**Title Page**

Optimum growth temperature declines with body size in 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 how growth and key processes affecting it (e.g., metabolism and consumption) depend on both body mass and temperature within species. This limits our ability to inform growth models, to link experimental data to observed growth patterns, and to advance mechanistic food web models. To resolve the combined effects of body size and temperature on growth, and examine the link between metabolism, maximum consumption and body growth, we compiled a large dataset of experimental results from studies combining body mass and temperature treatments. We estimate how these three processes scale jointly with temperature and within-species body mass, by fitting hierarchical models while accounting for variation between species. Maximum consumption rate scaled with a mass exponent smaller than for metabolism, and was unimodal over the full temperature range. These features contribute to unimodal thermal responses of growth, characterized by peak temperatures for growth declining within species with body mass. Small individuals will therefore likely be able to increase their growth rates with initial warming, whereas larger individuals of the same species could be the first to experience negative effects of warming on growth. 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 individual 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, understanding how growth 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 declining body sizes 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; Ohlberger 2013). 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). In fishes, reconstructed individual growth histories often reveal positive correlations between growth rates and temperature in natural systems, in particular in young fish (Thresher *et al.* 2007; Neuheimer *et al.* 2011; Baudron *et al.* 2014; Huss *et al.* 2019). However, it is less clear if the positive effect of warming on growth is limited to small individuals within a species, as predicted from the temperature size-rule. Negative correlations between maximum or asymptotic body size and temperature have been found in commercially exploited fish species (Baudron *et al.* 2014; van Rijn *et al.* 2017). However, other studies, including large scale experiments, controlled experiments and latitudinal studies, have failed to find negative relationships between maximum size or growth of old fish and temperature (Barneche *et al.* 2019; Huss *et al.* 2019; van Denderen *et al.* 2019; van Dorst *et al.* 2019).

While the underlying mechanisms of the TSR are not well understood (Ohlberger 2013; Audzijonyte *et al.* 2018; Neubauer & Andersen 2019), theoretical growth models predict similar organism responses to warming. For instance, Pütter growth models (Pütter 1920), such as the von Bertalanffy growth model (VBGM) (von Bertalanffy 1938), predict declines in asymptotic body mass with temperature and optimum growth temperature with body mass (Morita *et al.* 2010; Pauly & Cheung 2018b). However, the physiological basis of such models has been questioned for multiple reasons. These include mass scaling exponents not being informed by empirical observations but rather conceptual arguments about geometric constraints, which leads to unrealistically large effects of temperature on asymptotic size (Lefevre *et al.* 2017; Marshall & White 2019a, b). Hence, despite attempting to describe growth from first principles, Pütter growth models can also be viewed as phenomenological if those principles are erroneous. Therefore, as empirical findings vary and theoretical predictions are questioned, it remains unclear if and how growth of large fish within populations is limited by temperature.

In more mechanistic growth models, the difference between energy acquisition and expenditure (Ursin 1967; Kitchell *et al.* 1977; Jobling 1997) is partitioned between somatic growth and gonads. Energy acquisition is normally the amount of energy extracted from consumed food and expenditure is defined as fasting, activity and feeding metabolism. Metabolic processes are in turn often assumed to be related to resting metabolism, measured as the oxygen consumption of unfed fish at rest (Jobling 1997). These components of the energetics of growth are found in 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 scale with body size and temperature.

The effect of body mass and temperature on growth, consumption and metabolism should ideally be evaluated at the intraspecific rather than interspecific level, as they represent individual-level processes, and because allometric and temperature relationships can differ within and between species (Glazier 2005; Rall *et al.* 2012; Jerde *et al.* 2019). However, despite this potential difference, body mass- and temperature scaling is often inferred from interspecific data. Hence, the intraspecific scaling of biological rates with mass and temperature is less understood than interspecific scaling relationships. In addition, the temperature and mass dependence of metabolism and other related rates are often assumed to follow the Arrhenius fractal supply model (AFS), including 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 []. Importantly, the model assumes a mass-scaling exponent of ¾ when estimating temperature effects, as well as independent effects of mass and temperature (Downs *et al.* 2008). However, deviations from the ¾ mass exponent are common (Clarke & Johnston 1999; Bokma 2004; Jerde *et al.* 2019), and 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)). In addition, 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), within-species thermal response curves are generally unimodal (Dell *et al.* 2011; Englund *et al.* 2011; Rall *et al.* 2012; Uiterwaal & DeLong 2020). Alternative approaches that overcome these obstacles include fitting multiple regression models where coefficients for mass and temperature are estimated jointly (Downs *et al.* 2008), as well as fitting 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).

