

Supporting Information for

Optimal energy allocation to growth and reproduction driven by
size dependent physiological and demographic responses to warming

Journal name

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S1. Effects of size and temperature on maintenance, consumption and energy budget

S1.1. Effects of mass and temperature on maintenance and consumption The effects of mass and temperature on maintenance and consumption in combination with mass dependent allocation determines somatic growth and reproductive reserve in the DEBIPM (Fig S1.1). In the DEB, the effect of mass on maintenance and consumption is modeled using a power function (Fig S1.1A), the interacting effects of temperature and mass (equation 3, main text) on maintenance rate is exponential (Fig S1.1B) and the effect of temperature on consumption rate is exponential and unimodal (Fig S1.1B, solid line). We consider allocation to reproductive reserve hyper-allometric (or supra-linear with mass) meaning that kappa (modeled as a function of mass, $k(m)$) decreases with mass (Fig. S1.1C). The resulting DEB, which includes assimilation efficiency ($\alpha=0.4$), thus describes the proportion of consumed energy that each compartment use up (Fig S1.1D).

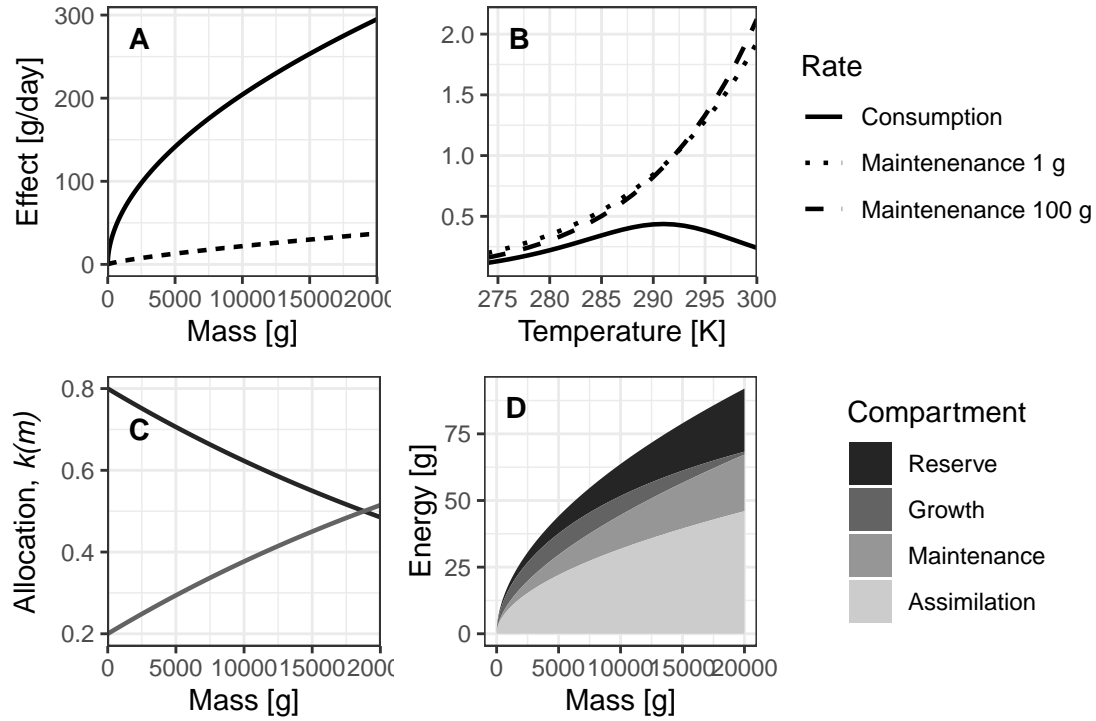


Figure S1.1. Size- and temperature dependence of the dynamic energy budget. The mass (A) and temperature (B) scaling of maintenance (A and B, dotted line for a 1 gram individual and dashed line for a 100 gram) and consumption (A and B, solid line) in combination with mass dependent energy allocation of reserve and growth (C, via $k(m)$) determines the size dependence of the energy budget (D).

S1.2. Effects of temperature on allocation to growth and reproduction The effects of mass and temperature on maintenance and consumption rate in fig. S1.1 makes rate of energy allocated to growth and reproductive reserve unimodal over temperature (Fig. S1.2). The optimum temperature for energy spent on reproduction is a function of consumption but not of mass and is therefore 291 Kelvin (Fig. S1.2, dashed line, Fig. S1.1B, solid line). The optimum temperature for somatic growth however decreases with mass (Fig. S1.2, solid line) due to the disparate effects of size on maintenance and consumption rate combined with a unimodal effect of temperature on consumption (Lindmark et al. 2021).

