancing trait-based approaches to ecology as well as for food web responses to warming.

In this study, we analyse how consumption, metabolism and body growth of fish scale intra-specifically with mass and temperature. To this end, we performed a systematic literature review by searching the Web of Science Core Collection to compile a dataset on individual growth, 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 acquire general intraspecific scaling predictions while also accounting for variation between species. For maximum consumption rates, we also fit quadratic models to a subset of the data to characterize the unimodal temperature dependence. We find that the temperature-dependence of growth, consumption and metabolism at below-peak temperatures is close to average intraspecific predictions (activation energies approximately 0.65 ), whereas the mass-exponent of maximum consumption is smaller than the predicted 3/4. Over the full temperature range, consumption rates are unimodal, suggesting declines in optimum growth temperatures with body mass. Finally, using an independent data set, we demonstrate that optimum growth temperatures decline with body mass.

**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 oxygen consumption rate as a proxy for metabolic rate (Nelson 2016). We used three different searches on the Web of Science Core Collection. For growth rate, we used the following topic terms: (growth) AND (mass OR weight OR size) AND (temperature\*) AND (optimum), as well as: (growth) AND (mass OR weight OR size) AND (temperature\*) AND (optim\*). For metabolic rate we used: (metabolism OR "oxygen-consumption" OR "oxygen consumption") AND (mass OR weight OR size) AND (temperature\*). For maximum consumption we used: (consumption or feeding$rate or food$intake or bio$energ\* or ingestion or food-intake) AND (mass or weight or size) AND (temperature\*), as well as: (feeding-rate or bio-energ\*) AND (mass or weight or size) AND (temperature\*). We also applied additional filters on subject: ‘marine freshwater biology’, ‘fisheries’, ‘ecology’, ‘zoology’, ‘biology’, ‘physiology’. For growth rates, we in addition included ‘limnology’ and for maximum consumption we included ‘limnology’ and ‘evolutionary biology’. The broader searches for growth and consumption reflects the lower data availability compared to metabolism. For more detailed information about the search protocol, we refer to Appendix S1.

We selected studies with a factorial body mass-temperature setup in order to estimate how these rates depend on both body size and temperature within species. While this reduces the number of data sets available in the literature (as most experimental studies only use size or temperature treatments), it allows us to fit multiple regression models and estimate the effects of mass and temperature jointly, and to evaluate the probability of interactive mass- and temperature effects within species. We excluded larval studies as they represent a small fraction of the ontogeny of most fish. Studies were included if (i) a unique experimental temperature was recorded for each trial (1), (ii) fish were provided food at *ad libitum* for consumption and growth data, fish were unfed for measurements of resting, standard or routine metabolic rate, (iii) fish exhibited normal behaviour. 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 (for details, see Appendix S1). A more detailed description of the search protocol, criteria to select data, data acquisition procedure, quality control, collation of additional information and standardizing rates to common units can be found in Appendix S1.

We compiled four datasets: growth, metabolic, and maximum consumption rate, and the optimum growth rate temperature for each combination of body mass group and species. We compiled in total 154 (45 optimum temperatures), 2790 and 626 data points from published articles for each 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).

Between experiments, individuals differed in their body masses, both in absolute values and relative to their maximum body size. Experimental temperatures also varied in relation to the species normal temperature-range between studies (Fig S2, S6-S7). For the analysis of optimum growth temperature, we therefore rescaled body mass and temperature to relative variables, by species. Relative body mass is defined as mass relative to maximum mass (based on literature estimates taken from FishBase (Froese & Pauly 2016) between 2019-06-01 and 2019-12-01), as we were interested in examining relationships within species while accounting for variation in relative body masses between experiments, and because we assume there is no interspecific relationship between optimum growth temperature and body mass. We expressed optimum growth temperature as mean-centered within species (of different size-classes), to control for species having different thermal optima. The optimum growth and consumption temperatures were also evaluated in relation to the minimum, mid-point and maximum of the ranges in experienced environmental temperatures (taken from FishBase), which was subtracted from the experimental temperature. In the growth data, this information was not available on FishBase for marbled sole (*Pseudopleuronectes yokohamae*), hence 3-24 (mid-point 13.5) was used (Joh *et al.* 2013; Mitamura *et al.* 2020).

