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

Max Lindmarka,1, Jan Ohlbergerb, Anna Gårdmarkc

a Swedish University of Agricultural Sciences, Department of Aquatic Resources, Institute of Coastal Research, Skolgatan 6, Öregrund 742 42, Sweden

b School of Aquatic and Fishery Sciences (SAFS), University of Washington, Box 355020, Seattle, WA 98195-5020, USA

c Swedish University of Agricultural Sciences, Department of Aquatic Resources, Skolgatan 6, SE-742 42 Öregrund, Sweden

1 Author to whom correspondence should be addressed. Current address:

Max Lindmark, Swedish University of Agricultural Sciences, Department of Aquatic Resources, Institute of Coastal Research, Skolgatan 6, Öregrund 742 42, Sweden, Tel.: +46(0)104784137, email: [max.lindmark@slu.se](mailto:max.lindmark@slu.se)

**KEY WORDS**:

**WORD COUNT**:

Abstract: ~260

Introduction: ~1375

Methods: ~1693

Results: ~786

Discussion: ~1400 (missing one section currently)

Total: ~ 3900

**Abstract**

1. Warming of aquatic communities is generally predicted to increase 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 estimates of intraspecific scaling of key processes such as metabolism and consumption. This limits our ability to link experimental data to empirical patterns of growth as well as developing growth models.
2. To estimate the effect of body size and temperature on growth, and to examine the link between growth and metabolic- and maximum consumption rates, we performed a systematic review and collated experimental data on these rates. We used only studies with body mass and temperature treatments and fit hierarchical models to evaluate how these rates scale with jointly with mass and temperature within species, while accounting for variation between species.
3. We find clear support for a declining optimum growth temperature with body mass within species, and a positive effect of warming on growth rates. We find mass-dependent effects of temperature on metabolism at sub-optimum temperatures but not for consumption, and that activation energies at sub-optimum temperature generally conform to theoretical predictions while mass-scaling does not.
4. Thus, small individuals within a species will likely be able to increase their growth rates with initial warming and that larger individuals will first experience deleterious effects of warming on growth. Size-dependent changes in growth dynamics due to climate warming may have implications for the structure and functioning of future aquatic ecosystems.

**Introduction**

Individual body growth is a fundamental process that 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.* 2009a; Barneche & Allen 2018). Therefore, understanding not only how body growth scales with body size and temperature but also the underlying processes affecting growth rates, 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; Forster *et al.* 2012a), as well as latitudinal gradient studies of insects (Horne *et al.* 2015), and is stronger in aquatic than terrestrial environments. The underlying mechanisms are not well understood, but are likely results of interplay between ecology and physiology (Ohlberger 2013a; Audzijonyte *et al.* 2018; Neubauer & Andersen 2019). However, the empirical examples identifying climate signals in time series of growth trajectories are accumulating. For instance, reconstructed growth histories of individual fish through ageing based on bony structures (otoliths) often show positive correlations between growth rates and warming (Thresher *et al.* 2007; Neuheimer *et al.* 2011; Baudron *et al.* 2014; Huss *et al.* 2019). This increased growth can also be predicted from numerous experimental studies showing that at intermediate temperatures, growth increases with temperature until a peak is reached, after which additional warming is deleterious (Brett *et al.* 1969; Elliott & Hurley 1995; Jobling 1997; Morita *et al.* 2010; García García *et al.* 2011). Less clear however is the negative effect of warming on the growth or body size of large fish. Time series of asymptotic or maximum body mass have shown negatively correlations with temperature (Baudron *et al.* 2014; van Rijn *et al.* 2017). However, a contributing factor could be that these examples stem from commercially exploited species and fishing disproportionally targets large fish. In a large scale semi-natural heating experiment, only small fish of a non-exploited species increased their specific growth rates with warming and the growth of larger fish was comparable to the non-heated control area. The lack of clear relationship between asymptotic or large fish size and temperature was also found in an experiment of ontogenetic growth (Barneche *et al.* 2019). Predictions about declines in asymptotic body mass have also been made from theoretical growth models (Pauly & Cheung 2018). However, the physiological mechanisms in these models (e.g. oxygen-limitation) have been questioned, both for the cause of asymptotic growth curves in the first place (resource limitation) (Marshall & White 2019a) and the mechanism for why warming leads to smaller asymptotic sizes (Lefevre *et al.* 2017). As empirical findings differ and theoretical predictions are questioned, is still remains unclear to which extent the growth of large fish within a population is limited by warming from purely physiological constraints (e.g. when accounting for other factors such as food availability. More accurate predictions about the effect of body size and temperature on growth from controlled experimental studies can aid both the development of theoretical growth models as well as providing predictions about the effect of temperature on growth. This includes also the scaling og key processes affecting growth, such as metabolic- and consumption rates.

