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

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**KEY WORDS**:

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*UPDATE ALL FIGURES*

**Abstract**

1. Understanding how temperature affects processes such as metabolism and consumption rates in ectotherms is important for predicting physiological limitations, ecological processes and trophic energy transfer in future climates.

2. To link physiological rates to ecological processes such as growth and predation we need to understand how they scale within species. , and it allows analysis of the unimodal rate-temperature relationships. However, empirical assessments of the body mass- and temperature-dependence of biological processes are usually on the between-species level, likely due to data limitations. Hence, biological rates are often assumed to scale identically within and between species, which may not be correct as different mechanisms may apply.

3. Here we search Web of Science for experimental studies on consumption and metabolic rates using a factorial body mass and temperature setup and compile a novel dataset, using fish as study taxa. We fit hierarchical Bayesian models that account for repeated measures within species and differences in regression coefficients.

4. By using a similar protocol and analysis, we are able to identify difference in the intra-specific thermal and mass-dependence of metabolism and consumption. We find clear support for mass-dependent effects of temperature on metabolism at sub-optimum temperatures but no mass-dependence in the optimum temperature. For consumption, we find the opposite pattern.

5. Based on bioenergetic principles, these findings suggest that large individuals within a species will be the first to experience negative effects of warming. Our results also highlight that progress towards unification of theory and empirical findings can be made through systematic data-analysis, which can guide process-based predictions of climate change impacts on growth and body size of ectotherms.

**Introduction**

The rate of energy acquisition and metabolic losses largely determine individual biomass production, which is a fundamental process in ecology. On the individual level, it shapes fitness and affects key life history traits such as body growth, mass and time of reproduction and maximum body mass (Barneche & Allen 2018). At the community and food web level, it affects the strength of ecological interactions, trophic transfer, community stability and size-structure (Andersen *et al.* 2009). To predict and understand individual-, population- and food web responses (e.g., through development of mechanistic and process-based models of individuals and food webs), it is important to understand how these rates scale with body mass and temperature at the appropriate scale.

It has long been recognized that metabolically driven rates vary predictable with body mass and temperature (Kleiber, 1934), and many approaches exist to statistically describe these relationships (Downs et al 2004). Because of its mechanistic basis, the metabolic theory of ecology (MTE) (Brown *et al.* 2004a) is a popular framework for linking individual metabolism to ecological processes in a bio-energetic framework (Vasseur & McCann 2005; O’Connor 2009; Brose *et al.* 2012; Gilbert *et al.* 2014; Sentis *et al.* 2017). The MTE predicts metabolism to scale in proportion to , where is body mass and is the activation energy, is Boltzmann’s constant and is absolute temperature in , based on the assumption that metabolism is limited by resource uptake and distribution (West *et al.* 1999), and that organisms typically inhabit thermal environments where rates scale with temperature exponentially. However, it is now recognized that there is no universal temperature-scaling relationship for metabolically driven rates, but that this depends on other factors, including body mass, taxonomy and life history strategy (Englund *et al.* 2011; Ohlberger *et al.* 2012; Dell *et al.* 2014; Archer *et al.* 2019). The discrepancy with the universal scaling model is perhaps most evident in intraspecific data, both in terms of variation in parameter estimates (Norin & Gamperl 2018) and functional form (Dell *et al.* 2011; Englund *et al.* 2011), as the rate-temperature relationship is typically asymmetrically unimodal (Dell *et al.* 2011; Englund *et al.* 2011). While suboptimum temperatures likely reflect average conditions for ecological processes (Brown *et al.* 2004a), and thus in general would fit the MTE equation (Dell *et al.* 2014), there are potentially important exceptions. First, even below optimum, thermal performance curves (TPCs) may not always be log-linear, which the Arrhenius-equation assumes (Englund, 2011). Second, it has been shown that sub-optimum temperatures are in fact optimal in varying environments, which makes it challenging to define the ascending part of a thermal response curve (Bernhardt et al 2019). Lastly, climate change is already causing populations at the edge of their distributions to experience lethal heat waves (Pörtner & Knust, 2007). Another observed deviation from scaling theories (including the MTE) is that body mass can affect the temperature scaling on physiological rates, both within (Beamish 1964; Xie & Sun 1990; Ohlberger *et al.* 2012; Fossen *et al.* 2019) and between species (Killen *et al.* 2010). This could lead to size-dependent thermal performance curves (e.g. body growth), with important effects on individuals and populations. This knowledge gap at the intraspecific level is likely due to the logistical challenges of replicating experiments for ranges of body masses and temperatures in a factorial setting (Jerde *et al.* 2019). Given that intra- and interspecific scaling can differ (Jerde *et al.* 2019), and that intraspecific processes and variation are important for understanding ecological dynamics (De Roos & Persson 2013), accurately describing the general intraspecific mass- and temperature dependence of biological rates is a high priority for understanding and predicting climate change impacts.