**Model fitting**

*Mass- and temperature scaling of growth, metabolism and consumption below optimum temperatures*

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 that individual growth, metabolism and maximum consumption rate scale as a generalized version of the Arrhenius fractal supply model (Gillooly *et al.* 2001; Brown *et al.* 2004). Note that the term optimum is misleading for metabolic rate data, but since we do not have data points beyond the temperature at which metabolism is at its maximum, optimum only refers to maximum consumption or growth data. Mass- and temperature dependence was not assumed a priori but estimated simultaneously. This is more appropriate than correcting for either variable if these parameters (mass-exponent or activation energy) are uncertain or vary across species and taxa (Downs *et al.* 2008; Isaac & Carbone 2010), and allows estimation of size-temperature interactions. We thus assumed the natural log of rate (growth, metabolism or maximum consumption) scales with mass and temperature as:

|  |  |  |
| --- | --- | --- |
|  | , | (1) |

which on normal scale becomes:

|  |  |  |
| --- | --- | --- |
|  | *,* | (2) |

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 fit hierarchical models with different combinations of group (species)-varying coefficients. This is in contrast to the Arrhenius fractal supply model, which assumes only the intercept varies between taxa. With such grouping in the models, the species-varying coefficients are estimated with shrinkage, which reduces the influence of outliers which could occur in species with small samples sizes (Gelman & Hill 2007; Harrison *et al.* 2018). The full model with uncorrelated species-varying intercepts, mass-, temperature- and interaction-coefficients, can be written as:

|  |  |  |
| --- | --- | --- |
|  |  | (3) |
|  |  | (4) |
|  | , | (5) |

where is the th observation of the natural log of the rate (growth, metabolism or consumption), and indexes regression coefficient (. In Eq. 4, is the mean centered (not by species) natural log of body mass (), and is mean-centered Arrhenius temperature (in unit ) (). For metabolism and maximum consumption rates, is mass in , whereas for growth rates, is either the geometric mean of the initial and final mass (in ) of the growth experiment, or the size-class (in ), as defined by the authors. Specific 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, e.g. lowest 10 % of measurements) to represent metabolic rate (Beamish 1964; Ohlberger *et al.* 2007). Routine and resting metabolism constitute 55% of the data used and standard metabolism constitutes 45%. We accounted for potential differences between these metabolic rate measurements by using a random species effect and a single experiment/dataset per species.

*Mass- and temperature scaling of consumption including beyond optimum temperatures*

Consumption rates are unimodal over a large enough thermal range, and we refer to the temperature where these rates are maximized as optimum temperature (Dell *et al.* 2011; Englund *et al.* 2011). To evaluate the intraspecific unimodal scaling of these rates, we fit quadratic models to a subset of these data containing only species with data points extending beyond the temperature at which the rate is maximized. The models were fit by species without any hierarchical structure accounting for species variation. This was due to the difficulty of standardizing thermal response curves 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 by pooling data, at the cost of losing the benefits of the hierarchical model for inferring general intraspecific scaling and for limiting the influence of extreme observations. The model of is for the data with the full temperature range defined as:

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| --- | --- | --- |
|  |  | (6) |
|  | , | (7) |

where in Eq. 6 refers to consumption rates divided by the mean value by species (), in Eq. 7 is mean-centered natural log of body mass () and is mean-centered rescaled temperature by species, where the rescaled 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 of our consumption data we did not fit an interaction term that alters the optimum temperature by mass, although this has been identified in data-rich single-species experiments (García García *et al.* 2011).

*Mass-dependence of optimum growth temperature*

To evaluate how the average optimum temperature () in degrees 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:

|  |  |  |
| --- | --- | --- |
|  |  | (8) |
|  |  | (9) |
|  |  | (10) |

Here is the *i*th observation of the mean-centered optimum growth temperature within species species : , is the natural log of the ratio between mass and maximum body mass within species: . The mass corresponds to either geometric mean body mass in the time interval where growth was measured in the experiments or size (mass) class depending on how it was defined in the original study. Subscript in Eq. 10 refers to regression parameters (0 for intercept and 1 for slope). We also fit a model with a global mass-coefficient (i.e. not varying by species). Body mass and temperature where in addition mean-centered for fitting, such that 0 corresponds to the mean across all data points.