The specific growth rate of a non-reproducing individual can be represented as the difference between energy acquisition and expenditure (von Bertalanffy 1938; Kitchell *et al.* 1977; Jobling 1997). Energy acquisition or assimilation is typically the amount of food consumed multiplied with a coefficient describing the available nutrients in the food. Expenditure is defined as fasting, activity and feeding metabolism. These different metabolic processes are in turn usually assumed to be proportional to resting metabolism, 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 models dynamic energy budget models (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 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 on average scale with body size and temperature. This scaling should ideally be at the intraspecific level rather than interspecific level to better represent the individual-level processes, as these can differ (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 representing individual processes. In addition, the temperature- and mass dependence of metabolism and other related rates are also often assumed to follow the mass-scaling model by (West *et al.* 1999) coupled with the Boltzmann-Arrhenius model (Gillooly *et al.* 2001), in the metabolic theory of ecology (Brown *et al.* 2004). This model, henceforth referred to as the Arrhenius fractal supply model (AFS), provides predictions from first principles and is therefore often empirically evaluated (Gillooly *et al.* 2001; Downs *et al.* 2008). The AFS assumes that metabolically-driven rates () (individual growth, metabolism and consumption), to scale as: , where is the activation energy, is Boltzmann’s constant and is temperature in Kelvin. Importantly, the model assumes mass-scaling of ¾ when estimating temperature effects, as well as independent effect 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 body mass and temperature can have interactive effects (Xie & Sun 1990; García García *et al.* 2011; Ohlberger *et al.* 2012; Lindmark *et al.* 2018). Moreover, while the AFS does tend 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)), thermal response curves are generally unimodal in intraspecific data (Dell *et al.* 2011; Englund *et al.* 2011; Rall *et al.* 2012). These assumption-violations, and model misspecifications, could affect the estimates of temperature-dependencies. Instead of mass-correcting according to the AFS, it could be more appropriate to fit multivariate models where coefficients are estimated jointly (Downs *et al.* 2008), or define models that can capture the negative rate-temperature relationships at higher temperatures (Dell *et al.* 2011; Englund *et al.* 2011). Overall, average intraspecific scaling is less understood, and contributing factors could be the logistical challenges of replicating experiments for ranges of body masses and temperatures in a factorial setting (Jerde *et al.* 2019) and due to the lack of comprehensive data bases (Dell *et al.* 2011). This appears to be especially true for consumption and growth rates. Inference about scaling parameters are therefore often limited to few detailed experiments, which makes inference about average intraspecific scaling across species difficult. However, individual-level processes shape ecological dynamics and structure (Andersen *et al.* 2009b; De Roos & Persson 2013), and therefore overcoming the knowledge gap about intraspecific scaling is highly warranted.

In this study, we performed a systematic literature review using search Web of Science core search to compile a dataset on individual growth rates, consumption and metabolic rates of fish from experiments in which the effect of fish body mass is replicated across multiple temperatures within species. To acquire both general and species-specific scaling, we fit hierarchical Bayesian models to account for variation between experiments or species and also to acquire general intraspecific scaling predictions based on partial pooling of data across species to minimize the influence of extreme observations. For maximum consumption rates, we also fit quadratic models to a subset of the data to characterize the unimodal temperature dependence. We find scaling patterns deviate from typical across-species patterns and scaling theory.

**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/standard/routine oxygen consumption rate (proxy for metabolic rate (Nelson 2016)), using three different searches on the Web of Science Core Collection. From the growth rate data search, we also compiled a data set containing the optimum growth rate temperature for each combination of body mass group and species. 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 a size- or temperature treatment), it allows us to fit multivariate models and fit the effects of mass and temeprature jointly rather than fixing one effect, as well as evaluate the probability if interactive effects within species. We found in total X, Y and Z data points from published articles on growth rate, maximum consumption and metabolic rate, for X, Y and Z 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 and growth data, no food for resting or routine metabolic rate for metabolism, (iv) fish exhibited normal behaviour. 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. 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 pool data across species. However, species differ in their body masses (both in absolute values and relative to their maximum body size), and in their experimental temperature (both in absolute values and relative to their mean environmental temperature) (Fig SX – add also distribution of relative mass by species). Therefore, we standardize our predictor variables by species. This was done by expressing temperature as the difference between the experimental temperature and the median environmental temperature. We used the median temperature in the environments of the respective species distribution using information available in FishBase, extracted between 2019.06.01-2019.12.01 (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). For the model of optimum growth temperature, as the difference between optimum temperature for each size-class and the mean optimum temperature across all body size classes of that species. For the analysis of mass-dependence of optimum growth temperature within species, we use relative mass as a predictor, as we are interested in examining relationships within species while accounting for variation in relative body masses between experiments. Relative mass is here body-mass data by dividing it with the maximum body mass by species, based on literature estimates, also taken from FishBase (extracted between 2019.06.01-2019.12.01). More detailed definitions of standardized variables are given below each model in the following sections.

**Model fitting**

*Mass-dependence of optimum growth temperature*

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

(1)

, (2)

, (3)

Here is the rescaled optimum temperature within species : to account for variation in the actual optimum growth temperature between species. is the natural log of body mass divided by the maximum body mass within species, in , defined as . In Eq. 3, the subscript referes to parameter (0 for intercept and 1 for slope). All predictor variables are in addition mean-centered, such that 0 corresponds to the overall mean (not by species). We also fit a model with non-varying mass-coefficient (i.e. , not indexed by ), and selected the best model based on predictive out-of-sample accuracy using the Widely Applicable Information Criterion (WAIC) (Vehtari *et al.* 2017).

*Scaling of growth, metabolism and consumption with temperature below optimum*

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 individual growth, metabolic rate 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.* 2004), in which neither the mass- or temperature dependence is assumed and corrected for. 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), which it not always is (Sibly *et al.* 2015; Jerde *et al.* 2019) and also to evaluate interactive effects of size and temperature (Ohlberger *et al.* 2012; Lindmark *et al.* 2018). We thus assumed rate (growth, metabolism or maximum consumption) scale with mass and temperature as:

, (4)

which on normal scale becomes:

, (5)

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 body mass and temperature coefficients (representing the mass-scaling exponent and activation energy, respectively) using hierarchical models with different combinations of group (species)-varying coefficients and select the final model using WAIC. The full model with uncorrelated species-varying intercepts, mass-, temperature- and interaction- coefficients, can be written as:

(6)

, (7)

, (8)

where is the th observation of the natural log of the rate (growth, metabolism or consumption), and indexes regression coefficient (. In Eq. 7, is the mean-centered natural log of body mass in unit by species (), and is standardized temperature on Arrhenius scale, defined as ), where Arrhenius temperature is defined as in Kelvin. For the analysis of growth rates, refers to natural log of the geometric mean of the initial mass and final mass of the growth experiment, unless stated otherwise (Appendix S1). All predictor variables are in addition mean-centered, such that 0 corresponds to the overall mean (not by species). We select our final model using WAIC.