In this study, we analyse how maximum consumption, metabolism and growth rate of fish scale intra-specifically with mass and temperature. We performed a systematic literature review by searching the Web of Science Core Collection to compile datasets on individual growth, maximum consumption and metabolic rates of fish from experiments in which the effect of fish body mass is replicated across multiple temperatures within species. We then fit hierarchical Bayesian models to estimate general intraspecific scaling parameters while accounting for variation between species. For consumption rates, we also fit polynomial models to a subset of the data to characterize the unimodal temperature dependence seen in data. 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 exponents are larger and smaller than ¾ for metabolism and maximum consumption, respectively. Over the full temperature range, consumption rates are unimodal, suggesting declines in optimum (peak) growth temperatures with body mass. Using an independent data set, we demonstrate that optimum growth temperatures indeed 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 maximum consumption we used: (consumption OR bioenerg\* 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\*) and: (“food intake”) AND (mass OR weight OR size) AND (temperature\*). For metabolic rate we used: (metabolism OR "oxygen-consumption" OR "oxygen consumption") AND (mass OR weight OR size) AND (temperature\*). \* represents any group of characters, including no character. We also applied additional filters by selecting only the following subjects: ‘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 use of additional subjects for growth and consumption reflects the lower data availability compared to metabolism.

We selected studies with a combination of body mass-temperature setup in order to estimate how these rates depend on both body size and temperature within species (at least two size and temperature treatments). This reduces the number of data sets available in the literature, as most experimental studies use either size or temperature treatments, not both. However, this criterion 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. Following common practice we excluded larval studies, because larvae can exhibit different isometric scaling and do not feed independently (Glazier 2005). Studies were included if (i) a unique experimental temperature was recorded for each trial (1), (ii) fish were provided food at *ad libitum* (consumption and growth data) or if they were unfed (resting, standard or routine metabolic rate), and (iii) fish exhibited normal behaviour during the experiments. We used only one study per species and rate 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, differences in experimental protocols or because different sub-populations were used (Armstrong & Hawkins 2008; Jerde *et al.* 2019). In cases where we found more than one study for a species for a rate, we selected the most suitable study based on our pre-defined criteria (for details, see Appendix S1). A more detailed description of the search protocol, data selection, acquisition, quality control, collation of additional information and standardizing rates to common units can be found in Appendix S1.

We compiled four datasets: growth rate, maximum consumption rate, metabolic rate and the optimum growth rate temperature for each combination of body mass group and species. We compiled in total 227 (growth rate) (and 45 optimum temperatures), 746 (maximum consumption rate) and 2695 (metabolic rate) data points from published articles for each rate, from 13, 20 and 34 species, respectively, representing a diverse range of taxonomic groups, habitats and lifestyles (Appendix S1). We asked all the corresponding authors of each article to share data, else data were extracted from tables or figures using Web Plot Digitizer (Rohatgi 2012).

**Model fitting**

*Mass- and temperature dependence of growth, consumption and metabolism below peak temperatures*

Peak temperatures (optimum in the case of growth), refers to the temperature at which the rate was maximized, by size group. For data below peak temperatures, we assumed that individual growth, maximum consumption rate and metabolism scale as a generalized version of the Arrhenius fractal supply model (Gillooly *et al.* 2001; Brown *et al.* 2004). The mass exponent was not assumed a priori but estimated simultaneously with the temperature coefficient. We thus assumed the natural log of rate (growth, maximum consumption or metabolism) scales with mass and temperature as:

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

where is the intercept, is the mass scaling exponent on a linear scale when () and is the interaction coefficient. On a linear scale, this becomes:

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| --- | --- | --- |
|  |  | (2) |

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. The species-varying coefficients are thus 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 coefficients can be written as:

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

where is the th observation for species of the natural log of the rate (growth, consumption or metabolism), is the standard deviation and are coefficients. Species-level coefficients, (where ) follow a normal distribution with hyperparameters (grand mean) and (between-species standard deviation). In Eq. 4, is the natural log of body mass and is Arrhenius temperature ( in unit ), both variables are mean-centred when fitting. Body mass is the mass in , specific growth rate has unit , consumption rate , and metabolic rate . 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 58% of the data used and standard metabolism constitutes 42%. We accounted for potential differences between these metabolic rate measurements by using a random species effect and a single study per species.