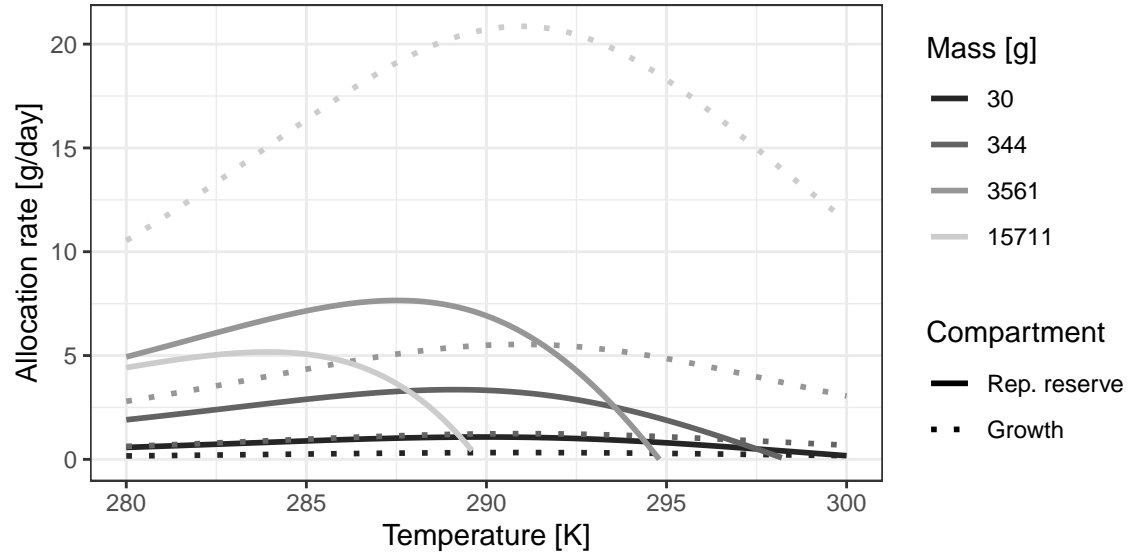


Figure S1.2. Energy allocation rate to reproductive reserve (dashed lines) and growth (solid lines) dependent on temperature for four different sizes.

S2. Comparison of modelled growth and reproduction (Fecundity) with data on Windermere pike

We adjust the parameter values of mass dependent consumption and allocation in the DEB model to fit data on the observed growth and fecundity of Windermere pike (see main text for details). Figure S2 shows how our estimates compare with growth mean (growth trajectories, Fig. S2A) and variance (Fig. S2B) and reproduction (S2C, estimated fecundity in October?) with data