*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 (Table 1). Weakly informative priors were given mean values around average prediction from the MTE (Brown *et al.* 2004), with increased variances to make them less informative. We used 3 Markov chains with 10000 iterations each saving every 5th sample, following a burn-in of 10000 iterations and 5000 iterations for adaptation. Model convergence was assessed by visually inspecting trace plots and potential scale reduction factors () (Gelman *et al.* 2003) (Appendix S1). compares chain variance with the pooled variance, and values <1.1 ensures all three chains converged to a common distribution. 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.

*Model comparison*

We compared the parsimony of models with different hierarchical structures, and with or without mass-temperature interactions, using the Watanabe-Akaike information criterion (WAIC) (Watanabe 2013; Vehtari *et al.* 2017), which is based on the posterior predictive distribution. We report WAIC for each model descried above (Table 2), and examine models with WAIC values < 2, where WAIC is each models difference to the lowest WAIC across models, in line with common convention (Olmos *et al.* 2019).

**Table 1** Description of model parameters and their prior distributions. refers to a normal distribution and to a uniform distribution.

|  |  |  |  |
| --- | --- | --- | --- |
| Model | Parameter | Description | Prior distribution |
| 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 |  |
| Quadratic model  for consumption and growth  (Eqns. 9-10) |  | Intercept |  |
|  | Mass coefficient |  |
|  | Temperature coefficient |  |
|  | Quadratic temperature coefficient |  |
|  | Variance |  |
| Linear  model  (Eqns. 1-3) |  | Hyperparameter (intercept) |  |
|  | Hyperparameter (mass coefficient) |  |
|  | Hyperparameter (intercept variance) |  |
|  | Hyperparameter (mass coefficient variance) |  |
|  | Variance |  |

**Results**

We find that the global intraspecific scaling of whole-organism metabolic rate can be described by the equation , and consumption rate at temperatures below optimum as (Fig. 1). In the models of consumption, all coefficients vary by species (M5) whereas for metabolism, all but the interaction coefficient vary by species (M2) (Table 2). Metabolic rate scales with a slightly larger mass-scaling exponent (0.77 [0.7, 0.83]) than maximum consumption (0.64 [0.56, 0.73), inferred from the only slightly overlapping Bayesian 95% credible intervals (indicated in square brackets) (Fig. 2). This difference implies that metabolic processes increase faster with body mass than maximum consumption rates. We also find it probable that the mass-scaling exponent of maximum consumption differs from the predicted 0.75 from the metabolic theory of ecology, because 99.5% of the posterior distribution is below 0.75 (Fig. 2). The mass-exponent for metabolism is closer to 0.75, with 70% of the posterior distribution above 0.75 (Fig. 2). Activation energies of metabolism and maximum consumption rate are both similar (-0.61 [-0.67, -0.56] and -0.66 [-0.83, -0.49], respectively; Fig. 2) and largely fall within the prediction from the MTE (0.6-0.7 eV) (Brown *et al.* 2004)).

We find strong statistical support for a negative global interaction between the effect of body mass and temperature on metabolic rate (99.9% of the posterior distribution of is above 0, Fig, S9), yet the effect size is relatively small. We estimate it to be 0.017 [0.0067, 0.03] on an Arrhenius temperature scale, which corresponds to a decline in the mass scaling exponent of metabolic rate by ~0.0023 . For metabolism, the model with a species-varying interaction term (M1) has a WAIC of 1.2, suggesting it is comparable to the global-interaction only model (M2). We chose the latter to illustrate predictions (Fig. 1A) because of its simpler model structure. For maximum consumption, the model with a global interaction term, , (M2) has a WAIC of 2 compared to the best model (M5) without an interaction term, meaning that WAIC offers little support for one of these models over the other (Table 2). For illustration of model predictions (Fig. 1B), we therefore chose model M5 (without interaction) because it is simpler and the estimate of in M2 is small (posterior median of -0.018 on Arrhenius temperature scale).

We find that the average intraspecific mass- and temperature dependence of specific growth at below optimum temperatures can be described by the equation: (Fig. 3). This model (M1, Table 2) also contains a body mass-temperature interaction. However, the estimated interaction coefficient is uncertain (-0.02 [-0.1, 0.06]) as about 72% of the posterior density is above 0 (Fig. 3D), and only leads to marginal better fits to data (WAIC of the model without interaction [M5] is 2.4, Table 2). We estimate the mass-scaling exponent of growth to be -0.3 [-0.43, -0.17]. The activation energy, , of growth is estimated to be -0.76 [-0.99, -0.54]. This is lower, i.e. more temperature-sensitive, than what is typically found for metabolic rate (Downs *et al.* 2008) and for growth based on field data (Sibly *et al.* 2015). We also find that 86% of the posterior density of the temperature effect is below -0.65 (approximately the value predicted by the metabolic theory of ecology) (Fig. 3C). To illustrate this in terms of specific growth, an increase in temperature from 15 (overall mean in data) to 25 leads to an increase in predicted natural log of growth by a factor of 2.9 for a fish of mean mass (~190).

