

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

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KEY WORDS:

WORD COUNT:

Abstract: ~260

Introduction: ~1400

Methods: ~1700

Results: ~800

Discussion: ~1900

Total: ~ 6100

Commented [Ca1]: Wondering if a title about the results would be more appealing?
I guess that means focusing on optimum growth temperature though ("Optimum temperature for growth declines with body size across fish species"), which is not optimal (ha!) either... other ideas?

Commented [ML2R1]: I agree that it would (but I'd prefer after the thesis then, because this title already circulates in some documents).

The problem is then we'd have to choose one result from many! (maybe too many...)

Abstract

1. Warming of aquatic communities is generally predicted to increase individual growth rates and reduce asymptotic body sizes of ectotherms. However, we lack a comprehensive overview of average intraspecific scaling of growth with body mass and temperature from controlled experiments, and mechanistic growth models are usually not informed by empirical scaling relationships of key processes such as metabolism and consumption. This limits our ability to link experimental data to observed patterns of growth, as well as developing models of growth and food web dynamics.
2. 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 with both body mass and temperature treatments, and fit hierarchical models to evaluate how these rates scale jointly with mass and temperature within species while accounting for variation between species.
3. Mass-scaling exponents of maximum consumption are smaller than both the predicted $\frac{3}{4}$ 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 growth, which we also find in growth data.
4. Thus, small individuals within a species will likely be able to increase their growth rates with initial warming and larger individuals will be the first to experience negative effects of warming on growth.

Introduction

Individual body growth is a fundamental process powered by metabolism, and thus depends on body size and temperature. 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, understanding 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 are likely results of an interplay between ecology and physiology (Ohlberger 2013; Audzijonyte *et al.* 2018; Neubauer & Andersen 2019). However, empirical evidence of climate signals in time series of individual growth rate is accumulating. For instance, reconstructed growth histories of individual fish through ageing based on bony structures (otoliths) often show positive correlations between growth rates and increasing temperatures (Thresher *et al.* 2007; Neuheimer *et al.* 2011; Baudron *et al.* 2014; Huss *et al.* 2019). This increased growth rate can also be predicted from numerous experimental studies showing growth increases with temperature until a peak is reached, after which additional warming is deleterious (Brett *et al.* 1969; Elliott & Hurley 1995; Jobling 1997; Morita *et al.* 2010a; García García *et al.* 2011). Less clear, however, is the negative effect of warming on the growth of large fish within populations, as would be predicted from the temperature size-rule. Some studies have found negative correlations

Commented [ML3]: I think it's good to be specific about this since growth is a broad term, but after a couple of times I'd rather just use "growth" © It should be evident for the reader if they get so deep into the paper it's individual growth

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 (Barneche *et al.* 2019; Huss *et al.* 2019; van Denderen *et al.* 2019). Predictions about declines in asymptotic body mass have also been made from theoretical growth models (Pauly & Cheung 2018b). However, the physiological basis of these models has been questioned for multiple reasons, both for the mechanism leading to asymptotic growth (resource limitation) (Marshall & White 2019a) as well as the mechanism causing the asymptote to decline with warming (Lefevre *et al.* 2017). As empirical findings vary and theoretical predictions are questioned, it remains unclear to which extent the growth of large fish within populations is limited by 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). Around the maturation size, the remaining excess energy is partitioned between somatic growth and gonads. Energy acquisition, or assimilation, is typically the amount of energy available in consumed food and expenditure is defined as fasting, activity and feeding metabolism. Metabolic processes are in turn usually assumed to be related to resting metabolism, often measured as the oxygen consumption of unfed fish at rest (Jobling 1997). These components of the biomass dynamics of growth are found in simple mechanistic Pütter-type growth models, such as the von Bertalanffy Growth Model (VBGM), or the Ontogenetic Growth Model (OGM) (Pütter 1920; von Bertalanffy 1938; Ursin 1967; West *et al.* 2001), as well as more complex dynamic energy budget models (Kitchell *et al.* 1977; Kooijman 1993; Kearney 2019) including multispecies dynamics models such as physiologically structured population models (PSPMs) (Roos & Persson 2001) and size-spectrum models (Hartvig *et al.* 2011; Maury & Poggiale 2013; Blanchard *et al.* 2017). In order to understand growth dynamics

Commented [Ca4]: This needs better explanation, or shorten the second part of the sentence to say 'for multiple reasons... (see refs)'

Commented [ML5R4]: Tried to explain and change. Can also skip going into the details as you suggest!

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 interspecific, to better represent the individual-level processes, as scaling within and between species can differ (Glazier 2005; 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 which case body size is a trait of an individual rather than a species. In addition, the temperature- and mass dependence of metabolism and other related rates are also often assumed to follow Arrhenius fractal supply model (AFS) in the metabolic theory of ecology (Gillooly *et al.* 2001; Brown *et al.* 2004; Downs *et al.* 2008). The AFS assumes that metabolically-driven rates (I) (individual growth, metabolism and consumption), to scale as: $I = i_0 M^{3/4} e^{-E/kT}$, where E is the activation energy, k is Boltzmann's constant and T 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 could also fit intraspecific data depending on the temperature range (Brown *et al.* 2004; Clarke 2004) (but see (Englund *et al.* 2011)), within-species thermal response curves are generally unimodal (Dell *et al.* 2011; Englund *et al.* 2011; Rall *et al.* 2012; Uiterwaal & DeLong 2020). These assumption-violations, and model oversimplifications, are likely to affect the estimates of temperature-dependencies (Downs *et*

al. 2008). Instead of mass-correcting according to the AFS (Brown *et al.* 2004), it could be more appropriate to fit multivariate models where coefficients 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, 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 is of a species (Bolnick *et al.* 2011; Miller & Rudolf 2011; Persson & De Roos 2013; Brose *et al.* 2017). Therefore, overcoming the knowledge gap about intraspecific scaling is important for advancing trait-based approaches to ecology.

In this study, 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 through partial pooling 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 0.6 eV), whereas the mass-

Commented [AG6]: but isn't this how a mass-correcting AFS could be interpreted? e.g. fitting an AFS with a size-temp interaction term

Commented [ML7R6]: I'm sorry I don't follow! The AFS corrects for mass or temperature by assuming an exponent of $\frac{3}{4}$ or an activation energy of ~ 0.6 .

However, if those are not accurate parameters, the other coefficient will get an incorrect estimate. Instead of fixing one variable, you could estimate both simultaneously (interaction or no interaction, main idea is not simply not correct your data before based on some theoretical prediction)

Commented [AG8]: they could scale with heaps of things, so better be explicit. Try to avoid talking only about "scaling" of rates, without saying what scaling. ("Scaling" is also quite technical, can also state it more straightforward as "how rates depend on")

Commented [ML9R8]: True, although I'm hoping to not have to write that all the time, especially since we from first paragraph and the title make it clear it's about body mass and temperature 😊 but good point to remind every now and then!