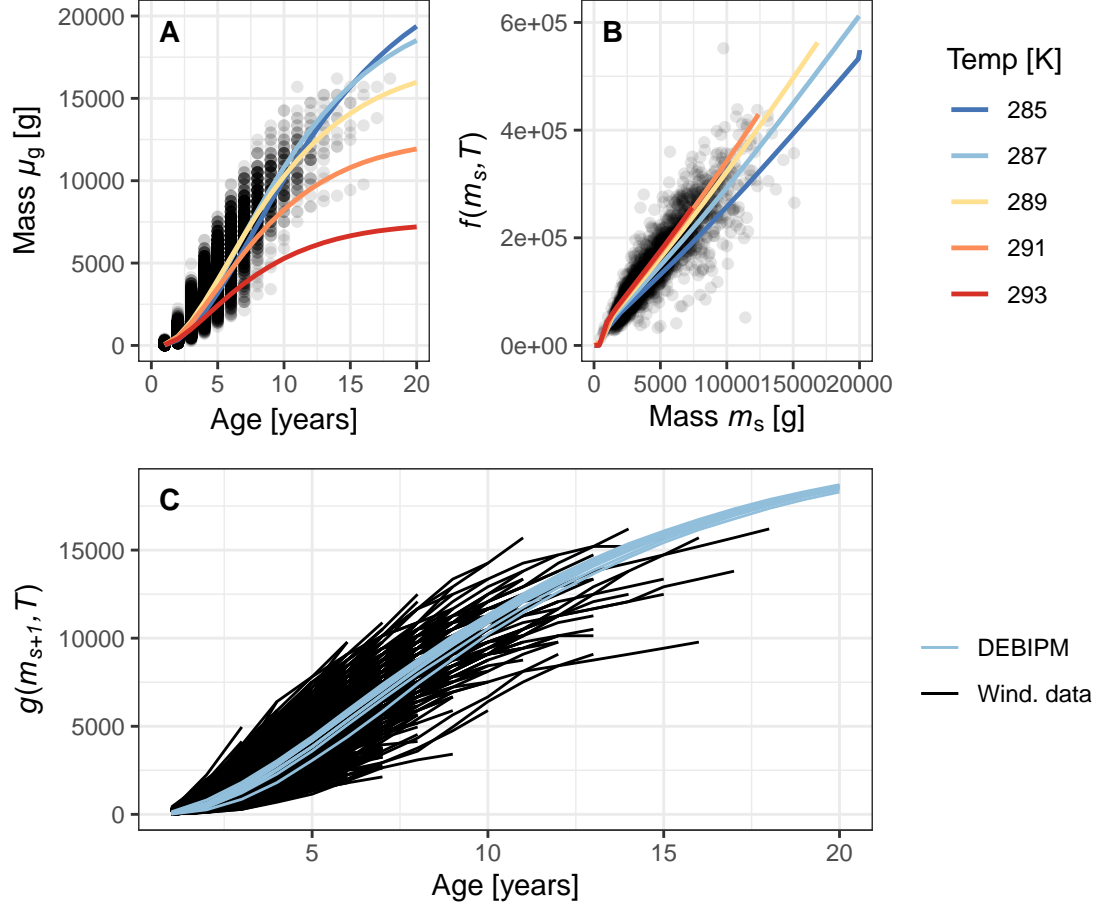


Figure S2. Comparison of DEBIPM and data on Windermere pike (black points in A and B and lines in C). Effects of size and temperature on demographic functions in the DEBIPM for $k_0=0.8$ (i.e. 80 % of daily assimilated energy is allocated to growth and maintenance): mean size at age (A) and size specific fecundity (eggs produced in year $s+1$ by individuals of size m_s in year s) (B). Growth trajectories in C are based on individual back calculated growth from wing bones from Windermere (black) and 10 random growth trajectories produced by the DEBIPM at 287 K (blue).

S3. Effect of number of size classes (n) on long-term population growth rate (λ) and stable population size structure.

When analyzing the IPM, the number of size classes in the (n , or matrix mesh size) should not affect the estimation of λ and stable size structure (w). We therefore estimate λ for DEBIPMs with $0 < n < 2400$ (Fig. S3A) to find the minimum number size classes that does not affect λ to an accuracy of four decimal points nor the qualitative shape of the w .

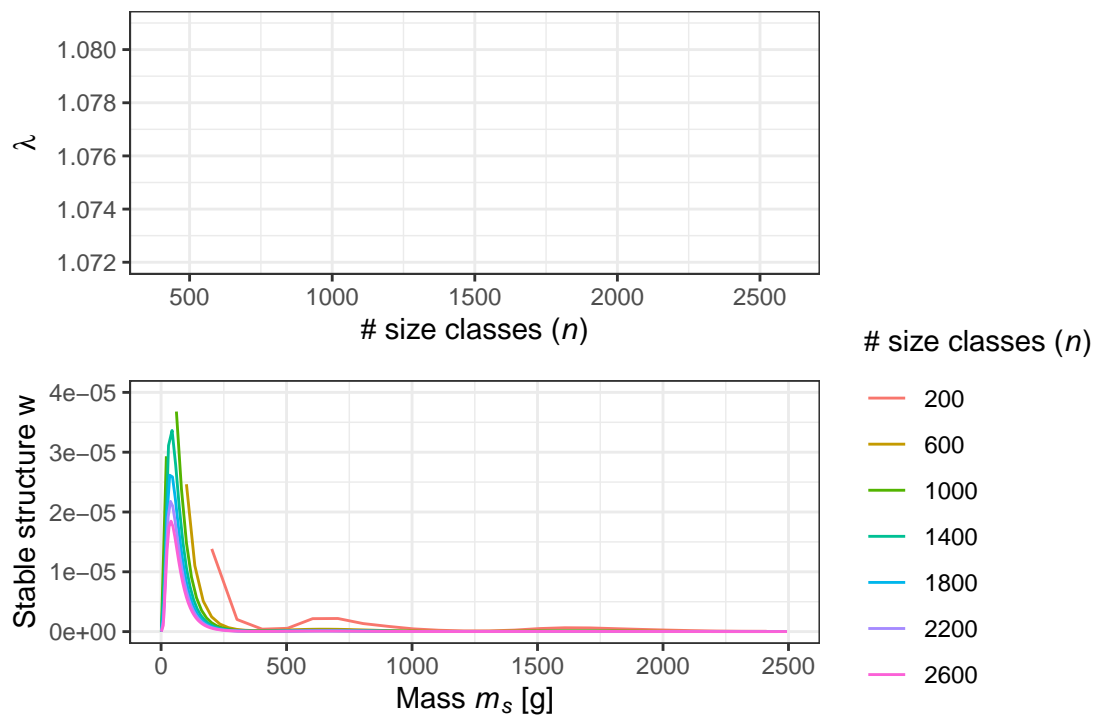


Figure S3. Effect of number of size classes (n) on long-term population growth rate (λ , top panel) stable size structure (w , bottom panel). We use $n = 1400$ in the main analysis of the DEBIPM.

