**Title Page**

Optimum growth temperature declines with body size within fish species

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**Abstract**

According to the temperature-size rule, warming of aquatic ecosystems is generally predicted to increase individual growth rates but reduce asymptotic body sizes of ectotherms. However, we lack a comprehensive understanding of how growth and key processes affecting it, such as metabolism and consumption, depend on both temperature and body mass 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 conducted a systematic review and compiled experimental data on fishes from 59 studies combining body mass and temperature treatments. By fitting hierarchical models accounting for variation between species, we estimated how these three processes scale jointly with temperature and body mass within species. We found that maximum consumption scaled with a smaller mass-exponent than metabolism, and is unimodal over the full temperature range. These two conditions lead to the prediction that optimum growth temperatures (*Topt*) decline with size. Analyses of an independent data set confirmed that *Topt* declined with mass. Small individuals will therefore likely be able to increase growth with initial warming, whereas larger conspecific individuals could be the first to experience negative effects of warming on growth. By synthesizing existing intraspecific experimental data on key physiological rates, while accounting for uncertainty at the species-level, can help overcome the mismatch between mechanistic growth models, general scaling theory, and single-species observations.

**Significance statement**

Predicting the consequences of rising temperatures requires understanding of how physiological processes such as growth, feeding and metabolism depend on body size and temperature within species. Common growth models predict declining optimum temperatures for growth with body size if energetic costs increase faster than gains with body size (net energy for growth decreases with size). However, the generality of this pattern has not been evaluated at the within-species level, and neither has the prediction about declining optimum temperatures. By collating data through a systematic literature review, we find support for both declining net energy gain with size and declines in optimum growth temperatures with body size using an independent dataset. These results provide a mechanistic basis for the common prediction that large individuals within populations may be the first to suffer negative consequences of warming on growth, with potential implications for fisheries yield and food web structure in warmer climates.

**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), is reflected in latitudinal gradients of insects (Horne *et al.* 2015), and is stronger in aquatic than terrestrial organisms (Forster *et al.* 2012; Horne *et al.* 2015).

Partial support for the TSR exist in in fishes, where 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 indeed limited to small individuals within a species, as predicted by 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 (Denderen *et al.* n.d.; Barneche *et al.* 2019; Huss *et al.* 2019; van Dorst *et al.* 2019) and differences between species may be related to life history traits and depend on local environmental conditions (Denderen *et al.* n.d.; Wang *et al.* 2020).

While the support for TSR is mixed, and the underlying mechanisms are not well understood (Ohlberger 2013; Audzijonyte *et al.* 2018; Neubauer & Andersen 2019), theoretical growth models, such as Pütter growth models (Pütter 1920), including the von Bertalanffy growth model (VBGM) (von Bertalanffy 1938), predict declines in asymptotic body mass with temperature and declines in optimum growth temperature with body mass – i.e. partly in line with the TSR (Morita *et al.* 2010; Pauly & Cheung 2018b). Yet, the physiological basis of these models has been questioned, as the scaling parameters (mass exponents) tend to differ from empirical estimates (Lefevre *et al.* 2017a; Marshall & White 2019a, b). Hence, despite attempting to describe growth from first principles, Pütter growth models can also be viewed as phenomenological. In more mechanistic growth models, the difference between energy gain and expenditure is partitioned between somatic growth and gonads (Ursin 1967; Kitchell *et al.* 1977; Jobling 1997; Essington *et al.* 2001). Energy gain 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). Therefore, it is important to understand how metabolism and consumption rates scale with body mass and temperature in order to understand if and how growth of large fish within populations is limited by temperature, and to evaluate the physiological basis of growth models.