Over a larger temperature range, biological rates are unimodal. We identified such tendencies in nine species in the consumption data set, and fit quadratic models to those species separately (Fig. 4). The unimodal temperature dependence implies that even if maximum consumption rates increase at the same rate as metabolism with temperature initially, consumption rates eventually 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 (i.e. ) in unit , we find large variations in the relative temperature at which consumption is maximized (“optimum”) (Fig. 4). These temperatures range from -2.3 to +17, but we also note these two extreme values could be due to inaccurate descriptions of the thermal environment. Across species, the mean distance between the mid-point of the environmental temperature and temperature where consumption is maximized is +6 with standard deviation of 6.

The implication of unimodal thermal response curves for maximum consumption is that the net energy gain, i.e. the difference between exponentially increasing metabolic rate (proportional to energetic costs) and consumption (proportional to energetic gains) also is unimodal (Fig. 5). This is a common observation at a specific body size (Jobling 1997), but it is not often compared between different body sizes. We exemplify the thermal response of net-energy gain using two body sizes and the mass- and temperature-dependent statistical models for metabolism and consumption (using the species *C. argus* because of the amount of data available and clear unimodal thermal response curve, Fig. S10), and show that the optimum of net energy gain declines with body size (Fig. 5). Empirical estimates of optimum temperature for growth across different body sizes within species corroborate this prediction. Specifically, we find that the optimum temperature for growth declines with body size by 0.3 per unit increase in the natural log of relative body mass (Fig. 6). This decline in optimum temperature with mass is very clear, because 99% of the posterior density of the slope estimate () is below 0 (Fig. S11). The two models, with and without species-varying slopes, were indistinguishable in terms of WAIC (WAIC = 1.3), and we therefore present the results for the global slope model for parsimony. The general relationship is given by the model: , where is the natural log relative mass. We also find that the mean across species difference between the mean intraspecific growth optimum temperature (across body sizes within species) and the mid-point of the species environmental temperature is 6.5 (Fig. 7).

**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 and absolute WAIC in brackets, rounded to the nearest decimal, where WAIC is the difference between each models’ WAIC and the lowest WAIC across models. Bold indicates models with WAIC < 2.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Model | m\*t | Species-varying parameter(s) | WAIC  metabolism | WAIC consumption | WAIC growth |
| M1 | Yes |  | **1.2 (291.3)** | 3.5 (530.3) | **0 (43)** |
| M2 |  | **0 (290)** | **2 (528.7)** | 2.7 (45.6) |
| M3a |  | 297.8 (587.9) | 132.5 (659.2) | 27.4 (70.4) |
| M3b |  | 844.5 (1134.6) | 48 (574.7) | 48.2 (91.2) |
| M4 |  | 1063.6 (1353.7) | 157.4 (684.1) | 59.2 (102.2) |
| M5 | No |  | 6.4 (296.5) | **0 (526.7)** | 2.4 (45.3) |
| M6 |  | 1167.6 (1457.6) | 185.5 (712.2) | 56.8 (99.8) |
| M7 |  | 2363.7 (2653.9) | 681.9 (1208.7) | 191.1 (234.1) |
| M8 |  | 4200 (4491) | 672 (1198.8) | 138.3 (181.2) |

A close up of a map

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***Fig. 1****. Natural log of metabolic rate (A) and maximum consumption rates (B) vs. natural log of mass [g]. Lines are global predictions for an average species at temperatures 15 (blue line and ribbon) and 25 (red line and ribbon). The average temperatures in the data are 19 and 18 for metabolism and maximum consumption, respectively. Note the model is fitted using mean-centered (ct) Arrhenius temperature (1/kT), and then converted for easier interpretation. Shaded areas correspond to 80% and 95% credible intervals. Point colors correspond to species (n=18 and n=35 for consumption and metabolism, respectively).*