*Mass- and temperature dependence of consumption including beyond peak temperatures*

To characterize the decline in consumption rates beyond peak temperature, we fit second and third degree polynomial regressions (with and without in Eq. 7) to a subset of these data containing only species with data points extending beyond such a peak temperature. The models were fit with a random intercept ( to account for variation across species. The models of are:

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| --- | --- | --- |
|  |  | (6) |
|  |  | (7) |
|  |  | (8) |

where in Eq. 6 refers to the th observation of mass-specific consumption rates for species divided by the mean value for species (), is the standard deviation and are coefficients. (species-level intercepts) follow a normal distribution with hyperparameters (grand mean) and (between-species standard deviation). in Eq. 7 is mean-centred body mass () and is the mid-point of the temperature in the environment of species subtracted from the temperature used in the experiment (). This rescaling is done to control for differences between species with respect to the experimental temperatures relative to the temperature that maximizes their consumption rate.

*Mass-dependence of optimum growth temperature*

To evaluate how the optimum temperature (, in degrees Celsius) for individual growth depends on body mass, we fit the following hierarchical model to account for variation between species in both the intercept and slope:

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| --- | --- | --- |
|  |  | (9) |
|  |  | (10) |
|  |  | (11) |

Here is mean-centred optimum growth temperature within species (), to account for species being adapted to different thermal regimes, is the standard deviation and are coefficients. Species-level coefficients, , (where ) follow a normal distribution with hyperparameters (grand mean) and (between-species standard deviation). is the natural log of the ratio between mass and body mass at maturation within species: , as we were interested in examining relationships within species while accounting for variation in relative body masses between experiments, and because we do not expect an interspecific relationship between optimum growth temperature and body mass. Subscript in Eq. 11 refers to regression parameters (0 for intercept and 1 for slope). We also fit the model with only a random intercept.

*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 large variances to make them less informative. We used 3 Markov chains with 5000 iterations for adaptation, followed by 15000 iterations burn-in and 15000 iterations sampling where every 5th iteration saved. 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 suggest all three chains converged to a common distribution. We relied heavily on the R packages within ‘*tidyverse’* (Wickham 2017) for data processing, as well as ‘*ggmcmc*’ (Fernández-i-Marín 2016), ‘*mcmcviz*’ (Youngflesh 2018) 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 other studies (Olmos *et al.* 2019).

*Net energy gain*

The effect of temperature and mass dependence of maximum consumption and metabolism (proportional to biomass gain and losses, respectively) (Ursin 1967; Kitchell *et al.* 1977; Essington *et al.* 2001) on growth is illustrated by visualizing the net energy gain. The model for the net energy gain (growth) can be viewed as a Pütter-type model, which is the result of two antagonistic allometric processes: , where is body mass and is temperature. We convert metabolism from oxygen consumption to by assuming 1 = 295 (based on an oxycaloric coefficient of 14.2 ) (Hepher 1988), 1 = 4184 and an energy content of 5600 (Rijnsdorp & Ibelings 1989). Consumption and metabolic rate are calculated for two sizes (10 and 100 g), using the global allometric relationships found in the log-log models fit to sub-peak temperatures. These allometric functions are further scaled with the temperature correction factor , (subscript for consumption and for metabolism). For maximum consumption, is based on Eq. 7 (but without a mass-coefficient and an intercept as it is rescaled to become a multiplier), as it reaches a peak over temperature. It can be written as: , where is temperature in and is a constant that scales the term to 1 at the mean temperature in the data (19). is defined as where , is in unit K and is a constant that scales the term to 1 at the mean temperature in the data (19). Note that when estimating these parameters, temperature is centred to the median temperature in the environment for species in the polynomial, whereas for the log-log model it is centred to the overall mean in the data.