*Scaling of consumption rates with temperatures including optimum*

As biological rates are unimodal over a large enough temperature range, we fit polynomial models to a subset of the maximum consumption data containing only species with data points beyond the temperature at which the rate is maximized, by species (Dell *et al.* 2011; Englund *et al.* 2011). No clear optimum curves were indicated in the metabolic rate data. 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 optimum-data to a common scale, as species have different consumptions rates at optimum temperature, different widths of the thermal performance curves and different optimum temperatures. By fitting models by species, we thus remove the risk of removing true effects in data, at the cost of benefits of the hierarchical model for inferring general intraspecific scaling. The model of is for the full data set defined as:

(9)

(10)

where in Eq. 9 refers to consumption rates divided by the mean rate value by species (), in Eq. 10 is mean-centered natural log of body mass in unit by species (, i.e. not normalized to maximum body mass as we fit this model by species) and is mean-centered standardized temperature by species, where the standardized temperature is defined as ().

For illustrations of model fits, we predict over the temperature range of the data for species while keeping body mass at 0 (corresponding to the mean mass across each species in ) (Fig. SX). The species predictions and data are plotted together in Fig. X, to illustrate the spread in optimum temperature measured as distance to environmental median. We also illustrate model fits by rescaling both data and predictions to the maximum predicted rate within species and subtract the optimum temperature from each temperature and add the overall mean optimum temperature, as in (Englund *et al.* 2011) (Fig. SX). Due to general data limitation we did not fit an interaction term which alters the optimum temperature by mass, however this has been identified in data-rich 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 (<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 and by ensuring (Appendix S1), which 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.

**Table 1** Description of model parameters and their prior distributions

|  |  |  |  |
| --- | --- | --- | --- |
| Model | Parameter | Description | Prior distribution |
| Linear model  (Eqns. 1-3) |  | Hyperparameter (intercept) |  |
|  | Hyperparameter (mass coefficient) |  |
|  | Hyperparameter (intercept variance) |  |
|  | Hyperparameter (mass coefficient variance) |  |
|  | Variance |  |
| Log-linear regression (Eqns. 6-8) |  | Hyperparameter (intercept) |  |
|  | Hyperparameter (mass exponent) |  |
|  | Hyperparameter (activation energy) |  |
|  | Hyperparameter (interaction) |  |
|  | Hyperparameter (intercept variance) |  |
|  | Hyperparameter (mass exponent variance) |  |
|  | Hyperparameter (activation energy variance) |  |
|  | Hyperparameter (interaction variance) |  |
|  | Variance |  |
| Polynomial  (Eqns. 9-10) |  | Intercept |  |
|  | Mass coefficient |  |
|  | Temperature coefficient |  |
|  | Quadratic temperature coefficient |  |
|  | Variance |  |

**Results**

The temperature at which optimum growth is achieved declines with body size declines with per unit increase in the natural log of relative body mass (Fig. 1). This decline in optimum temperature with mass is clear, as 99% of the posterior density of the slope estimate () is below 0. The selected model contains a species-level effect on the intercept () and a common slope across species ().

At below optimum temperatures, we find that the average intraspecific size-and temperature dependence of specific growth across-species can be described by the equation: . The model with best fit to data contains a body size-temperature interaction (Table 2). However, the predicted value of the interaction is close to 0 (only 55% of the posterior density is above 0), and the 95% intervals around the WAIC value (assuming a z-score of 1.96) are largely overlapping (, . We therefore find that mass-temperature interactions are not evident in data and only slightly improves fit, and thus exemplify the growth scaling predictions from model M5, which assumes independent but species-varying mass- and temperature coefficients. We estimate the (relative) mass-scaling exponent of growth, i.e. the mass-coefficient on log-log scale, to be to be [] (brackets indicate 95% Bayesian credible intervals). We estimate the activation energy, , (coefficient to the relative Arrhenius temperature, ) to be [], which is lower than what is typically found for metabolic rate, i.e. more temperature-sensitive (Downs *et al.* 2008) and growth based on field data (Sibly *et al.* 2015). To illustrate this in terms of specific growth (normal scale), an increase in relative temperature from approximately +to (relative to median environmental temperature) increases growth rates by a factor of 86% for a fish of with a mass of 30g (corresponding to the overall mean mass in data).

We find that the average intraspecific scaling of whole-organism metabolic rate can be described by the equation: , and consumption rate as: (See Fig. 3 a general intraspecific prediction for a given mass and two temperatures). Some notable differences exist in the scaling of these two rates. First, metabolic rate scales with a larger mass-scaling exponent ( []) than maximum consumption ( [), inferred from non-overlapping Bayesian 95% credible intervals (indicated in square brackets) (Fig. 4). This difference implies that metabolic processes increase faster with body mass than maximum consumption rates, and that both differ from the predicted mass-scaling exponent from the metabolic theory of ecology. We also find that maximum consumption rate is more temperature sensitive than metabolism when measured at temperatures below optimum. The activation energy for metabolism is estimated to be [] and for maximum consumption rate we estimate it to: ([]). However, this difference is less clear than the mass-exponents, as can be inferred from the overlapping credible intervals, partly due to the larger uncertainty of the temperature sensitivity of consumption (Fig. 4). In addition, both fall within within the prediction from the MTE (0.6-0.7 eV) (Brown *et al.* 2004). This implies that at temperatures below optimum, maximum consumption rates on average faster with temperature than metabolic rates. We also found support for a negative interaction between body mass and temperature (99.7% of the posterior distribution of is above 0, Fig, 5). However, the effect size is relatively small. We estimate it to be on an Arrhenius temperature scale, which on a Celsius temperature scale corresponds to a decline in the mass scaling exponent of metabolic rate by 0.002. In the selected model for consumption all coefficients vary by species whereas for the models of metabolism, all but the interaction coefficient varies by species (Table 2).