It may sound more technical, but it's a common term in this context (and it's in the title). It also has a slightly different meaning in my view. "how rates depend on" doesn't quite signal the universality of allometry, and how it can be used to "scale" things across levels of biological organization. Here's from a chapter I like:

"Change in organism size could be based on different measures, such as length, surface area, or, most commonly, mass. The change in size is then a change in scale and, in the language of practitioners, the question becomes: How does metabolic rate "scale" with size? The study of how changes in size influence other organism traits is known as allometry."

exponent of maximum consumption is smaller than the predicted $3/4$. Over the full temperature range, consumption rates are unimodal, and we find indications of consumption rates being maximized at similar relative temperatures as growth. Unimodal growth curves are predicted to cause declines in optimum growth curves with body mass, which we can demonstrate clearly in an independent data set.

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. For more detailed information about the search protocol, we refer to Appendix S1.

Commented [AG10]: say which (list of three within brackets) and refer to appendix where search criteria (and search dates) are given

Commented [Ca11R10]: yes, we need a bit more information on the basic searches

Commented [ML12R10]: Ok, now I have listed the search terms here, but refer to the appendix for more details because it takes up quite some space!

We selected studies with a factorial body mass-temperature setup in order to estimate how these rates depend on body size and temperature within species. While this reduces the number of data points available in the literature (as most experimental studies only use size or temperature treatments), it allows us to fit multivariate models and estimate the effects of mass and temperature jointly, and to evaluate the probability of interactive mass- and temperature effects within species. We 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 ($\pm 1^\circ\text{C}$), (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 behavior. We used only one study per species to ensure that all data within a given species are comparable as measurements of these rates can vary between studies due to e.g. measurement bias or differences in experimental protocols (Armstrong & Hawkins 2008; Jerde *et al.* 2019). In cases where we found more than one study for a species, we selected the study we found most suitable, based on how well it fit with our pre-defined criteria (Appendix S1). A more detailed description of the search protocol, criteria to 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, 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

Commented [Ca13]: What happened to 'contacting authors'? It would of course be better to be able to say we have the original data. Some authors I know and would be happy to contact (e.g. Hovel *et al.* paper, Jerde *et al.* paper – in case any of those are relevant)

Commented [ML14R13]: Yes, after the thesis, the idea is to go through the list of papers (just to make sure they are all there) for all rates, just to tick that of the list. This includes the recent Jerde paper, which I haven't looked at yet. When I have the absolute-final set of studies, I'll go ahead and send a similar e-mail to all authors in that list.

I preferred to not send e-mails to authors along the way, as it seemed more efficient to simply plough through the literature and extract data (to ensure I got at least something for the thesis). I hope I will be able put that sentence back into the paper though! I agree it would be really good to get the actual data, and also looks nicer...

Commented [ML15]: Check this is true for Björnsson data and other papers that combine old and new data.

.. although, what was the argument for that again? I'm a bit hesitant of removing data. I thought it was mainly to get one study per species to avoid uncertainty due to different experimental setups and such, but in this case it is the same lab group that did the same experiment, and since they analyzed all together they must have thought the data were comparable? I think this is the only known case in the data were it explicitly says data from different experiments were combined.

Commented [Ca16]: Not entirely clear how that was decided. Can we give a hierarchy of criteria, e.g. including the number of sizes and temperatures measured etc.? Or is this in the appendix? Then never mind...

Commented [ML17R16]: It is in the appendix, so I guess not needed here?

Commented [AG18]: you never got any data from authors in the end?

Commented [ML19R18]: No but I did not contact the majority yet. See reply to Jan's comment!

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 temperature ranges corresponding to the environmental or from predictions from distributional maps (both metrics 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°C (mid-point 13.5°C) was used (Joh *et al.* 2013; Mitamura *et al.* 2020).

Model fitting

Mass-dependence of optimum growth temperature

To evaluate how the average optimum temperature in Celsius ($T_{opt,i}$) for individual growth depends on body mass (M_i), we fit the following hierarchical model to account for variation in both intercept and slope with respect to species:

$$T_{opt,i} \sim N(\mu_i, \sigma^2) \quad (1)$$

$$\mu_i = \beta_{0j[i]} + \beta_{1j[i]} m_i \quad (2)$$

$$\beta_{pj} \sim N(\mu_{\beta_p}, \tau_{\beta_p}) \quad (3)$$

Commented [Ca20]: Would be nice to have one recent date...

Commented [ML21R20]: You mean a single date rather than an interval? Agree. I highly doubt the temperature parameters have changed for any of the species since this data collection was started. But for the paper I can go through them again and check they're the same, and in that case just put the last date.

Commented [Ca22]: In how many cases? If just a couple, could we afford to drop those?
These are metrics that likely differ for a given species so it does introduce some error. I'm also wondering if we can get population-specific information for most experiments, which would probably be a more relevant metric (e.g., median environmental temperature for Atlantic cod in Greenland is very different from that for Atlantic cod in the southern North Sea – and both are pretty far from the species-wide average...).

Commented [ML23R22]: I just wrote it all down instead.

I agree though we should look into this, i.e. getting more better "reference" that in addition take into account which population it is.

Commented [AG24]: clarify what index i is. at least the first time (from below, and from eqs 6-8, it seems as it is observation number i , but that doesn't make sense to me, as you should only have one estimate of T per species? what am I missing?). To me it would be clearer (I think...) if we wrote $j[i]$ as the index both on the left-hand-side of eq 2, and on both sides in eq. 1

Commented [Ca25R24]: I've seen both used, either an index for the individual observations only or indices for individuals by groups.

Commented [ML26R24]: No i is the observation number (as is written). We don't have one but multiple observations per species (to get the intraspecific decline).

And as I said in the e-mail, I also sort of reacted to the lack of indexing on the left-hand side. But since I've never seen it really I suspect there must be a good explanation ☺ For instance that it represents the global effect which doesn't not vary with j , or something like that maybe.

Here $T_{opt,i}$ is the i th observation of the mean-centered optimum growth temperature within species j : $T_{opt,i} = T_{opt,i,j} - \overline{T_{opt,i,j}}$, m_i is the natural log of the ratio between mass and maximum body mass within species: $m_i = \ln(M_{i,j}/M_{i,j,\infty})$. The mass corresponds to either geometric mean body mass in the time interval where growth was measured or size class depending on how it was defined in the original study. Subscript p in Eq. 3 refers to parameter (0 for intercept and 1 for slope). We also fit a model with a global mass-coefficient β_1 (i.e. not varying by species). Body mass and temperature were in addition mean-centered for fitting, such that 0 corresponds to the mean of all across all data points.