Moreover, the effect of body mass and temperature should be evaluated at the intraspecific rather than interspecific level (Marshall & White 2019b). Despite this, intraspecific body mass- and temperature scaling is often inferred from interspecific data. This could be because we know surprisingly little about the relationship between consumption and metabolic exponents within species (Marshall & White 2019b). Yet, the effects of mass and temperature for a rate can differ within and between species (Glazier 2005; Rall *et al.* 2012; Jerde *et al.* 2019). For instance, across species, rates are often assumed (and found) to scale as power functions of mass with exponents of 3/4 for whole organism rates (-1/4 for mass-specific rates), exponentially with temperature, and with independent mass and temperature effects (e.g., in the Arrhenius fractal supply model (AFS) applied in the metabolic theory of ecology, MTE (Gillooly *et al.* 2001; Brown *et al.* 2004; Downs *et al.* 2008)). However, within species, deviations from a general 3/4 mass exponent are common (Clarke & Johnston 1999; Bokma 2004; Jerde *et al.* 2019), rates are typically unimodal and the effects of mass and temperature can be interactive (Xie & Sun 1990; Glazier 2005; García García *et al.* 2011; Ohlberger *et al.* 2012; Lindmark *et al.* 2018) (but see Jerde *et al*. (2019)). Alternative approaches that overcome these obstacles include fitting multiple regression models where coefficients for mass and temperature are estimated jointly instead of a prior determined (Brown *et al.* 2004; Downs *et al.* 2008), as well as fitting non-linear or polynomial 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). However, this requires intraspecific data with variation in both mass and temperature within species.

In this study, we analyse how maximum consumption, metabolism and growth rate of fish scale intraspecifically 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 (total n=3672, with data from 13, 20 and 34 species for each rate, respectively). We then fit hierarchical Bayesian models to estimate general intraspecific scaling parameters while accounting for variation between species. The estimated mass dependence and temperature sensitivity of mass-specific growth, consumption and metabolism, are used to quantify the changes in net energy gain (growth) of a general fish over temperature and body mass. Lastly, we compare our predicted changes in optimum growth temperature over body mass with an independently compiled experimental data set on optimum growth temperatures individuals of different size within species.

**Results**

We identified that within species of fish, mass-specific metabolic rates increase faster with body mass than maximum consumption rates, and neither of these rates conform to the commonly predicted -1/4 scaling with body mass (Fig. 2-3). We also find that consumption rate is unimodal over the full temperature range (Fig. S13). Based on this scaling of these rates, growth models predict a decrease in optimum growth temperature with body size (Fig. 4). The prediction of declining optimum growth temperatures with size is corroborated by our analysis of experimental growth rate data, where we find that within species, the optimum growth temperature declines with body size by 0.31 per unit increase in the natural log of relative body mass (Fig. 5). Below we present the underlying results in more detail.

At below peak temperatures, the intraspecific mass- and temperature dependence of specific growth (% increase in size day-1) can be described by the equation: (Fig. 1), based on posterior medians of the global parameters, thus representing an average (unmeasured) fish. The estimated temperature-mass interaction coefficient is both small and uncertain, and only leads to marginally better fits to growth data compared to the model without the interaction (WAIC 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 0.74 [0.95, 0.53]. This is similar to the predicted mass scaling of net energy at sub-optimum temperatures, defined as the difference between consumption and metabolism in the same unit (Fig. 4; see also methods on *net energy gain*), which scales with a mass-specific exponent of -0.43.

We find that the global intraspecific scaling of mass-specific maximum consumption rate can be described by the equation (Fig. 2). For mass-specific metabolic rate, the relationship is: . In the models for consumption and metabolic rate, all coefficients vary by species (M5 and M1, respectively) (*SI Appendix*, Table S4). Consumption scales with a smaller mass exponent (-0.38 [-0.45, -0.30) than metabolic rate (-0.21 [-0.26, -0.16]), based on the non-overlapping Bayesian 95% credible intervals (Fig. 3). It is also probable that the mass-specific scaling exponents differ from -0.25 (predicted by the MTE). 99.7% of the posterior distribution of the mass exponent of maximum consumption is below -0.25 whereas 95.5% 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 0.62 [0.57, 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). In contrast, we find statistical support for a species-varying mass and temperature interaction for metabolic rate. 98.3% of the posterior distribution of the global interaction coefficient is above 0 (Fig. S12). The estimated coefficient is 0.018 [0.0011, 0.0364] on the Arrhenius temperature scale, which corresponds to a decline in the mass scaling exponent of metabolic rate by 0.0026 .

We estimate the parameters of the Sharpe-Schoolfield equation (Eq. 4) to: = 0.58 [0.45, 0.74], = 0.70 [0.52, 0.89], = 4.03 [2.81, 4.98], and = 2.64 [2.17, 3.22], which shows that the decline in consumption rate is steeper than the increase (Fig. S13).

There is a strong statistical support for a decline in optimum growth temperature with body mass, as 92% of the posterior density of the global slope estimate () is below 0. The models with and without species-varying slopes were indistinguishable in terms of WAIC (*SI Appendix*, Table S5), and we present the results for the species-varying intercept and slope model, due to slightly better model diagnostics (*SI Appendix*, Fig. S31-34). The global relationship is given by the model: , where is the natural log of the rescaled body mass.