Over a larger temperature range, biological rates tend to be unimodal. We identified such tendencies in 9 species in the consumption data set, and fit polynomial models to 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 metabolic costs-feeding gains mismatch depends on the current temperature relative to optimum. However, when standardizing the temperature data to a common unit, here relative to median temperature in the environment to overcome that experiments are performed at different temperatures relative to the species’ preferred temperature, we find large variations in the temperature at which consumption is maximized (“optimum”) (Fig. 6). These temperatures range from -2.3 to +17, in units median environment temperature subtracted from optimum temperature, by species (i.e. , in Celsius). Across species, the mean in intraspecific is 6 in the same unit (with a standard deviation of 6).

**Table 2**. Model comparison for the log-linear regressions of how consumption, metabolism and growth scale with mass and temperature (below optimum temperature). M1 is the full model and is described in text (Eqns. 3-5). The WAIC columns shows dWAIC (WAIC, SE), where dWAIC is the difference between each models’ WAIC and the lowest AIC across models, and SE is the standard error of the WAIC (calculated as the square root of the product number of observations and the variance of individual observation’s WAIC). Bold indicates best fitting model (lowest WAIC).

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Model | M\*T | Species-varying parameter(s) | WAIC consumption | WAIC  metabolism | WAIC growth |
| M1 | Yes |  | 2.9 (530.9, 103.3) | 0.7 (289.5, 120.4) | **0 (35.5, 31.5)** |
| M2 |  | 0.9 (528.6, 102.3) | **0 (288.8, 120.5)** | 3.9 (39.4, 32.1) |
| M3a |  | 132.3 (674.7, 101.7) | 298 (586.9, 118) | 35.3 (70.8, 31.4) |
| M3b |  | 60.5 (588.2, 88.8) | 392.4 (681.2, 110.3) | 43.8 (79.3, 31.3) |
| M4 |  | 168 (710.5, 91) | 646.3 (935.2, 109.2) | 65.9 (101.2, 31.9) |
| M5 | No |  | **0 (527.6, 102.6)** | 6.1 (294.9, 121.1) | 0.9 (36.3, 32.3) |
| M6 |  | 185 (712.1, 93.5) | 682.2 (971.1, 109.7) | 63.1 (98.6, 31.7) |
| M7 |  | 598.6 (1931.9, 59.1) | 4002.7 (4291.6, 143.2) | 171.5 (206.9, 25) |
| M8 |  | 822.4 (2094.1, 48.2) | 10662.5 (10951.3, 111.4) | 187.9 (223.4, 19) |

**A screenshot of a cell phone

Description automatically generated**

**Fig. 1**. *Optimum temperature for growth (standardized to optimum temperature within species and mean-centered) as a function of natural log of standardized body mass (mass/maximum mass within species). Probability bands represent 80% and 95% credible intervals and solid line represent the median prediction from the average across-species effect ( and ).*

A close up of a map

Description automatically generated

**Fig. 2**. *Effects of temperature and body mass on growth depends A) Growth rate [% day-1] as a function of body mass, both on natural log scale. Lines are mean marginal predictions at temperatures -0.75 and 0 in unit mean-centered Arrhenius temperature standardized to median environmental temperature, which is approximately median environment temperature +10 and +5 respectively. Shaded areas correspond to 80% and 95% credible interval and the solid line is the median prediction from the average across-species effect ( and ). The slope corresponds to the mass-scaling exponent. Posterior distributions of mass-scaling exponent (B) and activation energy (C) are shown in the bottom row. The dashed white line shows the posterior median.*

A close up of a map

Description automatically generated

***Fig 3****. Natural log of metabolic rate (A) and maximum consumption rates (B) vs. natural log of standardized mass. Shaded areas correspond to 80% and 95% credible interval and the solid line is the median prediction from the average across-species effect ( and ) for two temperatures on Arrhenius scale: warm (red) and cold (blue), which is approximately the median environment temperature +10 and +2.5 respectively*

A screenshot of a cell phone

Description automatically generated

***Fig. 4****. Posterior medians of species-varying activation energies and mass-coefficients from the hierarchical model fitted to below temperature optimum data, and their 80% and 95% credible interval. Vertical dashed lines correspond to the median prediction for a general species (i.e. and for the mass and temperature coefficient, respectively). The shaded vertical area corresponds to posterior median of the posterior median.*

A close up of a map

Description automatically generated

***Fig. 5*** *Posterior distributions of the between-species average intraspecific parameters () for metabolic rate (top row) and maximum consumption rate (bottom row). Text in top left corner corresponds to the posterior median. Note that the final model for maximum consumption rate did not include a mass-temperature interaction term. The scale is the same within parameters across rates for comparison.*

A close up of a map

Description automatically generated

***Fig. 6****. Standardized maximum consumption rates (relative to mean within species) as a function of temperature from the data subset containing only species with data points at temperatures higher than where the rate is maximized (“optimum”). Points show data and lines are predictions from the polynomial model where the centered body mass is held at 0 (corresponding to mean mass within species), by species (indicated by color). The shaded areas show 80% credible interval for the median prediction. Arrows depict the optimum temperature for each species, in units “difference from median environmental temperature”, and the vertical dashed and dotted lines correspond to the mean optimum temperature 1 standard deviation.*

**Discussion**

The scaling of individual growth, consumption and metabolic rate with 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). It is common to inform scaling relationships from either single-species studies or interspecific relationship. However, meta-analytical approaches of multiple single species studies can reveal large variation in intraspecific scaling parameters, and former can, and the latter relies on the assumption that rates scale identically within and between species, which is often found not to be the case (Rall *et al.* 2012; Jerde *et al.* 2019).