Commented [ML27]: This is very annoying! I really want to use i and j for subscripts here but the dots are not showing... gaaaaah

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

$$\ln B = \ln g_0 + (b_0 + cT) \ln M - E/kT, \quad (4)$$

which on normal scale becomes:

$$G = g_0 M^{b_0 + cT} e^{-E/kT}, \quad (5)$$

where g_0 is the intercept, b_0 is the mass-scaling exponent when $T = 0$, c is the interaction coefficient, E is the activation energy, and k is Boltzmann's constant in eV K^{-1} ($= 8.617 \times 10^{-5} \text{ eV K}^{-1}$). We fit hierarchical models with different combinations of group (species)-varying coefficients. The full model with uncorrelated species-varying intercepts, mass-, temperature- and interaction-coefficients, can be written as:

$$y_i \sim N(\mu_i, \sigma^2) \quad (6)$$

$$\mu_i = \beta_{0j[i]} + \beta_{1j[i]} m_i + \beta_{2j[i]} t_{A,i} + \beta_{3j[i]} m_i t_{A,i} \quad (7)$$

$$\beta_{pj} \sim N(\mu_{\beta_p}, \tau_{\beta_p}), \quad (8)$$

where y_i is the i th observation of the natural log of the rate (growth, metabolism or consumption), and p indexes regression coefficient (0,1,2,3). In Eq. 7, m_i is the mean centered (not by species) natural log of body mass ($m_i = \ln(M_i) - \overline{\ln(M_i)}$), and $t_{A,i}$ is mean-centered Arrhenius temperature ($1/kT$ in unit Kelvin) ($t_{A,i} = T_{A,i} - \overline{T_{A,i}}$). For metabolism and maximum consumption rates, M_i is mass in g, whereas for growth rates, M_i is either the geometric mean of the initial and final mass of the growth experiment, or the size-class, as defined by the authors. Specific growth rates were expressed as unit $\% \text{ day}^{-1}$, consumption rates as unit g day^{-1} and metabolic rates as unit $\text{mg O}_2 \text{ h}^{-1}$ (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 45%. We accounted for potential differences between these metabolic rate measurements by using a random species effect and a single experiment/dataset per species.

Commented [AG28]: was it something else for consumption and metabolism?

Commented [ML29R28]: Yes, just the mass. In growth trials either size-classes were used or geometric means of initial and final masses.

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 and then aggregated, i.e. 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 consumption 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 μ_i is for the full data set defined as:

$$y_i \sim N(\mu_i, \sigma^2) \quad (9)$$

$$\mu_i = \gamma_0 + \gamma_1 m_i + \gamma_2 T_{C,i} + \gamma_3 T_{C,i}^2, \quad (10)$$

where y_i in Eq. 9 refers to consumption rates divided by the mean value by species j ($y_i = y_{i,j}/\bar{y}_{i,j}$), m_i in Eq. 10 is mean-centered natural log of body mass ($m_i = \ln(M_i) - \ln(\bar{M}_i)$) and $T_{C,i}$ is mean-centered rescaled temperature by species, where the rescaled temperature is defined as $T_{C,i} = T_{C,i,j} - \overline{T_{env,C,i,j}}$.

For illustrations of model fits, we predict over the temperature range of the data for species j while keeping body mass at 0 (corresponding to the species-specific mean body mass in g). The species predictions and data are plotted together in Fig. S21 to illustrate the spread in optimum temperature measured as distance to environmental median. Due to general data limitation we did not fit an interaction term that alters the optimum temperature by mass,

Commented [AG30]: isn't it a bit strange to give the model for the full data set when you never fitted a full model? (rather give the species-specific model form)

Commented [ML31R30]: Note sure I follow, the "full" part refers to the data, not model, as we do not consider alternative model formulations.

This is also the non-hierarchical model.

Commented [ML32]: This was necessary to fit the models even by species, I don't actually know why but maybe has something to do with trimming the y-axis to a smaller scale?

Commented [AG33R32]: or because your predictor mass was mean-centred?

Commented [ML34R32]: No, I mean that when I fit the model with the raw consumption data as the dependent the fits look crazy. When I divide the consumption (not the predictor variables, which are mean centered in both cases) by the mean it model fits look ok.

So, the only thing that differs is the scale of the axis, which I didn't think would have such a large effect since we anyway fit it within species.

Commented [ML35]: I use overline for mean and tile for median!
https://www.rapidtables.com/math/symbols/Basic_Math_Symbols.html

although this has been identified in data-rich single-species experiments (García García *et al.* 2011).

Parameter estimation

We fit the models in a Bayesian framework, using R version 3.5.0 (R Core Team 2018) and JAGS (Plummer 2003) through the R-package ‘*rjags*’ (Plummer 2019). We used a mix of flat, weakly informative and non-informative priors to facilitate convergence depending on how well known the parameter is, based on previous literature (Table 1). 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 \hat{R} (Appendix S1). \hat{R} compares chain variance with the pooled variance, and values < 1.1 ensures all three chains converged to a common distribution (Gelman & Rubin 1992). We relied heavily on the R packages within the *tidyverse*’ (Wickham 2017) for data processing, as well as ‘*ggmcmc*’ (Fernández-i-Marín 2016) and ‘*bayesplot*’ (Gabry *et al.* 2019) for visualization. All data and R code (data manipulation, analyses and figures) can be downloaded from a GitHub repository (<https://github.com/maxlindmark/scaling>) and will be archived on Zenodo upon publication.

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 described above (Table 2), and evaluate models within with Δ WAIC values < 2 , where Δ WAIC is each models difference to the lowest WAIC across models, in line with common convention (Olmos *et al.* 2019).

Commented [Ca36]: Not clear if this refers to the recommendation on how to set priors or the actual values used as priors. I guess the former, but we should also mention if any priors are informed by independent data.

Commented [ML37R36]: Yes, you’re right.

The link <https://github.com/stan-dev/stan/wiki/Prior-Choice-Recommendations> was a reference to how to set priors, more to show both of you where I got the terms from, not really intended as a citation.

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

Model	Parameter	Description	Prior distribution
Linear T_{opt} model (Eqns. 1-3)	μ_{β_0}	Hyperparameter (intercept)	$N(0, 5)$
	μ_{β_1}	Hyperparameter (mass coefficient)	$N(0, 5)$
	$\sigma^2_{\beta_0}$	Hyperparameter (intercept variance)	$U(0, 10)$
	$\sigma^2_{\beta_1}$	Hyperparameter (mass coefficient variance)	$U(0, 10)$
	σ^2	Variance	$U(0, 10)$
Log-linear regressions for growth, consumption and metabolism (Eqns. 6-8)	μ_{β_0}	Hyperparameter (intercept)	$N(0, 0.5)$
	μ_{β_1}	Hyperparameter (mass exponent)	$N(-0.25, 0.5)$
	μ_{β_2}	Hyperparameter (activation energy)	$N(-0.6, 0.5)$
	μ_{β_3}	Hyperparameter (interaction)	$N(0, 0.5)$
	$\sigma^2_{\beta_0}$	Hyperparameter (intercept variance)	$U(0, 10)$
	$\sigma^2_{\beta_1}$	Hyperparameter (mass exponent variance)	$U(0, 10)$
	$\sigma^2_{\beta_2}$	Hyperparameter (activation energy variance)	$U(0, 10)$
	$\sigma^2_{\beta_3}$	Hyperparameter (interaction variance)	$U(0, 10)$
	σ^2	Variance	$U(0, 10)$
Quadratic model for consumption and growth (Eqns. 9-10)	γ_0	Intercept	$N(0, 5)$
	γ_1	Mass coefficient	$N(0, 5)$
	γ_2	Temperature coefficient	$N(0, 5)$
	γ_3	Quadratic temperature coefficient	$N(0, 5)$
	σ^2	Variance	$U(0, 10)$

Commented [ML38]: The “weakly informative” priors are not based on any specific study but are rather broadly centered around average MTE predictions with extra variability added. If we would use a specific study to inform the prior it would be more informative, because the variance would be much smaller. So, do I cite a specific paper? Maybe I can say that we use the MTE predictions (or more broadly the $\frac{3}{4}$ rule, for the mass exponent) as the mean but increase the variance?