The need to understand the mechanistic basis of growth scaling is more evident now than ever, since reductions in average adult body sizes of ectotherms have been proposed as a third universal response to warming (Daufresne *et al.* 2009). Yet we know little about the mechanisms underpinning the empirical observations of temperature-size responses (Ohlberger 2013; Audzijonyte *et al.* 2018; Lefevre *et al.* 2018; Pauly & Cheung 2018). Metabolism and maximum consumption rate are key processes describing the dynamics of individual-level biomass production or body growth. This is captured in numerous models based on simple dynamic energy budget theory, including individual-level models such as Wisconsin-type bioenergetic growth models (Kitchell *et al.* 1977), to Pütter-type growth models (Ursin 1967; Essington *et al.* 2001; Marshall & White 2019) and population and food web models, such as physiologically structured population models (PSPMs) (De Roos & Persson 2001) and size-spectrum models (Blanchard *et al.* 2017). As these are examples of mechanistic models of growth – an ontogenetic process – it is important that scaling assumptions are validated on intraspecific rather than interspecific data. More accurate estimates of scaling relationships at the individual level could contribute to better understanding of this fundamental process through mechanistic models (Marshall & White 2019).

In this study, we search Web of Science to compile a dataset on 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 share information across species and account for replication within species when estimating general- and species-varying scaling parameters, both at sub-optimum and full temperature-ranges. We find clear temperature-size interactions for metabolic rates at sub-optimum temperature, and that the optimum temperature for both metabolism and consumption declines with a mass. These scaling patterns deviate from typical across-species patterns and scaling theory. Based on simple bioenergetic principles, the observed scaling of consumption and metabolism could contribute to altered growth dynamics and reduced growth potential with warming, with implications for ecological interactions and potentially trophic transfer efficiency.

**Methods**

**Data acquisition**

We searched the literature for experimental studies measuring the temperature and mass dependence of maximum consumption rate (feeding rate at unlimited food supply, *ad libitum*) and resting/standard/routine oxygen consumption rate (proxy for metabolic rate), using the Web of Science Core Collection. We also reviewed published applications of Wisconsin-type Bioenergetics models, collated in (Deslauriers *et al.* 2017). This allowed us to estimate how these rates depend on body size and temperature simultaneously using multivariate models, rather than normalizing data assuming a specific scaling with one of the predictors separately. We found in total X and Y data points from published articles on maximum consumption and metabolic rate, for X and Y species representing a diverse taxonomic, habitat and lifestyle range. We asked authors for these data in most cases, but given the age of most studies found, we also extracted the data from figures using Web Plot Digitizer (Rohatgi 2012) or from tables.

We excluded larvae-only studies to ensure that parameter estimates were representative over ontogeny. Studies were selected if (i) the original study could be found, (ii) a unique experimental temperature was recorded for each trial (), (iii) fish were provided food at *ad libitum* for consumption data and no food for resting or routine metabolic rate for metabolism, (iv) fish exhibited normal feeding behavior. We used only one study per species. While this reduces the number of data points, it ensures that all data within a given species are comparable as measurements of these rates can vary between studies due to e.g. measurement bias or differences in experimental protocols (Armstrong & Hawkins 2008; Jerde *et al.* 2019). In cases where we found more than one study for a species, we selected the study we found most suitable, based on how well it fit with our pre-defined criteria (Appendix S1). A more detailed description of the search protocol, criteria to selected data, data acquisition procedure, quality control, collation of auxiliary information and standardizing rates to common units can be found in Appendix S1 in the Supporting Information.