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***Fig. 2****. Posterior medians of the global activation energies and mass-exponent of metabolism and maximum consumption from the hierarchical model fitted to below temperature optimum data (white triangles and circles, respectively), and their 80% and 95% credible interval (vertical short and long lines, respectively). Vertical dashed lines correspond to the median prediction for an average species (i.e. and in Eqs. 6-8 for the mass and temperature coefficient, respectively). Shaded vertical areas correspond to posterior median standard deviations.*

A close up of a map

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**Fig. 3**. *Effects of temperature and body mass on body growth. Panel A) shows growth rate [% day-1] as a function of mean centered body mass, both on natural log scale. Lines are global predictions from model M1 for an average species at temperatures 15 (blue line and ribbon), which is close to the mean temperature (14.3) in data, and 25 (red line and ribbon). Note the model is fitted using mean-centered Arrhenius temperature (1/kT), and then converted for easier interpretation. Shaded areas correspond to 80% and 95% credible intervals and the solid line is the median prediction across-species. Point colors indicate species (n=13, legend not shown). The slope corresponds to the mass-scaling exponent. Posterior distributions of the average mass-scaling exponent, , (B) activation energy,, (C) and mass-temperature interaction, , (D) are shown in the bottom row. Dashed white line shows the posterior median, red vertical line in (D) indicates zero.*

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***Fig. 4.*** *Rescaled maximum consumption rates (consumption divided by mean consumption within species) as a function of rescaled temperature (), where colors indicate species. The data is a subset of the maximum consumption data containing only species with observations at temperatures higher than where the rate is maximized (“optimum”). Lines are predictions from the quadratic model where the mean-centered body mass is held at 0 (corresponding to mean mass within species), and open circles are data. The shaded areas show 80% credible interval for the median prediction. Arrows depict the optimum temperature for each species and the vertical dashed and dotted lines correspond to the across-species mean optimum temperature 1 standard deviation.*

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***Fig. 5.*** *Illustration of normalized thermal response of maximum consumption (green), metabolism (purple) and their difference (orange) for two body sizes (100g = solid, 500g = dashed). The example consumption-curve is based on the quadratic model for C. argus (Fig. 4, Appendix S1, Fig S10), and metabolism is calculated from the global model (M2, see ‘Results’). Both rates are expressed as relative to their maximum, separately for each body size, for illustration purposes as they are in different units, and the curve depicting the difference is based on the normalized curves. Arrows indicate the temperature where the difference in net energy acquisition is maximized for the two body sizes.*

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**Fig. 6**. *Optimum temperature for growth (rescaled to optimum temperature within species) as a function of mean centered natural log of rescaled 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. 7.*** *Experimental temperatures (grey) overlap environmental temperatures (green) and optimum growth temperatures (orange) are typically at the upper end or above the environmental range. Vertical green lines show the minimum and maximum environmental temperature based on either temperature in distribution range (triangles) or modelled distribution maps (circles), both taken from FishBase, and green points show the midpoint. The optimum growth temperatures are depicted for all size-classes per species, where the circle size is proportional to number of observations at that temperature. The average distance between environmental mid-point temperature and mean optimum temperature (per species) is 6.5 with a standard deviation of 2.6.*

**Discussion**

Individual growth, consumption and metabolism represent fundamental processes in ecology, and their scaling with body mass and temperature is used to predict the effects of warming on individual growth, body size, and 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 (Glazier 2005) or interspecific relationships (Brown *et al.* 2004). However, the former can result in large variation in intraspecific scaling parameters, and the latter relies on the assumption that rates scale identically within as between species, which is often not the case (Glazier 2005; Rall *et al.* 2012; Jerde *et al.* 2019). As growth, consumption and metabolism represent individual-level processes, it is important to understand how these rates depend on temperature and mass within species. At temperatures below optimum, we find it probable that activation energies of metabolism, consumption and growth are close to predictions from the metabolic theory of ecology (MTE), i.e. with an activation energy of ~0.65 , which indicates that a “metabolic” mismatch does not occur at temperatures sub optimum. However, intraspecific thermal responses for maximum consumption rate are unimodal (Englund *et al.* 2011; Rall *et al.* 2012; Jutfelt *et al.* 2020) (Fig. 4), such that the mismatch occurs first at higher temperatures, and this likely contributes to unimodal thermal responses of growth (Jobling 1997). An important feature is that accounting for body-mass scaling of consumption and metabolism (and of their temperature effects) is that it leads to a decline in optimum growth temperature with body size, which we find also in experimental growth data.