**Table 1** Description the parameters in the full models (parameter type, as well as its interpretation in brackets), and their prior distributions. refers to a normal distribution (mean and standard deviation s.d.) and to a uniform distribution (interval). For simplicity, only the parameters of the full model are shown here (i.e. with most coefficients varying by species). When a model is fitted with a common rather than species-varying coefficient, e.g. instead of , the same prior is used for as for .

|  |  |  |  |
| --- | --- | --- | --- |
| Model | Parameter | Description | Prior distribution |
| Log-linear regressions  for growth, consumption and metabolism (Eqns. 3-5) |  | Hyperparameter (average intercept across species) |  |
|  | Hyperparameter (average mass coefficient across species) |  |
|  | Hyperparameter (average temperature coefficient across species) |  |
|  | Hyperparameter (average interaction coefficient across species) |  |
|  | Hyperparameter (s.d. of species-intercepts) |  |
|  | Hyperparameter (s.d. of species mass coefficients) |  |
|  | Hyperparameter (s.d. of species temperature coefficients) |  |
|  | Hyperparameter (s.d. of species interaction coefficients) |  |
|  | Parameter (s.d.) |  |
| Polynomial models  for consumption (Eqns. 6-8) |  | Hyperparameter (average intercept across species) |  |
|  | Parameter (common mass coefficient) |  |
|  | Parameter (common temperature coefficient) |  |
|  | Parameter (common quadratic temperature coefficient) |  |
|  | Parameter (common cubic temperature coefficient) |  |
|  | Hyperparameter (s.d. of species-intercepts) |  |
|  | Parameter (s.d.) |  |
| Linear  models  (Eqns. 9-11) |  | Hyperparameter (average intercept across species) |  |
|  | Hyperparameter (average mass coefficient across species) |  |
|  | Hyperparameter (s.d. of species-intercepts) |  |
|  | Hyperparameter (s.d. of species mass coefficients) |  |
|  | Parameter (s.d.) |  |

**Results**

*Below peak temperatures*

At below peak temperatures, the intraspecific mass- and temperature dependence of specific growth can be described by the equation: (Fig. 1). The parameters are posterior medians of the global parameters, thus representing an average, unmeasured fish. The estimated interaction coefficient is both small and uncertain, and only leads to marginally better fits to data compared to the model without the interactions (WAIC of the model without interaction, M5, is 2.4; Table 2). The estimated interaction coefficient is 0.0046 [-0.064, 0.075], where Bayesian 95% credible intervals are indicated in square brackets. The mass exponent of growth is estimated to be -0.36 [-0.5, -0.23] and the activation energy (-) of growth is estimated to be 0.74 [0.95, 0.53].

We find that the intraspecific scaling of mass-specific maximum consumption rate for an average fish can be described by the equation (Fig. 2). For mass-specific metabolic rate, the relationship is: . In the model for consumption rate, all coefficients vary by species (M5) whereas for metabolism, all coefficients except the interaction coefficient vary by species (M2) (Table 2). Maximum consumption scales with a smaller mass exponent (-0.38 [-0.45, -0.30) than metabolic rate (-0.20 [-0.25, -0.15]), based on the non-overlapping Bayesian 95% credible intervals (Fig. 3). This difference implies that metabolic rates increase faster with mass than maximum consumption rates. We also find it probable that the mass-specific scaling exponents differ from -0.25 as predicted by the Metabolic Theory of Ecology. 99.7% of the posterior distribution of the mass exponent of maximum consumption is below -0.25 whereas 96.2% of the posterior distribution of the mass exponent of metabolic rate is above -0.25. Activation energies of maximum consumption rate and metabolism are both similar (0.69 [0.54, 0.84] and 0.61 [0.56, 0.67] respectively; Fig. 3) and largely fall within the prediction from the MTE (0.6-0.7 eV) (Brown *et al.* 2004)).

For maximum consumption, the model with a global interaction term, , (M2) has a WAIC of 1.3 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. 2B), we therefore chose model M5 (without interaction) because it is simpler and the estimate of in M2 is small and uncertain (posterior median of -0.01 [-0.04, 0.02] on Arrhenius temperature scale).