In order to estimate general intraspecific parameters with hierarchical models, we standardized the data as the experiments were conducted at different temperatures, both absolute and in relation to average temperatures for that species. This was done by subtracting the experimental temperatures with a representative temperature of the species natural environment. We used the median temperature in the environments of the respective species distribution using information available in FishBase (Froese & Pauly 2016) (<https://fishbase.org/>). When this information was missing, we used other comparable metrics (e.g. median preferred temperature or temperature of spawning habitat) (Appendix S1). The body masses used in the experiments also correspond to different life stages. Hence, we standardized all body-mass data by dividing it with the asymptotic mass, also taken from FishBase. In the regression models presented below, body mass and temperature thus always correspond to mean-centered and standardized values.

**Data analysis**

*Below optimum temperatures*

Below optimum temperatures (i.e., a subset of the data sets including only data points for a given size-group that were below the temperature at which the rate was maximized), we assumed metabolic and maximum consumption rate to scale with size using a generalized version of the core equation in the metabolic theory of ecology (Gillooly *et al.* 2001; Brown *et al.* 2004b). This allowed us to evaluate the effects of temperature and body mass simultaneously, which is more appropriate if the mass-scaling exponent is not exactly 3/4 (Downs *et al.* 2008) and also to evaluate interactive effects of size and temperature (Ohlberger *et al.* 2012; Lindmark *et al.* 2018). We thus assumed rate (metabolism or maximum consumption) scale with mass and temperature as:

, (1)

which on normal scale becomes:

, (2)

where is the intercept, is the mass-scaling exponent when , is the interaction coefficient, is the activation energy, and is Boltzmann’s constant in (). We estimate these parameters using hierarchical models with different combinations of group (species)-varying coefficients (Table 2) and select the final model using widely applicable information criterion (WAIC) (Vehtari *et al.* 2017). The full model with uncorrelated species-varying intercepts, mass-, temperature- and interaction- coefficients, can be written as:

(3)

, (4)

with the following second level (species) models, where (:

, (5)

where is the th observation of the natural log of the rate (metabolism or consumption) for species , is the natural log of body mass relative to asymptotic mass and is standardized temperature (mean environmental temperature subtracted from the median environmental temperature, both on Arrhenius temperature scales: ). Both predictors are mean centered.

*Full temperature range*

To the full data set we instead fit polynomial models, as in (García García *et al.* 2011), because it includes data points beyond optimum temperatures. We consider two models of in Eq. 3 (with and without interaction. ) with the full data set. These models with species varying coefficients can be written as:

(6)

or:

, (7)

where the term () allows the optimum temperature to vary with mass. The second level models with the following second level (species) models, where (:

, (8)

Note that here here refers to the natural log of data normalized to the max rate value within species to reduce the variation between species, is centered and standardized temperature on Celsius scale.

*Model fitting*

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 (<https://github.com/stan-dev/stan/wiki/Prior-Choice-Recommendations>) (Table 1). We used 3 Markov chains with 10000 iterations each, following on 10000 iterations burn-in and 5000 for adaptation. Model convergence was assessed by visually inspecting trace plots (Appendix S1) and by ensuring , suggesting 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.