Results

We find that the average intraspecific mass- and temperature dependence of specific growth at below optimum temperatures across species can be described by the equation: $\ln(G) = 0.4 - 0.3 \times \ln(m) - 0.76 \times t_A - 0.02 \times t_A \times \ln(m)$. This model (M1, Table 2) contains a body mass-temperature interaction. However, the estimated interaction coefficient is small (-0.02 [-0.1, 0.06], where brackets indicate 95% Bayesian credible intervals) and uncertain, as about 72% of the posterior density is above 0 (Fig. 2), and only leads to marginal better fits to data (Δ WAIC around 2.4 compared to model without interaction, Table 2). We estimate the mass-scaling exponent of growth, i.e. the mass-coefficient on log-log scale, to be -0.3 [-0.43, -0.17]. The activation energy, E , 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. To illustrate this in terms of specific growth, an increase in temperature from 15°C (overall mean in data) to 25°C leads to an increase in predicted natural log of growth by a factor of 2.9 for a fish of mean mass (~190 g).

We find that the global intraspecific scaling of whole-organism metabolic rate can be described by the equation $\ln(\text{metabolism}) = 1.59 + 0.77 \times \ln(m) - 0.61 \times t_A + 0.017 \times \ln(m) \times t_A$, and consumption rate at temperatures below optimum as $\ln(\text{consumption}) = 0.55 + 0.64 \times \ln(m) + 0.66 \times t_A$ (see Fig. 3 for a general intraspecific prediction for a given mass and two temperatures). 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).

Some notable differences exist in the mass- and temperature-dependences of these two rates. First, 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 largely non-overlapping Bayesian

Commented [AG39]: same as above; looks like a dependence on absolute mass; include your indices to show that it is the relative that you've explained in the methods

Commented [ML40R39]: In this case it's actually absolute mass. But agree it's a problem when it differs between models.

Because I use m in the models, and define m when the statistical model is described (to not make the statistical indexing look weird), I would prefer to just use m and t_A and reiterate in words which units/scale etc.

I don't think it's needed to index here because that's our general, global prediction for an unmeasured fish and not limited to our data.

Commented [ML41]: Note that for the consumption model I end up in a similar situation. Tricky thing here is that this delta waic is always around 2, not really smaller or bigger. So in this case, but not the other with close WAICs, I'll go with this one but explain the interaction is uncertain and the gains are small of including it.

Commented [Ca42]: Maybe better in the discussion...

Commented [ML43R42]: I've been trying to sneak in borderline discussion-sentences here in case I couldn't fit them in the discussion (because we already have too much to discuss in this wide-spanning ms...). If you think it's too much of a discussion I can remove it!

Commented [ML44]: It was 0.8 before, now it's 0.77. This isn't because we now use non-scaled variables, but because I discovered a unit-conversion error when I plotted the data on the non-rescaled values.

There I noticed a really small bodied fish with really high values and checked it out further. The reason I didn't see that cluster being to large before was because the body masses are close to observed max for that species (desert pupfish).

I will go through all data really thoroughly after the thesis so this won't happen again...

95% credible intervals (indicated in square brackets) (Fig. 4). This difference implies that metabolic processes increase faster with body mass than maximum consumption rates. We also find it probable that both mass-scaling exponent of maximum consumption differ from the predicted 0.75 from the metabolic theory of ecology, because 99.5% of the posterior distribution is below 0.75. The mass-exponent for metabolism is closer to 0.75, with 70% of the posterior distribution above 0.75. 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) 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 β_3 is above 0, Fig. 5), 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 °C⁻¹. For maximum consumption, the model with a global interaction, β_3 , term has a ΔWAIC of 2, meaning that WAIC offers little support for one of these models over the other. For illustration of model predictions we therefore chose model M5 because it is simpler and the estimate of β_3 is uncertain (82% of posterior is < 0) and small (posterior median of -0.018 on Arrhenius temperature scale). For metabolism, the model with a species-varying interaction term has a ΔWAIC of 1.2, suggesting it is comparable to the global-interaction only model. We chose the latter to illustrate predictions for the simpler model structure.

Over a larger temperature range, biological rates tend to be unimodal. We identified such tendencies in nine species in the consumption data set, and fit quadratic models to the consumption rate in those species (Fig. 6). The unimodal temperature-dependence implies that even if maximum consumption rates increase faster than metabolic rates with temperature at sub-optimum temperatures (due to larger activation energy), eventually consumption rates

decline relative to metabolism with further warming. In other words, the effect of temperature on the mismatch between metabolic costs and feeding gains depends on the current temperature relative to optimum temperature. However, when standardizing the temperature data to a common unit, here relative to median temperature in the environment (i.e. $T_{c,j} - \widetilde{T_{env,c,j}}$) in unit °C, we find large variations in the relative temperature at which consumption is maximized (“optimum”) (Fig. 6). These temperatures range from -2.3 to $+17$. Across species, the mean in intraspecific $T_{opt,j}$ is 6 in the same unit (with a standard deviation of 6).

The optimum temperature for growth declines with body size by -0.3°C per unit increase in the natural log of relative body mass (Fig. 1). This decline in optimum temperature is very clear, because 99% of the posterior density of the slope estimate (β_1) is below 0. The two models, with and without species-varying slopes, were indistinguishable in terms of WAIC ($\Delta\text{WAIC} = 1.3$), and we therefore present the results for the global slope model for parsimony. The general relationship is given by the model: $T_{opt} = 0.0124 - 0.3 \times m$, where m is relative mass.

Commented [Ca45]: Those are rather extreme values, esp. the highest and lowest values.

About the strong difference for the Mandarin fish: maybe the mean environmental (or preferred?) temperature is not representative of the population used in the experiments? Lui et al. 1998 report maximum water temperatures in that lake of up to 35°C , so 13°C as preferred seems rather low.

The negative value for brown trout is also questionable. Optimum for consumption should be higher than mean experienced temperature.

The overall mean of 6°C , on the other hand, seems reasonable. That's of course where a hierarchical approach would be better...

I know this seems very picky - but somehow these are extreme enough to warrant further scrutiny in my view

Commented [ML46R45]: I agree those are extreme values, and maybe the environment-temperatures for mandarin fish refer to a specific population (35C is 13C warmer than the upper range of temperatures, which seems lethal...).