We find strong statistical support for a negative global interaction between the effect of body mass and temperature on metabolic rate, as 99.7% of the posterior distribution of is above 0 (Fig. S12). The estimated coefficient is 0.014 [0.0039, 0.024] on the Arrhenius temperature scale, which corresponds to a decline in the mass scaling exponent of metabolic rate by 0.002 . For metabolism, the model with a species-varying interaction term (M1) has a WAIC of 0.6, suggesting it is comparable to the model with a single global interaction term (M2). We chose the latter to illustrate predictions (Fig. 2A) because of its simpler model structure.

*Including beyond peak temperatures*

Over a larger temperature range, many biological rates reach a peak and then decline. We identified such tendencies in 11 species in the consumption data set, and fit hierarchical polynomial models with a random intercept (). Based on WAIC and visual inspection of residual patterns we chose a model with a cubic temperature variable and an increasing rather (than constant) sigma with temperature (see Table SX for details). The equation for rescaled mass-specific consumption rate over the full temperature range in the data can therefore be written as: (Fig. S13).

The implication of a peak in consumption rate over temperature is that even if maximum consumption rates increase at the same rate as metabolism with temperature initially (at below peak temperature), consumption rates eventually decline relative to metabolism with further warming. This means that the effect of increasing temperature on net energy gain depends on the current temperature relative to peak temperature. In addition, the thermal response curve of net energy gain is characterized by optimum temperatures declining with body masses, as shown when predicting consumption, metabolism and net energy gain from our fitted models for two different body sizes (Fig. 4). This decline in optimum temperature of net energy gain with body size emerges from the unimodal curve over temperature and the smaller mass-scaling exponent of consumption compared to that of metabolism (as shown analytically by Morita *et al.* (2010)).

The prediction of declining optimal growth temperatures with size is further corroborated by our analysis of experimental growth rate data. We find that within species, the optimum growth temperature declines with body size by 0.35 per unit increase in the natural log of relative body mass (Fig. 5). Statistical support for the decline in optimum growth temperature with body mass is strong, as 99% of the posterior density of the common slope estimate () is below 0. The models with and without species-varying slopes were indistinguishable in terms of WAIC (Table SX), and we present the results for the random intercept model, due to slightly better model diagnostics (Fig SX). The general relationship is given by the model: , where is the natural log the rescaled body mass.

**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 |  | **0.6 (271.9)** | 3.9 (564.5) | **0 (47.2)** |
| M2 |  | **0 (271.3)** | **1.3 (561.9)** | 7.4 (55.6) |
| M3a |  | 306 (577.3) | 147.5 (708.1) | 24 (71.2) |
| M3b |  | 388.6 (659.9) | 69.7 (630.3) | 33 (80.1) |
| M4 |  | 652.3 (923.6) | 190.6 (751.2) | 43.7 (90.8) |
| M5 | No |  | 6.3 (277.6) | **0 (560.6)** | 5.5 (52.7) |
| M6a |  | 347.8 (619.1) | 166.1 (726.7) | 21.7 (68.9) |
| M6b |  | 390.5 (661.8) | 73.7 (634.3) | 34.8 (82) |
| M7 |  | 684.6 (955.9) | 212.9 (773.5) | 44.8 (92) |

**Table X**. Comparison of different polynomial models fitted to maximum consumption rate including beyond peak temperatures. Due to increasing variance with temperature, we modify the general model structure (Eqns. 6-8) to allow the standard deviation of the likelihood to increase linearly with the predictor variables. In these models, we put a uniform prior for the intercept and a gamma prior for the slope(s) . 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. One outlier was removed prior to fitting (value > 4 times higher than mean for the same size).

|  |  |  |  |
| --- | --- | --- | --- |
| Model | Temperature-variables | Standard deviation of likelihood | WAIC |
| M1 | Quadratic | Constant () | 31.2 (619.5) |
| M1b | Increasing with mass () | 5.3 (593.4) |
| M1c | Increasing with temperature () | **0 (588.1)** |
| M1d | Increasing with mass () | 1241.5 (1829.7) |
| M2 | Quadratic + Cubic | Constant () | 27.7 (615.8) |

**Table X**. Comparison of the two models fitted to optimum growth temperature data. 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 | Species-varying parameter(s) | WAIC  metabolism |
| M1 |  | **0 (177.3)** |
| M2 |  | **1 (178.3)** |