Table 1 Description of model parameters and their prior distributions

|  |  |  |  |
| --- | --- | --- | --- |
| Model | Parameter | Description | Prior distribution |
| Log-linear regression (Eqns. 3-5) |  | Hyperparameter (intercept) |  |
|  | Hyperparameter (mass exponent) |  |
|  | Hyperparameter (activation energy) |  |
|  | Hyperparameter (interaction) |  |
|  | Hyperparameter (intercept variance) |  |
|  | Hyperparameter (mass exponent variance) |  |
|  | Hyperparameter (activation energy variance) |  |
|  | Hyperparameter (interaction variance) |  |
|  | Variance |  |
| Polynomial  (Eqns. 6-8) |  | Intercept |  |
|  | Mass coefficient |  |
|  | Temperature coefficient |  |
|  | Quadratic temperature coefficient |  |
|  | Interaction coefficient |  |
|  | Variance |  |

**Growth models**

To exemplify the effects of the mass- and temperature-dependence estimated from the experimental studies, we apply a generic Pütter-type growth model of the form: , where is body mass and the first term is assumed proportional to maximum consumption rate and the second to metabolic costs (Ursin 1967). Parameters , , and can be derived theoretically (e.g. based on geometry (von Bertalanffy 1957) or the MTE (West *et al.* 1997)) or empirically (Ursin 1967) and we choose the latter here to link it to our data analysis. This growth model has an asymptote at (Ricklefs 2003), thus, declines with warming if and/or declines with warming.

**Results**

Table 2 Model selection for the log-linear regressions of how consumption and metabolism depend on mass and temperature (below optimum temperature). M1 is the full model and is described in text (Eqns. 3-5). Values in bold indicated the model selected based on the Widely Applicable Information Criterion (WAIC).

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Model | M\*T | Species-varying parameter | WAIC consumption | WAIC  metabolism |
| M1 | Yes |  | 530.9 | **290** |
| M2 |  | 528.62 | 290.25 |
| M3a |  | 674.66 | 626.95 |
| M3b |  | 588.24 | 681.28 |
| M4 |  | 710.46 | 973.36 |
| M5 | No |  | **527.64** | 294.28 |
| M6 |  | 712.1 | 971.2 |
| M7 |  | 1931.92 | 7988.26 |
| M8 |  | 2094.1 | 9523.1 |

Table 3 Model selection for the polynomial model of how consumption and metabolism depend on mass and temperature (including optimum temperature). M1 is the full model and is described in text (Eqns. 3-5). Values in bold indicated the model selected based on the Widely Applicable Information Criterion (WAIC).

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Model | M\*T | Species-varying parameter | WAIC  consumption | WAIC  metabolism |
| M1 | No |  | **942.63** | **901.4305** |
| M2 |  | 1363.59 | 4779.198 |
| M3 | , | 1258.1 | 5951.29 |
| M4 | Yes |  | 945.6 | 903.1162 |
| M5 |  | 1366.11 | 4781.286 |
| M6 | , | 1253.43 | 5942.267 |
| M7 |  | 1371.52 | 6184.961 |

**Figures**

A picture containing text, map

Description automatically generated

**Figure 1.** Natural log of metabolic rate (A) and maximum consumption rates (B) vs. natural log of standardized mass. Lines correspond to predicted average scaling relationships from the hierarchical model for two temperatures: warm (green) and cold (purple). Shaded areas correspond to 80% and 95% credible interval.