But just to clarify also, the reference temperature (T_{env}) is the midpoint between the minimum and maximum temperature on fishbase, so it's not necessarily the mean experienced temperature. Which is another reason for maybe coming up with another metric, something like average temperature in spatial area of distribution weighted by abundance, or something.

Since we only use for a few species now (only growth (maybe) and consumption), we can probably afford digging into it.

Commented [ML47]: Some confusion here in the last round, because I didn't put the WAIC for T_{opt} in any table. They are just two so I thought I could just put them in a text and keep the WAIC table to the log-linear models to make it clearer. I stick with that approach here, so don't look for these values anywhere else :)

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

Model	m*t	Species-varying parameter(s)	WAIC metabolism	WAIC consumption	WAIC growth
M1	Yes	$\beta_0, \beta_1, \beta_2, \beta_3$	1.2 (291.3)	3.5 (530.3)	0 (43)
M2		$\beta_0, \beta_1, \beta_2$	0 (290)	2 (528.7)	2.7 (45.6)
M3a		β_0, β_1	297.8 (587.9)	132.5 (659.2)	27.4 (70.4)
M3b		β_0, β_2	844.5 (1134.6)	48 (574.7)	48.2 (91.2)
M4		β_0	1063.6 (1353.7)	157.4 (684.1)	59.2 (102.2)
M5	No	$\beta_0, \beta_1, \beta_2$	6.4 (296.5)	0 (526.7)	2.4 (45.3)
M6		β_0	1167.6 (1457.6)	185.5 (712.2)	56.8 (99.8)
M7		β_1	2363.7 (2653.9)	681.9 (1208.7)	191.1 (234.1)
M8		β_2	4200 (4491)	672 (1198.8)	138.3 (181.2)

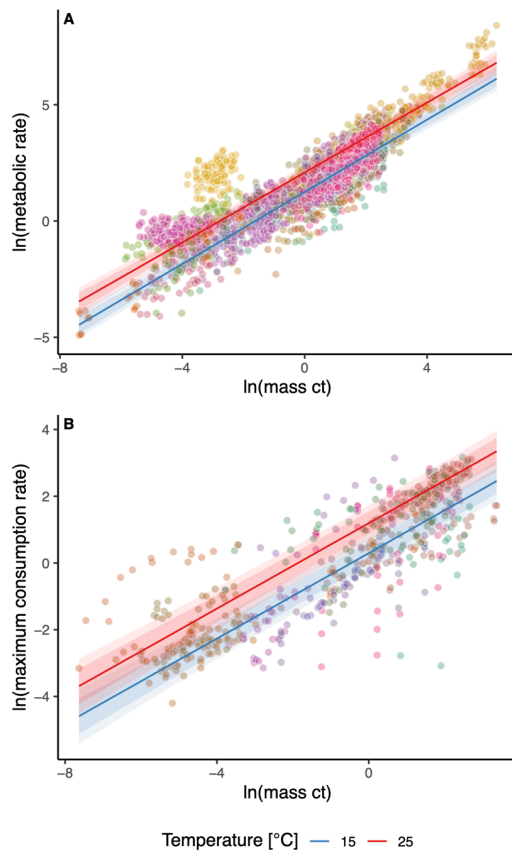


Fig. 1. Natural log of metabolic rate (A) and maximum consumption rates (B) vs. natural log of mass [g]. Lines are global predictions for an average species at temperatures 15°C (blue line and ribbon) and 25°C (red line and ribbon). The average temperatures in the data are 19°C and 18°C for metabolism and maximum consumption, respectively. 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 interval. Point colors correspond to species ($n=18$ and $n=35$ for consumption and metabolism, respectively).

Commented [ML48]: Later I can add transparent/dashed/narrow lines corresponding to predictions by species... that would maybe visualize better that we account for the clusters.

We could also remove the hot and cold predictions, I think they are best for illustration when we have strong interactions, which we don't. Then we can colors the global prediction with something more neutral, to not make it too confusing with the color-coded data points...

Commented [ML49]: The reason I had odd temperatures for predictions before was that they look nice on Arrhenius scale (-1 and 0). Now I instead choose the C-values and odd/specific Arrhenius temperatures instead.

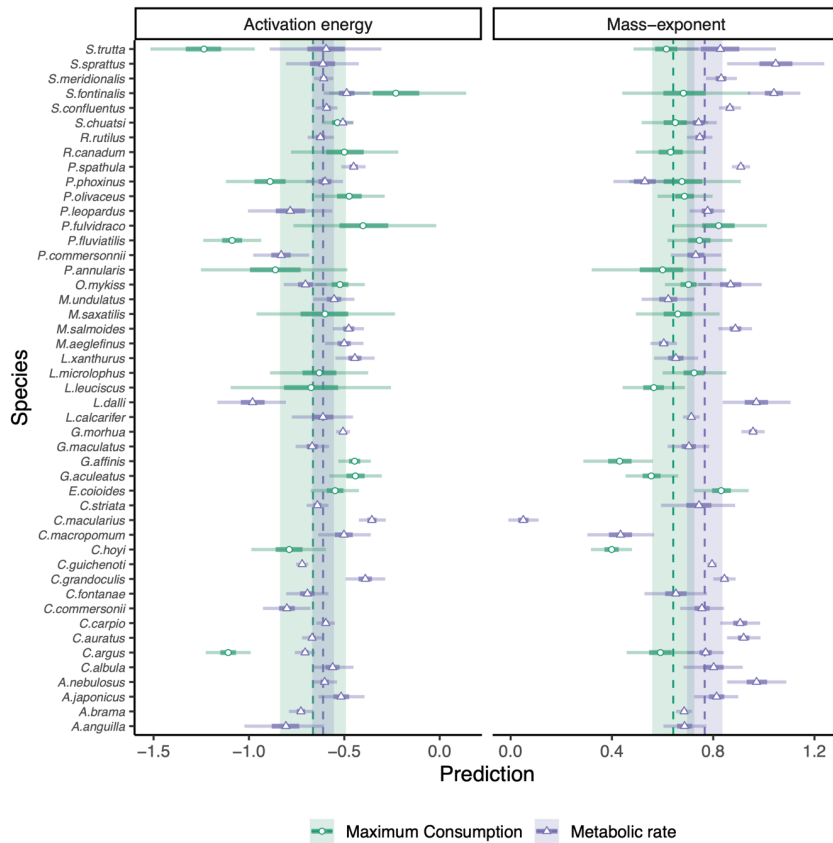


Fig. 2. Posterior medians of the global activation energies and mass-exponent of metabolism (model M2) and maximum consumption (model M5) from the hierarchical model fitted to below temperature optimum data (white triangles and circles, respectively), and their 80% and 95% credible interval (vertical short and long lines, respectively). Vertical dashed lines correspond to the median prediction for an unknown species (i.e. μ_{β_1} and μ_{β_2} in Eqs. 6-8 for the mass and temperature coefficient, respectively). Shaded vertical areas correspond to posterior median ± 2 standard deviations of the posterior median.