That optimum growth temperatures decline 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 temperature for an average fish declines as they increase in mass over ontogeny. The effect size – a decline in by 0.3 per unit increase in the natural log of relative mass, – also appears relatively large, considering the small range of body sizes used in the experiments (73% of individuals in the experiments assembled for this study are < 1% of maximum mass in their species). Individuals of such small relative size likely invest little energy in reproduction. This suggests that reduced growth performance of large fish with increased temperatures cannot only be explained by earlier maturation and changes in energy allocation from somatic growth to gonads but may also represent physiological constraints (as also predicted by supply and demand-based growth models (Pütter 1920; Marshall & White 2019b)).

Translating effects of experimentally 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 conditions but largely affects growth (Brett *et al.* 1969; Lorenzen 1996; Huey & Kingsolver 2019). Yet, these variables affect growth rates and optimum temperatures for growth, such that the field-optimum growth curves are likely closer to the environmental temperatures (Fig. 7). It is important to acknowledge that climate change may also introduce higher food limitation, which would further lower the optimum temperature for growth (Huey & Kingsolver 2019). With respect to the role of optimum thermal response for a species response to warming, temperate species in particular occupy thermal habitats below their optimum for growth as sub-optimum temperatures are in fact optimal when temperatures fluctuate (Bernhardt et al 2019). However, warming has already lead to negative (or lack of positive (Huss *et al.* 2019)) effects on populations living at the edge of their physiological tolerance in terms of growth (Neuheimer *et al.* 2011). While the optimum temperature for growth declines as individuals grow in size, the key question for predicting if large fish will be the first to suffer negative consequences of warming is to understand if they in general live closer to their thermal optimum for growth. Even if the optimum growth temperatures of large fish are lower, they may inhabit colder temperatures compared to small fish due to ontogenetic habitat shifts (Werner & Hall 1988), see also Heincke’s law (Heincke 1913; Audzijonyte & Pecl 2018). That said, there is already empirical evidence of the largest individuals being the first to suffer from (or not being able to benefit, (Huss *et al.* 2019)) negative impacts of warming from e.g. heatwaves (Pörtner & Knust 2007). Hence, assuming that species occupy thermal habitats where warming can lead to increased growth rate (i.e. the exponentially increasing part of a thermal response curves) 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 general Pütter-type growth models (Pütter 1920), where growth is the result of two antagonistic processes, anabolism and catabolism representing build up and break down of body materials: , where is body mass and is temperature. Here optimum growth temperatures decline with size under two conditions: (also a necessity for growth being asymptotic) and that growth is unimodal over temperature (Morita *et al.* 2010). While this is one of the most commonly applied growth models, the first condition has been debated recently. In the von Bertalanffy growth model (VBGM) – a species case of the Pütter model – . The assumption that catabolism is proportional to body mass originates from the argument that spontaneous denaturation occurs in every cell (von Bertalanffy 1957; Pauly & Cheung 2018a) (and likely also for mathematical convenience and lack of empirical data (Ursin 1967)). It is however common to restate this model in terms of energy, i.e. as a balance between energy assimilation and costs. From a physiological perspective, it is common to assume maintenance costs are proportional to standard metabolic rate (Ursin 1967; Jobling 1997; Lefevre *et al.* 2017), which has a mass-exponent typically around 0.8 (Clarke & Johnston 1999; Jerde *et al.* 2019) and not 1. In this case, classic Pütter models of growth, such as the VBGM or the similar ontogenetic growth model (West *et al.* 2001), either fail to represent the physiological processes they aim to capture, or fail to exhibit asymptotic growth (Marshall & White 2019b). This dichotomy can be resolved by considering the overlooked energetic investment into reproduction (and its hyper-allometric mass-scaling, i.e., with an exponent larger than 1) (Marshall & White 2019b), or by applying more complex energy pathways in dynamic energy budget models (Kearney 2019). The recent debate about scaling coefficients in growth models calls 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 gains. It is also worth noting that our estimate of the mass-scaling exponent of 0.77 is slightly smaller than what is found in other studies, e.g. (Clarke & Johnston 1999; Jerde *et al.* 2019). In natural systems, however, realized consumption is mediated by predator-prey encounter rates and search rates, whereas maximum consumption rates largely correspond to the physiological limits on digestion (Ursin 1967). Regardless, changes in the maximum feeding capacity could result in reduced growth efficiency over ontogeny, as illustrated in Fig. 5, 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 gain with body mass, it is important to understand how the balance between energy gains and costs 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; Rall *et al.* 2010; 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 within species. This is in contrast to other studies, e.g. (Lemoine & Burkepile 2012; Rall *et al.* 2012). However, it is in line 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.