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**Fig. 1**. *Effects of temperature and body mass on body growth below optimum temperature. Panel A) shows the natural log of specific growth rate as a function of body mass on a logarithmic x-axis (for readability, note the model is fitted with ln(mass) as a predictor), such that the slope corresponds to the mass-scaling exponent. The line in panel A is the global prediction from model M1 at the mean temperature (14, but note the model is fitted using Arrhenius temperature). Shaded areas correspond to 80% and 95% credible intervals. Point colours indicate species (n=13, legend not shown). The bottom row shows the posterior distributions of (B) the average mass-scaling exponent, , (C) the temperature coefficient, and (D) the mass-temperature interaction, . Dashed white line shows the posterior median and red vertical line in (D) indicates zero.*

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***Fig. 2****. Natural log of mass-specific maximum consumption rate (A) and metabolic rate (B) against body mass on a logarithmic x-axis. Lines are global predictions at the average temperature in each data set (both 19, but note the model is fitted using mean-centred Arrhenius temperature). Shaded areas correspond to 80% and 95% credible intervals. Species are grouped by colour (legend not shown, n=20 for consumption and n=34 for metabolism, respectively).*

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***Fig. 3****. Global and species-level effects of mass- and temperature on specific maximum consumption and metabolic rate. Vertical lines show the posterior medians of the global activation energies and mass exponents of maximum consumption and metabolism ( and in Eqs. 6-8 for the mass and temperature coefficients, respectively). The shaded vertical bars correspond to the posterior median standard deviations. Points and triangles show the posterior medians for each species-level coefficient (for maximum consumption rate and metabolic rate, respectively), and the horizontal bars show their 80% and 95% credible interval.*

A close up of a map

Description automatically generated

***Fig. 4.*** *Illustration of predicted whole-organism maximum consumption rate (green), metabolic rate (purple) and the difference between them (orange) for two body sizes (10g = solid, 100g = dashed). Vertical arrows indicate the temperature where the difference in net energy acquisition is maximized for the two body sizes, which occurs at different temperatures despite that consumption peaks at the same temperature for both body sizes.*

A close up of a map

Description automatically generated

**Fig. 5**. *Experimental data demonstrating optimum temperature for growth declines with body mass. The plot shows the optimum temperature within species (rescaled by subtracting the mean optimum temperature from each observation, by species) as a function of the natural log of rescaled body mass (ratio of mass to maturation mass within species). Probability bands represent 80% and 95% credible intervals and the solid line shows the global prediction ( and ). Colours indicate species (n=13, legend not shown) and the point size corresponds to the non-scaled mass in unit .*

**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 body size and size structure, and population and community dynamics (Vasseur & McCann 2005; Rall *et al.* 2010; Cheung *et al.* 2013). How biological rates scale with temperature and/or mass is commonly inferred from either meta-analysis of single-species studies (Bokma 2004; Glazier 2005) or interspecific relationships (Brown *et al.* 2004; Killen *et al.* 2010). However, the former can result in large variation in intraspecific scaling parameters due to variation between species, 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, ideally over ontogeny. At temperatures below those that maximize the rates (‘peak temperatures’), we find that temperature sensitivities 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 . This means that a “metabolic mismatch” (e.g. metabolism being more temperature sensitive than consumption) does not occur in this temperature range. However, over a larger temperature range, the relationship between maximum consumption rate and temperature is typically unimodal within species (Englund *et al.* 2011; Rall *et al.* 2012; Jutfelt *et al.* 2020) (Fig. 4), and a mismatch can therefore occur at higher temperatures. This likely contributes to growth rates reaching an optimum over temperature (Jobling 1997). An important aspect of accounting for the body mass dependence of consumption and metabolism is that it leads to a decline in optimum growth temperature with body size, which we verify using a conceptual model of biomass production as well as independent data from growth experiments.

Some previous studies have found declines in optimum growth temperatures with body size, including for fishes (Panov & McQueen 1998; Steinarsson & Imsland 2003; Björnsson *et al.* 2007; Handeland *et al.* 2008), while others have not (Brett *et al.* 1969; Elliott & Hurley 1995). We find that for an average fish, the optimum growth temperature declines as it grows in size, despite the small range of body sizes used in the experiments (only 10% of observations are larger than 50% of maturation size). Individuals of such small relative size likely invest little energy in reproduction. This suggests that reduced growth performance of large fish with warming cannot only be explained by earlier maturation and changes in energy allocation from somatic growth to gonads, but may also represent physiological constraints.