Commented [ML50]: Some species' mass-coefficients changed here since I rolled back to using non-scaled predictor variables. Seems also more extreme species-predictions came out this time, will look into it in more detail. Wonder what those extremes would be in a non-hierarchical single species model.

Commented [Ca51]: See comment above – if we keep it for metabolism we need to clearly state that we refer to the temperature at which the respective rate is at its maximum (in the intro or methods)

Commented [ML52R51]: Good point. Tried to say that early on now.

Commented [Ca53]: Maybe better?

Commented [ML54R53]: Or average?

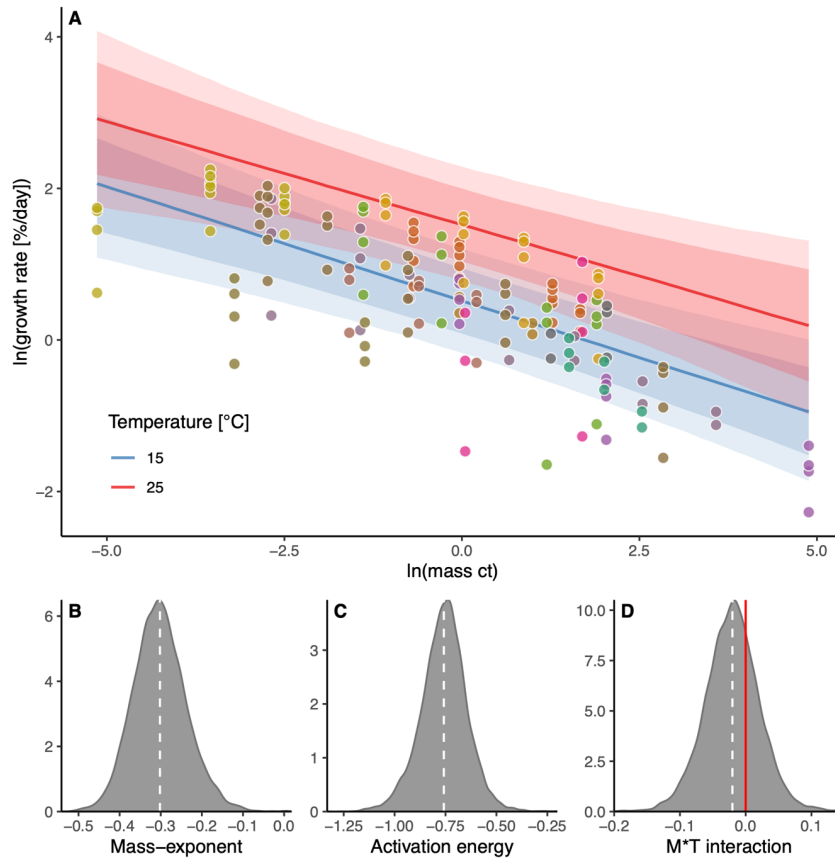


Fig. 3. Effects of temperature and body mass on body growth. Panel A) shows growth rate [% day⁻¹] as a function of mean centered body mass, both on natural log scale. Lines are global predictions from model M1 for an average species at temperatures 15°C (blue line and ribbon), which is close to the mean temperature (14.3°C) in data and 25°C (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 interval and the solid line is the median prediction from the average across-species prediction. 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, μ_{β_1} , (B) activation energy, μ_{β_2} , (C) and mass-temperature interaction, μ_{β_3} , (D) are shown in the bottom row. Dashed white line shows the posterior median.

Commented [ML55]: The reason I had odd temperatures for predictions before was that they look nice on Arrhenius scale (-1 and 0). Now I instead choose the C-values and odd/specific Arrhenius temperatures instead.

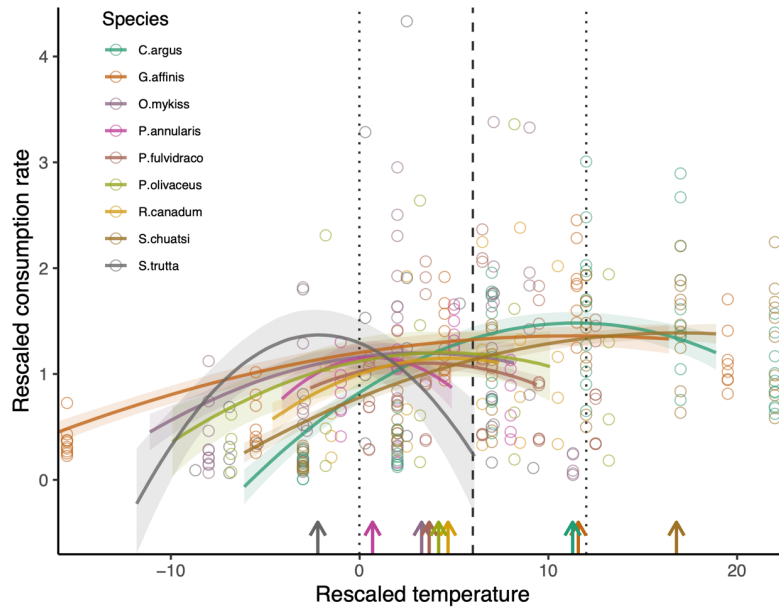


Fig. 4. Rescaled maximum consumption rates (consumption divided by mean consumption within species) as a function of rescaled temperature ($T_{c,j} - \widehat{T_{env,c,j}}$), where colors indicate species. The data is a subset of the maximum consumption data containing only species with observations 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.

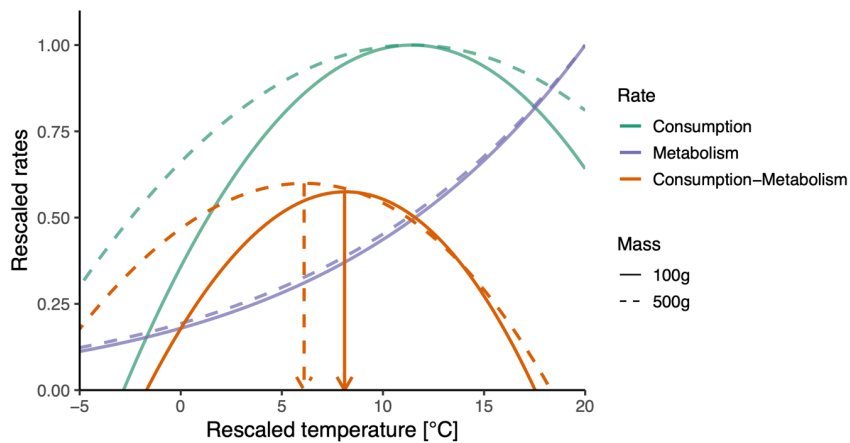


Fig. 5. Illustration of normalized thermal response of maximum consumption (green), metabolism (purple) and their difference (orange) for two body sizes (100g = solid, 500g = dashed). The consumption-curve is based on the quadratic model for *C. argus* (Appendix S1, Fig SX), and metabolism is calculated from the global model (see 'Results'). Both rates are expressed as relative to maximum their maximum, per body size separately, for illustration purposes are 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.