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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. Colors indicate species. 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. The bottom row shows the posterior distributions for (B) the global mass-scaling exponent, , (C) the global temperature coefficient, and (D) the global 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 rate 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.*

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***Fig. 4.*** *Illustration of predicted whole-organism maximum consumption rate (green), metabolic rate (purple) and the difference between them (orange) for two body sizes (top=1000g, bottom=5g) (see ´Materials and Methods´). Vertical arrows indicate the temperature where the difference in net energy gain (energy available for growth) is maximized for the two body sizes, which occurs at different temperatures despite that consumption peaks at the same temperature for both body sizes.*

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**Fig. 5**. *Experimental data demonstrating optimum growth temperature 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 and the area of the circle corresponds to body mass in unit .*

**Discussion**

Individual growth, consumption and metabolism represent fundamental processes in ecology, and their scaling with body mass and temperature has been used to predict the effects of warming on body size, size structure, and population and community dynamics (Vasseur & McCann 2005; Rall *et al.* 2010; Cheung *et al.* 2013). Over a large enough temperature range, the relationship between maximum consumption rate and temperature is typically unimodal within species (Englund *et al.* 2011; Rall *et al.* 2012) (Fig. 4), If in addition the whole-organism mass-exponent for metabolism is larger than that for consumption, optimum growth temperatures decline with body size in Pütter-type growth models such as the von Bertalanffy growth model (Morita *et al.* 2010). These growth dynamics would be in line with the temperature-size rule (Ohlberger 2013), as temperature initially increases growth but eventually leads to reduced growth performance of large fish. However, neither the difference between within-species exponents of consumption and metabolism, nor the generality of the predicted decline in optimum temperatures, have been evaluated across multiple species using systematic review.

In the von Bertalanffy growth model, the allometric exponent of energy gains ( is assumed to be smaller than that of costs (). However, this is based on the arguments that anabolism scales with the same power as surfaces to volumes () and catabolism, or maintenance metabolism, is assumed proportional to body mass (), as spontaneous denaturation occurs in every cell (von Bertalanffy 1957; Pauly & Cheung 2018a). These assumptions have been criticized by empiricists, as maintenance costs are thought to be proportional to standard metabolic rate, which in turn is proportional to intake rates (Lefevre *et al.* 2017a; Marshall & White 2019b). In this case, is close to , meaning growth trajectories and their temperature dependence can become unrealistic in a Pütter model (Lefevre *et al.* 2017a; Marshall & White 2019b). Hence, the prediction of shrinking of large fish has been questioned (Lefevre *et al.* 2017b). That said, we do not have a good understanding of the relationship between the *intraspecific* exponents for energy gains and costs, and instead rely on interspecific estimates (Peters 1983; Marshall & White 2019b). Similarly to how the existence of large fishes in tropical waters does not invalidate the hypothesis that large fish may shrink with warming, interspecific parameters cannot reject or support these model predictions on growth dynamics within species. By collating experimental data with intraspecific variation in both size and temperature, we are able to show that the mass scaling exponent of metabolism is larger than that of maximum consumption, which implies that on average within species of fish, maintenance costs increase faster with body mass than energy gains.

In addition to identifying the prerequisites to declining optimum growth temperatures with size within species, it is also important to verify the prediction. Some previous studies have found declines in optimum growth temperatures with body size in particular species of fishes and other aquatic ectotherms (Wyban *et al.* 1995; 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). Using our newly compiled growth data, 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, which suggests that physiological constraints contribute to reduced growth performance of large compared to small fish, in addition to increasing investment into reproduction (Barneche *et al.* 2018).

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). Moreover, effects in experiments reflect responses on shorter time scales than that of natural warming. In fact, the relationship between growth and temperature clines in a snapshot of time in natural populations tend to be weaker than predicted from metabolic theory, likely a result of acclimation, adaptation and thermal plasticity of life history traits (Denderen *et al.* n.d.). That said, ample evidence exist for positive associations between *warming* and reconstructed growth rates in time series studies (Thresher *et al.* 2007; Neuheimer *et al.* 2011; Baudron *et al.* 2014; Huss *et al.* 2019; van Dorst *et al.* 2019). This probably reflects that species generally live in temperatures cooler than those maximizing growth, such that initial warming can be beneficial, which would be in line with experimental predictions from the studies compiled here, all else equal (Fig. S14) (Bernhardt *et al.* 2018). These somewhat varying results from gradient studies, time series and experiments highlight the importance of understanding the time scale of environmental change in relation to that of immediate physiological responses, acclimation, adaptation and community reorganization for the specific prediction about climate change impacts.