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 much wider temperature range. A recent hypothesis suggests that the reason for unimodal consumption responses is to protect aerobic scope by not overshoot post-meal oxygen consumption, which would causally explain why also growth curves are unimodal (Jutfelt *et al.* 2020). While our data are limited in number of species and relative temperatures are simple approximations, we do find that the average optimum for consumption and growth occur at largely similar temperatures (measured in distance from environmental midpoint temperature). This suggests that consumption may be a driver of unimodal growth curves (as is often argued from a conceptual point of view (Jobling 1997). However, we cannot discriminate between other potential factors, such as temperature-dependent changes in assimilation efficiency or cost of growth (Barneche *et al.* 2019), and our samples sizes are small and uncertain. Nevertheless, unimodal thermal responses are likely important for understanding impacts of climate change (Neuheimer *et al.* 2011). Therefore, a priority should be to identify generalized approaches and parameters for characterizing the unimodal shape of consumption rate, which would require more data and experiments with factorial mass and temperature treatments.

We also find the general temperature scaling of metabolic and maximum consumption at temperatures below optimum are 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 hierarchical models and partial pooling to estimate higher level (across species) scaling from species-data. No pooling, by contrast is equivalent of fitting fixed species effect, which does not lead to shrinkage towards the mean which leads to larger variation in species predictions (Gelman & Hill 2007; Harrison *et al.* 2018).

In contrast to the MTE, we find that body mass can affect the temperature dependence of physiological rates, which previously has been reported only for single species studies (Beamish 1964; Xie & Sun 1990; Ohlberger *et al.* 2012; Lindmark *et al.* 2018; Fossen *et al.* 2019) and between species (Killen *et al.* 2010). This prediction is in line with the metabolic boundary-level hypothesis, which predicts a negative relationship between resting metabolic exponents and temperature (Glazier 2010). This was however not found in a recent study on the intraspecific mass-scaling exponent of metabolic rate in fishes (Jerde *et al.* 2019), which could be due to different data collection protocols, where we specifically used studies with temperature replicates within species. The effect size of the interaction is, however, relatively small. We do not find strong evidence for average effects of temperature-size interactions in growth or consumption, although it has been reported for some species (García García *et al.* 2011). A possible explanation is that we strictly exclude temperatures beyond optimum for the log-linear model, and inclusion of these could lead to significant negative interactions if optimum occurs at lower temperature for large fish. The ecological implications of temperature-size interactions at sub-optimum temperatures could therefore be small, although larger estimates have been reported in single species studies (Ohlberger *et al.* 2012). It could also be that the overall effect is masked by variation between species, as studies have found both positive and negative interaction between mass and temperature (Ohlberger *et al.* 2012; Messmer *et al.* 2016; Lindmark *et al.* 2018). Given the between species variation, one approach forward could be to control for taxonomic structure at multiple levels when assessing intra-specific mass- and temperature-scaling of these rates.

Because we evaluated the joint effect of body mass and temperature on rates of body growth, metabolism and consumption, the number of studies included in our analysis constitutes a small fraction of the available experimental data, which mostly consists of experiments testing only a single temperature or body size (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, compared to metabolism. 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. Therefore, the data collated here contains uncertainty from many sources, including differences in experimental protocols. Our selection criteria lead to using a small fraction of all available data being used, which limits the hierarchical model structures we can consider. 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 approach also has merit, because hierarchical models (e.g. in a Bayesian framework with literature-informed priors) can overcome difficulties with small data sets.

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 discrepancy between mechanistic models, general scaling theory, and data is the lack of data synthesis at the intraspecific level. Systematic data-analysis of existing experimental data combined with models that account for uncertainty at the species-level constitutes an approach that can guide process-based predictions of climate change effects, from individuals to food webs.

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**Author contributions**

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

**Data accessibility statement**

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.

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