Commented [ML56]: I don't think this matter so much in this case because we look at the temperature where optimum occurs. It's not needed – I also plotted without this normalization per size-class. The only qualitative difference is then that the small size (solid line) has a higher rate value for the difference (but not the other rates) at optimum, which looks strange since it's not mass-specific rates we plot here. That's why I normalized consumption and maximum also by size-class.

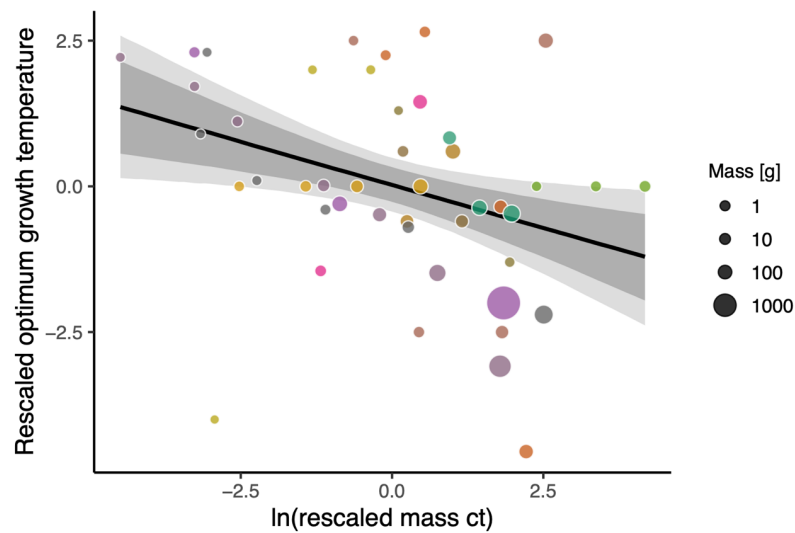


Fig. 6. Optimum temperature for growth (rescaled to optimum temperature within species) as a function of mean centered natural log of rescaled body mass (mass/maximum mass within species). Probability bands represent 80% and 95% credible intervals and solid line represent the median prediction from the average across-species effect (μ_{β_0} and μ_{β_1}). Colors indicate species ($n=13$) (see Appendix S1) and point size corresponds to mass in unit g.

Commented [Ca57]: I feel like I had this question before but can't remember if we talked about it: $\ln(M_i/\max(M_i))$ for a given species should be smaller or equal to zero – so how are there positive values?

Commented [ML58R57]: It's because they are mean-centered after that ☺ added that now!

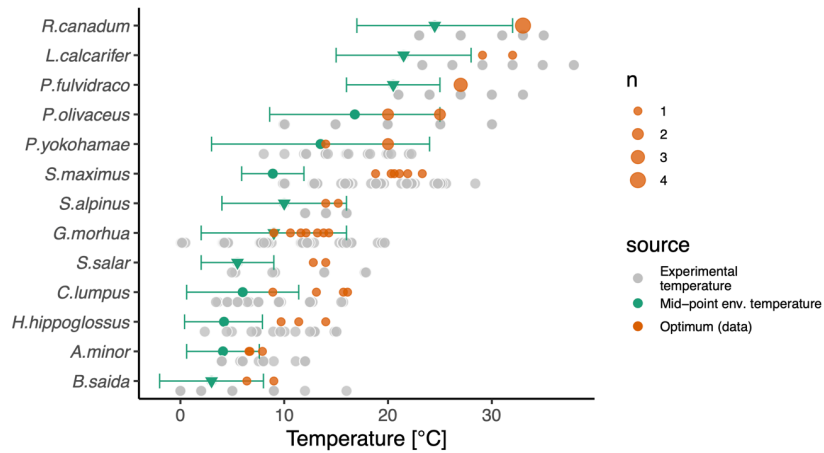


Fig. 7. Environmental temperature versus experimental and optimum growth temperature.

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. Gray points below each line indicates experimental temperatures and orange points show the optimum temperatures 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 $6.5^{\circ}\text{C} \pm 2.6 \text{ s.d.}$

Commented [ML59]: Anna: this is a colorblind friendly palette, from RColorBrewer

Discussion

Individual growth, consumption and metabolic rate represent fundamental processes in ecology, and their scaling with body mass and temperature is used to predict the effects of warming on individual growth, population and community dynamics using mechanistic models (Vasseur & McCann 2005; Rall *et al.* 2010; Cheung *et al.* 2013). 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. However, the former can result in large variation in intraspecific scaling parameters, and the latter relies on the assumption that rates scale identically within and between species, which is often not the case (Glazier 2005; Rall *et al.* 2012; Jerde *et al.* 2019). As growth, consumption and metabolic rate represent individual-level processes, it is important to understand how these rates depend on temperature and mass at the intraspecific level. We find that the optimum temperature for growth declines with body size. At temperatures below optimum, we generally find that activation energies metabolism, consumption and growth are close to predictions from the metabolic theory of ecology (MTE), which predicted mass-corrected rates to scale with temperature with an activation energy of ~ 0.6 eV. The mass-scaling exponent of metabolism is predicted to be 0.77, which is only slightly larger than $3/4$ in fish, e.g. (Clarke & Johnston 1999; Jerde *et al.* 2019). By contrast, the mass-exponent of maximum consumption is smaller than predicted by the MTE. This has implications for mechanistic models of individual growth, as well as population and food web dynamics.

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 the optimum growth temperature for an average fish decline as they in mass over ontogeny. The effect size also

Commented [Ca60]: Which meta-analyses would this be, for example?

Commented [ML61R60]: Good point! I think Glazier's 2005 paper where he collects scaling exponents from the literature is one example.

Commented [ML62]: Regarding your question Anna if MTE predicts higher activation energies of growth: well, no, but e.g. 95% credible intervals overlap 0.6, and X percent of the posterior is below, so similarly seemed like an ok description! (not identical, but not very different either!)

Commented [ML63]: Maybe state which exponents I find...

appears relatively large considering the small range of body sizes used in the experiments (a decline in T_{opt} by 0.3°C per unit increase in the natural log of relative mass, M/M_{max}). Because 73% of individuals in the experiments assembled for this study are < 1% of their maximum, the individuals in the experiments 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.

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 condition, yet these variable affect growth rates and optimum temperatures for growth (Brett *et al.* 1969). Nevertheless, the finding that large fish would be the first in a population to experience negative effects of warming suggests there might be purely physiological constraints to body growth of large fish. However, this also depends on if larger individuals within a species live closer to their thermal optimum for growth, which they may not do given that ontogenetic habitat shifts are common and could (partly) compensate for such negative effects of warmingss (see e.g. Heincke’s law (Heincke 1913; Werner & Hall 1988; Audzijonyte & Pecl 2018)). That said, there is already empirical evidence of the largest individuals being the first to suffer negative impacts of warming from e.g. heatwaves (Pörtner & Knust 2007). It is also commonly assumed that species occupy thermal habitats below their optimum for growth, as sub-optimum temperatures are in fact optimal in temperatures fluctuate (Bernhardt et al 2019). However, warming can have negative (or lack of positive) effects on populations living at the edge of their physiological tolerance in terms of growth (Neuheimer *et al.* 2011; Huss *et al.* 2019) or even survival (Pörtner & Knust 2007). This suggests that 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.