In natural systems, climate warming may also result in stronger food limitation (Huey & Kingsolver 2019). Hence, as optimum growth temperatures decline not only with size but also food availability (Brett *et al.* 1969; Brett 1971), and realized consumption rates are a fraction of the maximum consumption rate (e.g. 20-70%) (Kitchell *et al.* 1977; Neuenfeldt *et al.* 2019), species may be negatively impacted by warming even when controlled experiments show they can maintain growth capacity at these temperatures. Supporting this point is the observation that warming already has negative or lack of positive effects on body growth (Huss *et al.* 2019) in 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 (as suggested by our finding that growth temperature optimum declines with intraspecific body size) depends on whether they live closer to their thermal optimum for growth compared to smaller conspecifics. 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 in natural populations 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; van Dorst *et al.* 2019). Hence, assuming that warming can lead to increased growth rate for individuals of all sizes in a population is a simplification that can bias predictions of the biological impacts of climate change.

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 (all else equal). 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 gain. The lack of mismatch at sub-peak temperatures also illustrates to importance of accounting for unimodal thermal response curves, even in thermal regions below optimum (Fig. 4). In fact, our findings suggest that size-dependent differences in net energy gain only arise when consumption rates are unimodally related to temperature, and not at temperatures below peak where rates increase exponentially.

We find that body mass can affect the temperature dependence of metabolism, which has been reported in some single species studies (Beamish 1964; Xie & Sun 1990; Ohlberger *et al.* 2012; Messmer *et al.* 2017; Lindmark *et al.* 2018; Fossen *et al.* 2019; Christensen *et al.* 2020) and across species (Killen *et al.* 2010). Although t (typically smaller than abovementioned results for single species), it 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). A possible explanation is that overall effect is masked by variation between species and pooling of data, as studies have found both positive and negative interactions between mass and temperature for metabolism (Ohlberger *et al.* 2012; Messmer *et al.* 2017; Lindmark *et al.* 2018). Another difference could be that we specifically used studies with temperature replicates within species and hence evaluate within-species interactive effects of mass and temperature. We do not find strong evidence for temperature-size interactions in growth or consumption, although it has been reported for some species (García García *et al.* 2011). One explanation, in addition to variation across species, could be that we strictly exclude temperatures near or beyond those at which rates peak for the log-linear model, and inclusion of these could lead to negative interactions if rates for large fish peak at lower temperature.

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. The approach presented here, with systematic literature review followed by hierarchical modelling approaches in a Bayesian framework, can ing in a single modelling framework In order to predict the impacts of climate warming on individuals, populations and food webs, it is important to improve our understanding of the intraspecific scaling of key physiological rates such as growth, metabolism and consumption with body mass and temperature.

**Materials and 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 (see *SI Appendix*, for details). In order to estimate how these rates depend on both body size and temperature within species, we selected studies with a combination of body mass-temperature setup (at least two temperature [average number of unique temperatures rounded to nearest are 4.3 for metabolism and consumption data, 7.2 for growth] treatments and at least two body masses [average 3.4, 20 and 47 unique body masses rounded to nearest for growth, consumption and metabolism, respectively]). The criteraia for both mass and temperature variation in the experiments reduces the number of potential data sets, 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, which represents a life stage exhibiting different constraints and scaling relationships (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 populations were used (Armstrong & Hawkins 2008; Jerde *et al.* 2019). In cases where we found more than one study for a given rate and species, we selected the most suitable study based on our pre-defined criteria (for details, see *SI Appendix*). 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 *SI Appendix*.

We compiled four datasets: growth rate, maximum consumption rate, metabolic rate and the optimum growth 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, of which 666 are below peak) and 2699 (metabolic rate) data points from published articles for each rate, from 13, 20 and 34 species, respectively, from different taxonomic groups, habitats and lifestyles (*SI Appendix*). We asked all the corresponding authors of each article to share data. In cases where we did not hear from the corresponding author, we extracted data from tables or figures using Web Plot Digitizer (Rohatgi 2012).