While suboptimum temperatures likely reflect average conditions for ecological processes, 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).

This estimate is very similar to the estimated in (Barneche *et al.* 2019).

Rall, Dell Englund and Ecology paper – what do they say about scaling? What do I say that differs? What does it mean for growth?

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.

We have shown that temperature affects body growth rates of fishes differently depending on their body mass, through 1) small changes in the mass-scaling exponent 2) clear declines in optimum growth temperatures with body size. These results mean that smaller individuals within a population may benefit more in terms of faster growth rates with, but this potential to capitalize on warming declines with body size.

The empirical observation that higher temperatures lead to faster development and smaller adult body sizes within species (“temperature-size rule”, TSR) (Atkinson 1994; Daufresne *et al.* 2009), has fueled research into climate-driven changes in growth trajectories of also fish - especially since TSR-effects are predicted to be stronger in aquatic systems (Forster *et al.* 2012b; Horne *et al.* 2015). Studies on changes in individual growth trajectories typically utilize time series of age-at-length or catch data (Thresher *et al.* 2007; Baudron *et al.* 2014; van Rijn *et al.* 2017; Huss *et al.* 2019). In most cases such data are only available species with a long history of commercial exploitation and time-varying population abundances and food productivity, which could confound or dilute any climate change signals in individual growth data. Therefore, it is important to compare field studies with controlled environments. Our finding that growth rates increase with temperature is similar to finding positive correlations between and temperature, as was many have found also in field data.

While our data do not contain individuals that are close to their predicted asymptotic body sizes, we do see weak evidence of the positive effects of warming on growth leveling off over ontogeny. This would be analogous to declines in maximum body size, or in time series (Baudron *et al.* 2014; van Rijn *et al.* 2017). However, we estimate a relative small interaction-effect, meaning notable impacts on growth only manifest over large temperature and body mass ranges (see Fig. 3) (but we also note that this estimate is almost an order of magnitude lower than what has been reported for some single species studies, e.g. Björnsson *et al*. (2007)). On the contrary, we find clear effects of body mass on optimal growth temperatures. Assuming that fish exhibit similar temperatures in the environment over ontogeny, this would lead to warming lowering growth performance of the largest fish in a population first (we estimate roughly a 4 change in optimum over ontogeny). However, this may not always be the case, as for instance Heincke’s law states that individuals move to deeper habitats over ontogeny (Heincke 1913; Audzijonyte & Pecl 2018), and other type of ontogenetic habitat shifts are well documented, e.g. (Werner & Hall 1988). For inferences about impacts of climate change, the change in optimum growth temperature that we report here should be viewed in relation to size-dependent habitat temperatures if those change over ontogeny. That said, there are already empirical evidence of the largest individuals being the first to suffer negative impacts of warming from e.g. heatwaves (Pörtner & Knust 2007). Taken together, while temperature has a clear positive effect on growth at for small fish in a population, in line with empirical findings, the effect of temperature on the large fish within a species is still not properly understood. This was also mirrored in a recent experimental study by Barneche *et al*. (2019), where a negative relationship between asymptotic body size and temperature was evident only at high temperatures. The inability to capture clear temperature-effects on asymptotic size over a realistic temperature-range experimentally could mean other factors are involved in time series of field-sampled fish, e.g. life history evolution in response to intensive fishing. However, we are not really able to make that conclusion since large individuals are generally not covered in experimental studies, including those compiled in this study, and large fish may still find direct negative impacts of warming on body growth.

We still lack mechanistic understanding and theoretical models for the causes of TSR (Marshall & White 2019a; Pauly 2019). This is likely because it appears to be a response to several co-varying mechanisms at different levels of biological organization (Ohlberger 2013b; Audzijonyte *et al.* 2018). We are also still discussing what drives the asymptotic body size of fish, so perhaps it is not strange we cannot explain the causes of directional changes in asymptotic mass. One of the reasons could be to general lack of experimental data of ontogenetic growth rates. This is most likely an artefact of the logistical challenges of performing growth rate experiments in the factorial design (size x temperature) needed. Moreover, body growth is an ontogenetic process, and there is only so much interspecific comparisons can ultimately say about ontogenetic growth. In a step to overcome this, we have systematically compiled growth data for different size-classes at different temperatures in order to get as close as possible to the ontogenetic scaling of growth without limiting ourselves to “truly” ontogenetic data (in which case our data set would have been smaller). We argue that this approach to systematic review of already existing literature can be fruitful in combination with hierarchical models and variable-standardization, as this can address the general aspects of ontogenetic growth that are shared across species, which single species studies will struggle with. One example is the size-dependence of optimum growth temperatures, which we find clear signals of even when analyzing data from a diverse set of species on a common scale. In doing so, our study adds a new take on aspects of intra-specific growth scaling for a “general” fish, adds data to the literature and highlights the lack of representation of large individuals in growth experiments.

\*Add section here about limitations in experiments and all uncertainties from that\*, including pros and cons with standardization…

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.

Do as in Englund and discuss effects on population and community dynamics?

See notes about the scaling, important to do intraspecific aspect!