A close up of a device

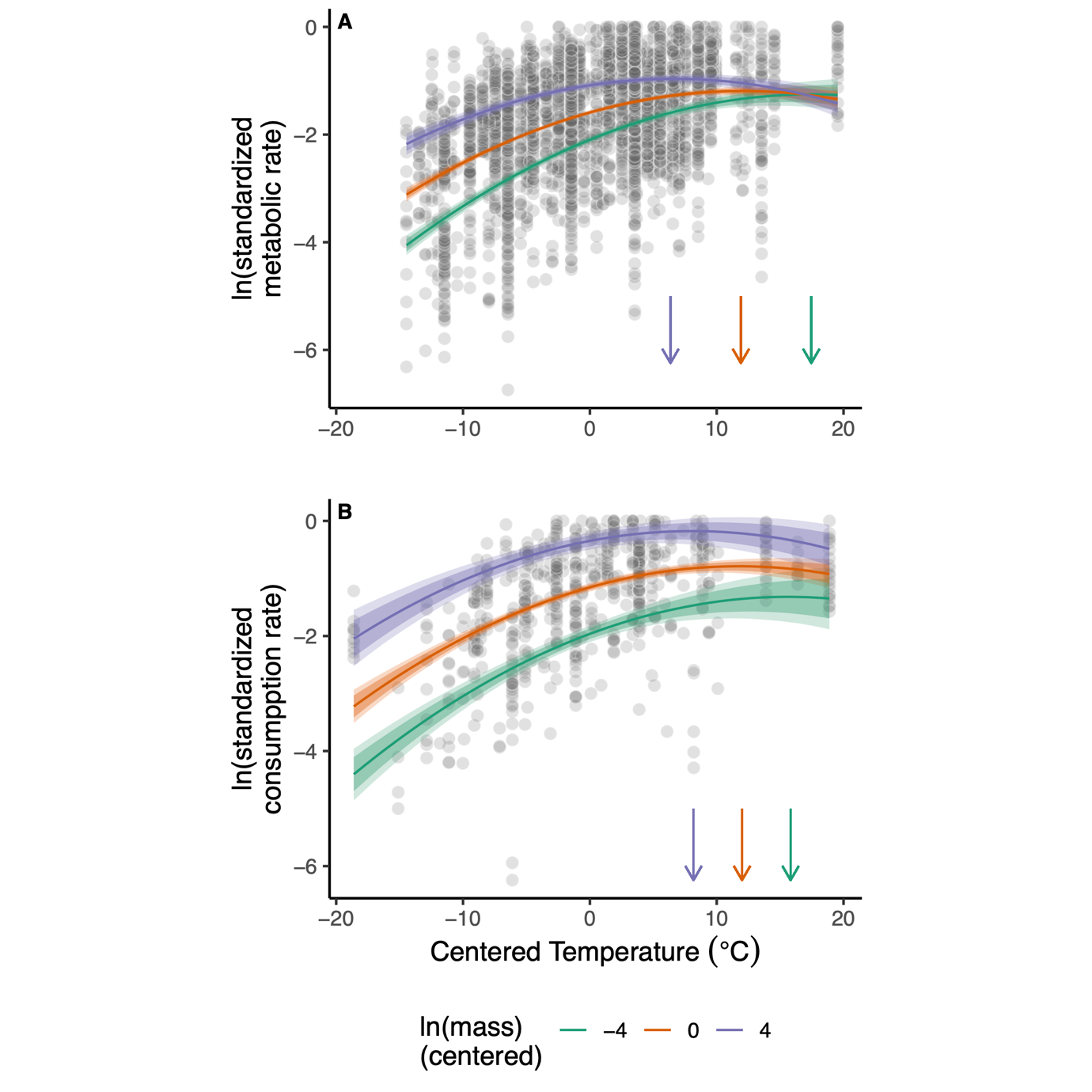
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**Figure 2.** Posterior medians of species-varying activation energies and mass-scaling exponents from the hierarchical model (triangles) fitted to below temperature optimum data, and their 80% and 95% credible interval. Vertical dashed lines correspond to the mean prediction for a general species and the shaded area correspond to the 95% credible interval of the mean prediction.

A picture containing boat, text, map

Description automatically generated

**Figure 3.** Posterior distributions of the grand mean parameters for how metabolic rate (top row) and maximum consumption rate (bottom row) scale with mass and temperature when fitted to below optimum temperature data. Text in top left corner corresponds to the median. Note that the final model for maximum consumption rate did not include a mass-temperature interaction term.



**Figure 4.** Natural log of normalized (0:1 within species) metabolic rate (A) and maximum consumption rate (B) vs. temperature (mean centered and on Celsius scale) from the full data, which includes beyond optimum temperatures. Lines correspond to predictions from polynomial models for three different values of mean-centered natural log of body masses relative to asymptotic masses, within species. Shaded areas correspond to 80% and 95% credible interval. Arrows indicate the optimum temperature (where the ln normalized rates are maximized for each relative body mass).