Commented [AG64]: this is true for optimum curves in general, but your paragraph (and finding) is about size-varying optima. Have a more specific conclusion/implication?

Commented [Ca65R64]: I also find this a bit too vague and complicated. Need something more specific or drop it – in fact: as you indicate above, the majority of comparisons between field data and experimentally determined thermal ranges indicates that species typically occupy thermal habitats that are below their optimum (due to variance in temperatures, hence more pronounced in temperate compared to tropical climates) – so I’m not sure this is a critical point to make, especially at end of this paragraph.

Commented [ML66R64]: I’m not sure, I think it’s a good point (but could be written differently, of course).

I mean yes it’s true for optimum in general, but size-dependent curves are just optimum curves for specific sizes. I just think it’s important to not only show it exists but talk about some implications. The major implication here is that it means rates (growth) does not increase as predicted from an exponential model – if they live close to their optimum. This is often not assumed, so it’s important to discuss that assumption.

I cut the paragraph to make it more clear, and also rewrote this section a bit, let me know if it works better now!

Interestingly, a decline in optimum growth temperature with mass is also predicted by the von Bertalanffy growth model (VBGM) $dM/dt = H(T)M^a - K(T)M^b$, where M is body mass and T is temperature), under two conditions: $a < b$ (which also is a necessity for asymptotic growth) and that growth has an optimum over temperature, as shown by (Morita *et al.* 2010b). While this is one of the most commonly applied growth models, the first condition has been debated recently. b in the classic VBGM is assumed to be proportional to body mass. This originates from the argument that maintenance should be proportional to mass, as spontaneous denaturation occurs in every cell (von Bertalanffy 1957; Pauly & Cheung 2018a) (and likely also from mathematical convenience and a lack of empirical data (Ursin 1967)). From a physiological perspective, it is more common to assume maintenance costs are proportional to standard metabolic rate (oxygen consumption of a resting and fasting organism) (Ursin 1967; Jobling 1997; Lefevre *et al.* 2017). In this case, supply and demand models of growth, such as the VBGM or the similar OGM (West *et al.* 2001), either fail to represent the physiological processes they aim to capture or fail to exhibit asymptotic growth. This is especially true if assuming a ‘universal’ mass scaling exponents of 3/4 for both assimilation and standard metabolic rate. This dichotomy can be resolved by considering the overlooked energetic investment into reproduction (and its hyper-allometric mass-scaling, i.e. exponent larger than 1) (Marshall & White 2019b), or by applying more complex energy pathways in dynamic energy budget models (Kearney 2019). This recent debate about scaling coefficients in growth models call for an investigation of the intraspecific scaling of metabolic rate in relation to assimilation or consumption. Our finding that the mass-scaling exponent of metabolism is larger than that for maximum consumption implies that “costs” for maintenance increase faster with body mass than energy assimilation – assuming no other processes such as assimilation efficiency scale in ways to counteract this. In natural systems, however, realized consumption is mediated by predator-prey encounter rates and search rates, whereas maximum

consumption rates largely correspond to the physiology of digestion (Ursin 1967). Regardless, changes in the maximum feeding capacity could result in reduced growth efficiency over ontogeny and bioenergetics models may need to account for this difference in the mass-scaling of metabolism and consumption, which is in contrast to universal mass-scaling predictions.

In addition to resolving the scaling of net energy gain (e.g. difference between energy assimilation and costs) with body mass, it is important to understand how this balance is affected by temperature. The match, or mismatch, between the temperature dependence of feeding vs. metabolic rates is a central question in experiments, meta-analyses and food web models (Vasseur & McCann 2005; 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. This is in contrast to other studies, e.g. (Lemoine & Burkepile 2012; Rall *et al.* 2012). However, it fits well with the finding that growth rates increase with temperature, which would be difficult to explain from a bioenergetics perspective if warming always reduced net energy gains.

We also find the general temperature scaling of metabolic and maximum consumption to be less uncertain than what has been reported previously (e.g. in (Downs *et al.* 2008; Englund *et al.* 2011)). A likely contributing factor is our use of hierarchal models and partial pooling to estimate higher level (across species) scaling from species-data as opposed to either aggregating all data (complete pooling) or summarizing single-species estimates (no pooling).

In contrast to the MTE, we also find that body mass can affect the temperature scaling physiological rates, which previously has been reported only for single species studies (Beamish 1964; Xie & Sun 1990; Ohlberger *et al.* 2012; Fossen *et al.* 2019) and between species (Killen *et al.* 2010). This prediction is in line with the metabolic boundary-level

Commented [AG67]: REFS for these examples? would be helpful

Commented [ML68R67]: Ref for what? I mean Downs and Englund as examples of non-hierarchical models (no pooling)

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 valued temperature replication over mass-replication), differences the body size or temperature-ranges, or that we specifically searched for studies with temperature replicates within species. The effect size of the interaction is, however, relatively small. **We do not find strong evidence for a global average of decl**The ecological implications could therefore also 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 terms (Ohlberger *et al.* 2012; Messmer *et al.* 2016; Lindmark *et al.* 2018).

While we find no clear evidence of mismatch between metabolic demands and maximum consumption induced by temperature at sub-optimum temperatures, we do find clear mismatches at higher temperatures. These are due to consumption rates being unimodally related to temperature, whereas metabolic rates increase exponentially over essentially all temperatures. **To what degree this is due to metabolic mismatch caused by the unimodal temperature-dependence of consumption vs the exponential one of metabolism (as is often argued from a conceptual point of view (Jobling 1997)) remains uncertain. This is perhaps best evaluated on a species level, given the large variation among species in their optimum temperature relative to their preferred temperature (Fig. 6).**

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 data on 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**

Commented [ML69]: Maybe check the references in the old document regarding growth. Say also what the implications for that are... cite garci Garcia and the dutch paper...

Commented [Ca70]: Not clear to me where this is going or whether it is essential for the discussion?

Commented [ML71R70]: See if the new figures can be discussed here!

Commented [Ca72]: Is this critical? If not, drop.

Commented [ML73R72]: Hmm I think it's important to link that to the first point. Otherwise people really interested in exact mass-scaling exponents, for instance, might wonder why we did not have more body masses or larger size-ranges.

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. Thus, our selection criteria leads to using a small fraction of all available data, which limits the hierarchical model structures we can consider (Jerde *et al.* 2019). 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. One approach for overcoming difficulties with these relatively small data sets is using hierarchical models (e.g. in a Bayesian framework with literature-informed priors), which can aid estimation of general scaling relationships.

Commented [AG74]: than?

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

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.

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