To illustrate the effects of the intraspecific mass- and temperature-dependence of metabolic and consumption rates estimated from the experimental studies, we apply a generic Pütter-type growth model (Pütter 1920) of the form: , where is body mass. von Bertalanffy assumed, based on theoretical arguments and mathematical convenience, that and represent anabolism and catabolism and scale with exponents (based on the scaling of surfaces to volumes) and (von Bertalanffy 1938). However, the mechanistic interpretation of these two terms varies (Marshall & White 2019b), and are often defined as energy assimilation and expenditure, respectively (Ursin 1967; Essington *et al.* 2001). With this definition, the model constitutes a simple mass-balance equation that resembles bioenergetic models (Ursin 1967; Kitchell *et al.* 1977; Essington *et al.* 2001). It can further be assumed that assimilation and expenditure are proportional to consumption rates (at constant food levels) and oxygen consumption rates (Ursin 1967). In this case, the temperature dependence of and can be approximated by Eq. 5 for temperatures below optimum. The growth model and assumptions are great simplifications of the factors influencing growth dynamics over size and temperature, omitting for example specific dynamic action, food dependence of respiration and energetic investment into reproduction (Ursin 1967; Kitchell *et al.* 1977; Marshall & White 2019b). However, it can illustrate an example of the ability of simple bioenergetic models to capture the size-and temperature dependence of ontogenetic growth, and the assumptions can also be relaxed by applying the allometric functions into more complex bioenergetic models.

In the context of climate change impacts on ecosystem functioning and productivity, it is important to acknowledge the now widespread finding in field and experimental studies that warming has the potential to increase growth rates – at least in the smaller end of the species’ size-spectrum. This poses a challenge to general theoretical growth models that feed into climate projections. Body growth is a fundamental process, and not being able to characterize it properly may limits our understanding of important aspects beyond individual body size, including energy transfer & efficiency of food webs and ecosystems.

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.

**Author contributions**

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

**References**

Andersen, K.H., Beyer, J.E. & Lundberg, P. (2009a). Trophic and individual efficiencies of size-structured communities. *Proceedings of the Royal Society B: Biological Sciences*, 276, 109–114.

Andersen, K.H., Farnsworth, K.D., Pedersen, M., Gislason, H. & Beyer, J.E. (2009b). How community ecology links natural mortality, growth, and production of ﬁsh populations, 7.

Armstrong, J.D. & Hawkins, L.A. (2008). Standard metabolic rate of pike, Esox lucius: variation among studies and implications for energy flow modelling. *Hydrobiologia*, 601, 83–90.

Atkinson, D. (1994). Temperature and Organism Size—A Biological Law for Ectotherms? In: *Advances in Ecological Research*. Elsevier, pp. 1–58.

Audzijonyte, A., Barneche, D.R., Baudron, A.R., Belmaker, J., Clark, T.D., Marshall, C.T., *et al.* (2018). Is oxygen limitation in warming waters a valid mechanism to explain decreased body sizes in aquatic ectotherms? *Global Ecology and Biogeography*.

Audzijonyte, A. & Pecl, G.T. (2018). Deep impact of fisheries. *Nature Ecology & Evolution*, 2, 1348–1349.

Barneche, D.R. & Allen, A.P. (2018). The energetics of fish growth and how it constrains food-web trophic structure. *Ecology Letters*, 21, 836–844.

Barneche, D.R., Jahn, M. & Seebacher, F. (2019). Warming increases the cost of growth in a model vertebrate. *Functional Ecology*, 33, 1256–1266.

Baudron, A.R., Needle, C.L., Rijnsdorp, A.D. & Marshall, C.T. (2014). Warming temperatures and smaller body sizes: synchronous changes in growth of North Sea fishes. *Global Change Biology*, 20, 1023–1031.

Beamish, F.W.H. (1964). Respiration of fishes with special emphasis on standard oxygen consumption: II. Influence of weight and temperature on respiration of several species. *Canadian Journal of Zoology/Revue Canadienne de Zoologie*, 42, 177–188.

von Bertalanffy, L. (1938). A QUANTITATIVE THEORY OF ORGANIC GROWTH (INQUIRIES ON GROWTH LAWS. II). *Human Biology*, 10, 181–213.

Blanchard, J.L., Heneghan, R.F., Everett, J.D., Trebilco, R. & Richardson, A.J. (2017). From Bacteria to Whales: Using Functional Size Spectra to Model Marine Ecosystems. *Trends in Ecology & Evolution*, 32, 174–186.

Bokma, F. (2004). Evidence against universal metabolic allometry. *Functional Ecology*, 18, 184–187.

Brett, J.R., Shelbourn, J.E. & Shoop, C.T. (1969). Growth Rate and Body Composition of Fingerling Sockeye Salmon, Oncorhynchus nerka, in relation to Temperature and Ration Size. *J. Fish. Res. Bd. Can.*, 26, 2363–2394.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004). TOWARD A METABOLIC THEORY OF ECOLOGY. *Ecology*, 85, 1771–1789.

Cheung, W.W.L., Sarmiento, J.L., Dunne, J., Frölicher, T.L., Lam, V.W.Y., Deng Palomares, M.L., *et al.* (2013). Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. *Nature Climate Change*, 3, 254–258.

Clarke, A. (2004). Is there a Universal Temperature Dependence of metabolism? *Functional Ecology*, 18.

Clarke, A. & Johnston, N.M. (1999). Scaling of metabolic rate with body mass and temperature in teleost fish. *Journal of Animal Ecology*, 68, 893–905.

Daufresne, M., Lengfellner, K. & Sommer, U. (2009). Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences, USA*, 106, 12788–12793.

De Roos, A.M. & Persson, L. (2013). *Population and community ecology of ontogenetic development*. Princeton University Press, Princeton, New Jersey, USA.