Translating results from experimental data to natural systems is challenging because unlimited food supply, lack of predation, and constant temperatures do not reflect natural conditions but affect growth rates (Brett *et al.* 1969; Lorenzen 1996; Huey & Kingsolver 2019). In natural systems, species live in temperatures cooler than those maximizing growth (Fig. S14) (Bernhardt *et al.* 2018), suggesting that initial warming increases growth rates. Moreover, realized consumption rates are not equal to maximum consumption rates but rather a fraction of the maximum consumption rate (e.g. 20-70%) (Kitchell *et al.* 1977; Neuenfeldt *et al.* 2019). Since optimum growth temperatures decline not only with size but also food availability, and climate warming may also introduce higher food limitation (Huey & Kingsolver 2019), species may be negatively impacted by warming even when controlled experiments show they can maintain growth capacity at these temperatures. In fact, there are examples of warming already having 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). Whether or not the negative effects of warming will be first experienced by the largest fish depends on if they live closer to their thermal optimum for growth. They may for instance 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 negative impacts of warming from heatwaves (Pörtner & Knust 2007), or not being able to benefit from warming (Huss *et al.* 2019). Hence, assuming that species occupy thermal habitats where warming can lead to increased growth rate for all individuals in a population is a simplification that can bias prediction of the biological impacts of climate change.

Interestingly, a decline in optimum growth temperature with mass is also predicted by general Pütter-type growth models (Pütter 1920). In these models, optimum growth temperatures decline with body size under two conditions: (1) the mass-exponent is for consumption than fore metabolism (also a necessity for growth being asymptotic) and (2) 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 (Lefevre *et al.* 2017; Pauly & Cheung 2018b). In the von Bertalanffy growth model (VBGM) – a special case of the Pütter model – it is assumed that catabolism is proportional to body mass (). This stems from the argument that spontaneous denaturation occurs in every cell (von Bertalanffy 1957; Pauly & Cheung 2018a), but likely also for mathematical convenience and lack of empirical data (Ursin 1967). The model can also be restated in terms of energy, as a balance between energy gains 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 around 0.8 in fishes (Clarke & Johnston 1999; Jerde *et al.* 2019). In this case, classic Pütter models of growth, such as the VBGM or the 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 hyperallometric mass scaling (exponent larger than 1) (Marshall & White 2019b), or by describing 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. Bioenergetics models may need to account for this difference in the mass scaling of metabolism and consumption, which is in contrast to predictions from the metabolic theory of ecology.

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 ecology that extends from experiments to meta-analyses to 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 temperatures below peak, the global (average intraspecific) predictions about the activation energy of metabolism and consumption do not differ substantially and 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 (Angilletta & Dunham 2003), which is difficult to reconcile from a bioenergetics perspective if warming always reduced net energy gains. However, we do find clear mismatches at higher temperatures, due to consumption rates reaching a peak whereas metabolic rates increase exponentially over much wider temperature ranges. A recent hypothesis suggests that the reason for unimodal consumption curves is to protect aerobic scope by not overshooting post-meal oxygen consumption (Jutfelt *et al.* 2020). This would causally explain why also growth curves are unimodal, as is often argued from a conceptual point of view (Jobling 1997). Thus, 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 combined mass and temperature treatments.

In contrast to the metabolic theory of ecology, 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 size variation (Killen *et al.* 2010). This finding is in line with the metabolic boundary-level hypothesis, which predicts a negative relationship between mass scaling exponents of resting metabolism and temperature (Glazier 2010). However, this interaction was not found in a recent study on the intraspecific mass scaling exponent of metabolic rate in fishes (Jerde *et al.* 2019), possibly due to different data collection protocols. 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 temperature-body 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 those at which rates peak for the log-linear model, and inclusion of these could lead to significant negative interactions if rates for large fish peak at lower temperature. The ecological implications of temperature-size interactions at sub peak 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 intraspecific 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 varying either temperature or body size, not both (Appendix S1). It also resulted in that the numbers of 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 growth experiments or automatically measuring oxygen depletion rates. 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, as presented in this study, 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.

**References**