A screenshot of a cell phone

Description automatically generated

Figure 5. Surface depicting proportional change in asymptotic mass between 10 and 12 predicted by a general Pütter-type growth model, as a function of the decline in mass-scaling exponent per unit temperature (parameter in Eqns. 1-2). The dashed line corresponds to the zero-change isocline. Points indicate where species with data on both rates are mapped onto this space, based on their species-specific parameters estimated using the log-linear regression model.

**Results**

\*I have not gotten so far as to write the results, but I will write them similarly as in the growth paper I think, i.e. in order describe the figures and give examples of predictions and their probability for some specific cases.

For now, I will summarize/interpret/discuss the results figure by figure:

1. We find an interaction for metabolism but not for consumption rate, however it’s very small. This can be seen in the posterior figure (#3). It can also be seen in the very small difference in slopes in Fig. 1. Overall the interaction term is smaller than in some other intraspecific single species studies.

(At this point, if we assume that metabolisms and consumption can be viewed as costs and gains, average intraspecific scaling of consumption and metabolism does not suggest warming introduces constraints on growth. In fact, the opposite, as the “cost” mass-exponent declines with warming. This would suggest an increase in asymptotic mass.)

1. Here we show that the mass-scaling exponent of consumption is smaller than that of metabolism. This supports the growth models we discuss here (in that there \*is\* an asymptotic body mass, so the bar is pretty low). We also show that the activation energies are by large similar, and the prediction (median) is that the value for consumption is actually larger (absolute value).

(Again, this does not cause shrinking in the model but the opposite, same as the result from the c-effect in Fig. 1)

1. This could perhaps go into the appendix, but it shows the uncertainty around the global estimates, including the interaction term which isn’t in Figure 2.
2. Ok, this is a bit interesting. Both rates show unimodal relationships over the full temperature range, and for both rates a model is selected that have size-dependent temperature optima. Also, it’s sometimes said that the optimum for metabolism is much higher than intake (e.g. Jobling 1997) and therefore can be approximated by an exponential curve. This doesn’t really show that, although to really say that I should make a prediction and get a credible interval around the predicted T when the derivative is 0.

(Still no shrinking here! The optimum for consumption would have to be at lower temperatures than metabolism for that to occur!)

1. So far none of our results have supported the conditions that lead to smaller sizes ( and/or declining with warming). In this figure, we show the change in asymptotic mass assuming identical activation energies and general parameters, the only thing changing here is the species -effect. Now, I have not been able to update this figure yet, but so far, the species we have fall below the zero-change isocline, i.e. a shrinking! Will this hold when I update it with more species? I do not now but I’m very curious to see, as the other results do not predict this. When I update this figure, I will also look into the parameters and functional forms. We might want to try different combinations, e.g. unimodal vs exponential etc. Currently though I’m using the most generic parameterization to bring out the effect of .

In conclusion: some mixed results here. My plan is to first get feedback from you. Then finalize the growth analysis (update the heat map with the new species) AND perform sensitivity analysis like I did in the growth paper, where I compared different ways of standardizing body mass (maturation vs asymptotic mass). Hopefully I will have that before the meeting, so that we can discuss what kind of paper this will be with all (most) results in hand…

**Discussion**

Key discussion points:

* Recap what’s new and how that relates to question
* What does this mean in terms of scaling? General for other species e.g. ectotherm? Here I can also cite papers that I couldn’t take data from but that support our findings
* What does this mean for mechanistic models (Putter, bioenergetic)? Does this suggest that mechanistic models (most/all of which are based on growth being constrained by biomass production, in turn constrained by decreasing net biomass production over mass, are fairly limited in what they can predict about empirical growth patterns? I.e. these models \*can\* be parameterized in a way that gives certain predictions (fast growth, smaller max size), but that’s not what we find in the data. One conclusion is then that other processes are perhaps quite important for the growth trajectory.
* Limitations. there are many. One is that the fish we look at are quite small in general… perhaps we can’t detect any negative effects of temperature in this size range.

**Author contributions**

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

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