Dell, A.I., Pawar, S. & Savage, V.M. (2011). Systematic variation in the temperature dependence of physiological and ecological traits. *Proceedings of the National Academy of Sciences*, 108, 10591–10596.

Dell, A.I., Pawar, S. & Savage, V.M. (2014). Temperature dependence of trophic interactions are driven by asymmetry of species responses and foraging strategy. *Journal of Animal Ecology*, 83, 70–84.

Downs, C.J., Hayes, J.P. & Tracy, C.R. (2008). Scaling metabolic rate with body mass and inverse body temperature: A test of the Arrhenius fractal supply model. *Functional Ecology*, 22, 239–244.

Elliott, J.M. & Hurley, M.A. (1995). The Functional Relationship between Body Size and Growth Rate in Fish. *Functional Ecology*, 9, 625.

Englund, G., Öhlund, G., Hein, C.L. & Diehl, S. (2011). Temperature dependence of the functional response. *Ecology Letters*, 14, 914–921.

Essington, T.E., Kitchell, J.F. & Walters, C.J. (2001). The von Bertalanffy growth function, bioenergetics, and the consumption rates of fish. *Canadian Journal of Fisheries and Aquatic Sciences*, 58, 2129–2138.

Fernández-i-Marín, X. (2016). ggmcmc: Analysis of MCMC Samples and Bayesian Inference. *Journal of Statistical Software*, 70, 1–20.

Forster, J., Hirst, A.G. & Atkinson, D. (2012a). Warming-induced reductions in body size are greater in aquatic than terrestrial species. *PNAS*, 109, 19310–19314.

Forster, J., Hirst, A.G. & Atkinson, D. (2012b). Warming-induced reductions in body size are greater in aquatic than terrestrial species, 109, 19310–19314.

Fossen, E.I.F., Pélabon, C. & Einum, S. (2019). Genetic and environmental effects on the scaling of metabolic rate with body size. *Journal of Experimental Biology*, 222.

Froese, R. & Pauly, D. (2016). *Editors. FishBase*. World Wide Web electronic publication. www.fishbase.org, (10/2016).

Gabry, J., Simpson, D., Vehtari, A., Betancourt, M. & Gelman, A. (2019). Visualization in Bayesian workflow. *J. R. Stat. Soc. A*, 182, 389–402.

García García, B., Cerezo Valverde, J., Aguado-Giménez, F., García García, J. & Hernández, M.D. (2011). Effect of the interaction between body weight and temperature on growth and maximum daily food intake in sharpsnout sea bream (Diplodus puntazzo). *Aquaculture International*, 19, 131–141.

Gardner, J.L., Peters, A., Kearney, M.R., Joseph, L. & Heinsohn, R. (2011). Declining body size: a third universal response to warming? *Trends in Ecology & Evolution*, 26, 285–291.

Gelman, A. & Rubin, D.B. (1992). Inference from Iterative Simulation Using Multiple Sequences. *Statist. Sci.*, 7, 457–472.

Gillooly, J.F., Brown, J.H., West, G.B., Savage, V.M. & Charnov, E.L. (2001). Effects of size and temperature on metabolic rate. *Science*, 2248–2251.

Hartvig, M., Andersen, K.H. & Beyer, J.E. (2011). Food web framework for size-structured populations. *Journal of Theoretical Biology*, 272, 113–122.

Heincke, F. (1913). Rapp. Proc. Verb. Réun. ICES 16, 1–70.

Horne, C.R., Hirst, Andrew.G. & Atkinson, D. (2015). Temperature-size responses match latitudinal-size clines in arthropods, revealing critical differences between aquatic and terrestrial species. *Ecology Letters*, 18, 327–335.

Huss, M., Lindmark, M., Jacobson, P., van Dorst, R.M. & Gårdmark, A. (2019). Experimental evidence of gradual size‐dependent shifts in body size and growth of fish in response to warming. *Global Change Biology*.

Jerde, C.L., Kraskura, K., Eliason, E.J., Csik, S.R., Stier, A.C. & Taper, M.L. (2019). Strong Evidence for an Intraspecific Metabolic Scaling Coefficient Near 0.89 in Fish. *Front. Physiol.*, 10, 1166.

Jobling, M. (1997). Temperature and growth: modulation of growth rate via temperature change. In: *Global Warming: Implications for Freshwater and Marine Fish* (eds. Wood, C.M. & McDonald, D.G.). Cambridge University Press, Cambridge, pp. 225–254.

Kearney, M. (2019). Reproductive Hyperallometry Does Not Challenge Mechanistic Growth Models. *Trends in Ecology & Evolution*, 34, 275–276.

Killen, S.S., Atkinson, D. & Glazier, D.S. (2010). The intraspecific scaling of metabolic rate with body mass in fishes depends on lifestyle and temperature. *Ecology Letters*, 13, 184–193.

Kitchell, J.F., Stewart, D.J. & Weininger, D. (1977). Applications of a bioenergetics model to yellow perch (Perca flavescens) and walleye (Stizostedion vitreum vitreum). *Journal of the Fisheries Board of Canada*, 34, 1922–1935.

Kooijman, S.A.L.M. (1993). *Dynamic energy budgets in biological systems*. Cambridge University Press.

Lefevre, S., McKenzie, D.J. & Nilsson, G.E. (2017). Models projecting the fate of fish populations under climate change need to be based on valid physiological mechanisms. *Global Change Biology*, 23, 3449–3459.

Lindmark, M., Huss, M., Ohlberger, J. & Gårdmark, A. (2018). Temperature-dependent body size effects determine population responses to climate warming. *Ecology Letters*, 21, 181–189.

Marshall, D.J. & White, C.R. (2019a). Aquatic Life History Trajectories Are Shaped by Selection, Not Oxygen Limitation. *Trends in Ecology & Evolution*.