**Model fitting**

*Model description*

To each dataset, we fit hierarchical models with different combinations of species-varying coefficients, meaning they are estimated with shrinkage. This reduces the influence of outliers which could occur in species with small samples sizes (Gelman & Hill 2007; Harrison *et al.* 2018). The general form of the model is:

(1)

(2)

(3)

where is the th observation for species for rate *y*, is a species-varying intercept, is a predictor and is its coefficient, with , where is the number of mean-centered predictors considered in the model (mass, temperature, and their interaction). Species-level intercepts follow a normal distribution with hyperparameters (global intercept) and (between-species standard deviation). For most models we also allow the effects of predictor(s) tovary between species, such that becomes and , where . For each dataset, we evaluate multiple combinations of species-varying coefficients (from varying intercept to varying coefficients). The models are completed with priors for parameters (see *SI Appendix*, Table S3). 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 standard deviations to make them less informative. Below we describe how the model in Eqns. 1-3 is applied to each data set.

*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 mass-specific growth, maximum consumption rate and metabolism to scale allometrically (as a power function of the form ) with mass, and exponentially with temperature. Hence, after log-log transformation of mass and the rate, and temperature in Arrhenius temperature ( in unit , where is Boltzmann’s constant [8.6210-5 ]), the relationship between the rate and its predictors becomes linear. This is similar to the MTE, except that we estimate all coefficients instead of correcting rates, and allow not only the intercepts but also slopes to vary across species.

When applied to Eqns. 1-3, is the th observation for species of the natural log of the rate (growth, consumption or metabolism), and the predictors are (natural log of body mass), (Arrhenius temperature, in unit ), both of which were mean-centred, and their interaction. Body mass is 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 allowing the intercept and slopes to vary between species and used a single study per species.

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

Over a large temperature range, many biological rates are unimodal. We identified such tendencies in 10 species in the consumption data set. To characterize the decline in consumption rates () beyond peak temperature, we fit a mixed-effecs version of the Sharpe Schoolfield equation (Schoolfield *et al.* 1981), as parameterized in (Padfield *et al.* 2018). Specifically, we model in Eq. 1 as:

(4)

(5)

(6)

where the right hand side of Eq. 4 is the Sharpe-Schoolfield equation, is the rate at a reference temperature (here set to -10 on a centred scale), [] is the activation energy, [] characterises the decline in the rate past the peak temperature and [] is the temperature at which half the rate is reduced due to high temperatures. We assume and that vary across species and follow a normal distribution (Eq. 5-6). Prior to rescaling maximum consumption by dividing with the mean within species , we mass-normalize it by dividing it with where is mass in and is the mass-exponent estimated with the log-linear model fitted to data below peak temperature. Temperature, , is centered by subtracting the peak temperature estimated separately for each species. The rescaling is done to control for differences between species with respect to the experimental temperatures relative to the temperature that maximizes their consumption rate such that data can be pooled.

*Mass-dependence of optimum growth temperature*

To evaluate how the optimum temperature (, in degrees Celsius) for individual growth depends on body mass, we fit Eqns. 1-3 with as the mean-centred optimum growth temperature within species (), to account for species being adapted to different thermal regimes. , the predictor variable for this model, is the natural log of the ratio between mass and mass at maturation within species: . This rescaling is done because we are 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. We consider both the intercept and the effect of mass to potentially vary between species.

*Parameter estimation*

We fit the models in a Bayesian framework, using R version 4.0.2 (R Core Team 2020) and JAGS (Plummer 2003) through the R-package ‘*rjags*’ (Plummer 2019). 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 () (*SI Appendix*). compares chain variance with the pooled variance, and values <1.1 suggest all three chains converged to a common distribution (Gelman *et al.* 2003). 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 (5 and 1000 g, which roughly correspond to the 25th percentile of both datasets and the maximum mass in the consumption data, respectively), 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 factors for consumption and for metabolism. is based on the Sharpe Schoolfield model and is given by the temperature dependence of metabolic rate from the log-linear model. Because and are fitted to data on different scales, we divide these functions by their maximum. Lastly, we rescale the product between the allometric function and and such that the rate at 19 (mean temperature in both data sets) equals the temperature-independent rate.

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**Author contributions**

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

**Data accessibility statement**

All data and R code (lists of studies in literature search, data preparation, 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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