Marshall, D.J. & White, C.R. (2019b). Have We Outgrown the Existing Models of Growth? *Trends in Ecology & Evolution*, 34, 102–111.

Maury, O. & Poggiale, J.-C. (2013). From individuals to populations to communities: A dynamic energy budget model of marine ecosystem size-spectrum including life history diversity. *Journal of Theoretical Biology*, 324, 52–71.

Morita, K., Fukuwaka, M., Tanimata, N. & Yamamura, O. (2010). Size-dependent thermal preferences in a pelagic fish. *Oikos*, 119, 1265–1272.

Nelson, J.A. (2016). Oxygen consumption rate v. rate of energy utilization of fishes: a comparison and brief history of the two measurements. *Journal of Fish Biology*, 88, 10–25.

Neubauer, P. & Andersen, K.H. (2019). Thermal performance of fish is explained by an interplay between physiology, behaviour and ecology. *Conserv Physiol*, 7.

Neuheimer, A.B., Thresher, R.E., Lyle, J.M. & Semmens, J.M. (2011). Tolerance limit for fish growth exceeded by warming waters. *Nature Climate Change*, 1, 110–113.

Ohlberger, J. (2013a). Climate warming and ectotherm body size – from individual physiology to community ecology. *Functional Ecology*, 27, 991–1001.

Ohlberger, J. (2013b). Climate warming and ectotherm body size - from individual physiology to community ecology. *Functional Ecology*, 27, 991–1001.

Ohlberger, J., Mehner, Thomas., Staaks, Georg. & Hölker, Franz. (2012). Intraspecific temperature dependence of the scaling of metabolic rate with body mass in fishes and its ecological implications. *Oikos*, 121, 245–251.

Pauly, D. (2019). Female Fish Grow Bigger – Let’s Deal with It. *Trends in Ecology & Evolution*.

Pauly, D. & Cheung, W.W.L. (2018). Sound physiological knowledge and principles in modeling shrinking of fishes under climate change. *Global Change Biology*, 24, e15–e26.

Plummer, M. (2003). JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. *Working Papers*, 8.

Plummer, M. (2019). *rjags*.

Pörtner, H.O. & Knust, R. (2007). Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science*, 315, 95–97.

Pütter, A. (1920). Studien über physiologische Ähnlichkeit VI. Wachstumsähnlichkeiten. *Pflügers Arch.*, 180, 298–340.

R Core Team. (2018). *R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing*. Vienna, Austria.

Rall, B.C., Brose, U., Hartvig, M., Kalinkat, G., Schwarzmuller, F., Vucic-Pestic, O., *et al.* (2012). Universal temperature and body-mass scaling of feeding rates. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, 367, 2923–2934.

Rall, B.C., Vucic-Pestic, O., Ehnes, R.B., Emmerson, M. & Brose, U. (2010). Temperature, predator-prey interaction strength and population stability. *Global Change Biology*, 16, 2145–2157.

van Rijn, I., Buba, Y., DeLong, J., Kiflawi, M. & Belmaker, J. (2017). Large but uneven reduction in fish size across species in relation to changing sea temperatures. *Global Change Biology*, 23, 3667–3674.

Rohatgi, A. (2012). *WebPlotDigitalizer: HTML5 based online tool to extract numerical data from plot images. Version 4.1. [WWW document] URL https://automeris.io/WebPlotDigitizer (accessed on January 2019).*

Roos, A.M.D. & Persson, L. (2001). Physiologically structured models – from versatile technique to ecological theory. *Oikos*, 94, 51–71.

Savage, V.M., Gillooly, J.F., Brown, J.H., West, G.B. & Charnov, E.L. (2004). Effects of body size and temperature on population growth. *The American Naturalist*, 163, 429–441.

Sibly, R.M., Baker, J., Grady, J.M., Luna, S.M., Kodric-Brown, A., Venditti, C., *et al.* (2015). Fundamental insights into ontogenetic growth from theory and fish. *Proceedings of the National Academy of Sciences, USA*, 112, 13934–13939.

Thresher, R.E., Koslow, J.A., Morison, A.K. & Smith, D.C. (2007). Depth-mediated reversal of the effects of climate change on long-term growth rates of exploited marine fish. *Proceedings of the National Academy of Sciences, USA*, 104, 7461–7465.

Ursin, E. (1967). A Mathematical Model of Some Aspects of Fish Growth, Respiration, and Mortality. *Journal of the Fisheries Research Board of Canada*, 24, 2355–2453.

Vasseur, D.A. & McCann, K.S. (2005). A mechanistic approach for modelling temperature-dependent consumer-resource dynamics. *The American Naturalist*, 166, 184–198.

Vehtari, A., Gelman, A. & Gabry, J. (2017). Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Stat Comput*, 27, 1413–1432.

Werner, E.E. & Hall, D.J. (1988). Ontogenetic Habitat Shifts in Bluegill: The Foraging Rate-Predation Risk Trade-off. *Ecology*, 69, 1352–1366.

West, G.B., Brown, J.H. & Enquist, B.J. (1999). The fourth dimension of life: Fractal geometry and allometric scaling of organisms. *Science*, 284, 1677–1679.

West, G.B., Brown, J.H. & Enquist, B.J. (2001). A general model for ontogenetic growth. *Nature*, 413, 628–631.

Wickham, H. (2017). *tidyverse: Easily Install and Load the “Tidyverse.”*

Xie, Xiaojun. & Sun, Ruyung. (1990). The Bioenergetics of the Southern Catfish (Silurus meridionalis Chen). I. Resting Metabolic Rate as a Function of Body Weight and Temperature. *Physiological Zoology*, 63, 1181–1195.