S4. Sensitivity of the DEBIPM: Methods and analytical expression for derivatives of demographic functions to κ_0 .

Methodological approach Our sensitivity analysis aims at explaining how κ_0 is optimized at different temperatures, i.e. how the ‘configuration’ of vital rates at optimal values of κ may shift with temperatures. To this end we decompose the sensitivity of λ into the respective size dependent sensitivity contribution from the demographic functions for age 1 size, somatic growth and fecundity at three temperatures (287, 289, 291 K). We use the chain rule of derivation based on numerical approximations of the derivatives for mass and temperature specific demographic functions with respect to κ_0 . We use numerical approximation as the integrals in the DEB (that approximates the energy budget and consecutive growth and fecundity) are also numerical approximations. Below, we however present analytical expressions for the sensitivity.

Notation when deriving sensitivity To describe this approach, we here use a simplified matrix notation instead of integrals (the underlying functions and analysis are the same as the main text DEBIPM). The expressions describing the derivation of the sensitivity below is thus a discrete version of the IPM with two main stages (eggs, and ‘non-eggs’, i.e. individuals with a given size, from age 1 and above), resulting in following four main parts of the projection matrix \mathbf{K} :

$$\mathbf{K} = \left[\begin{array}{c|c} \text{Egg to egg} & \text{Reproduction} \\ \hline \text{Egg to 'non-egg'} & \text{Size transitions for 'non-eggs'} \end{array} \right]. \quad (1)$$

As all eggs transition to 1-year olds (or die) next year, the upper left element of the matrix is zero. The other parts of the matrix are defined by the DEBIPM, the discretized version assumes the model consists of $n + 1$ stages, where the first stage is the egg stage and the last stages from 2 to $n + 1$ are size stages. The term g_{ij} is the probability of transitioning from size stage j to size stage i and are determined by the underlying DEB-function $g(y, x)$. The projection matrix is then given by

$$\mathbf{K} = \left[\begin{array}{c|ccc} 0 & f_2 a_2 & \cdots & f_{n+1} a_{n+1} \\ \hline a_1 g_{21} & g_{22} a_2 & \cdots & g_{2,n+1} a_{n+1} \\ \vdots & \vdots & \ddots & \vdots \\ a_1 g_{n+1,1} & g_{n+1,2} a_2 & \cdots & g_{n+1,n+1} a_{n+1} \end{array} \right]. \quad (2)$$

Here, g_{i1} is the probability that a surviving egg grows to stage i at age 1 (determined by $o_y(y)$ in the DEB-models) and is thus calculated differently from g_{ij} for $j > 1$. However, they both represent the same transition process (growth transitions) and have the same symbol here g_{ij} . Similarly, a_j is survival probability, given by the parameter el_{surv} for $j = 1$ and calculated by the $a(m_s, T)$ function for $j > 1$.

The κ_0 parameter affects growth g_{ij} and fecundity f_j in stage j , while survival a_j is not dependent on this parameter.

Sensitivity analysis

Decomposition of sensitivity of λ to κ_0 Using this projection matrix \mathbf{K} we can decompose the sensitivity $\frac{d\lambda}{d\kappa_0}$ (which should be zero at the optimum), into contributions from the different vital rates across different stages. Applying the chain rule (and the fact that $\frac{d\lambda}{dK_{ij}} = v_i w_j$), we get

$$\frac{d\lambda}{d\kappa_0} = \sum_{i=1}^{n+1} \sum_{j=1}^{n+1} \frac{d\lambda}{dK_{ij}} \frac{dK_{ij}}{d\kappa_0} \quad (3)$$

$$= \sum_{i=1}^{n+1} \sum_{j=1}^{n+1} v_i w_j \frac{dK_{ij}}{d\kappa_0} \quad (4)$$

$$= \sum_{j=2}^{n+1} v_1 w_j a_j \frac{df_j}{d\kappa_0} + \sum_{i=2}^{n+1} v_i w_1 a_1 \frac{dg_{i1}}{d\kappa_0} + \sum_{i=2}^{n+1} \sum_{j=2}^{n+1} v_i w_j a_j \frac{dg_{ij}}{d\kappa_0}. \quad (5)$$

In the last equation, the first term corresponds to contributions from fecundity, the second to contributions from first year growth, and the third to contributions from individuals age 1 and older. The contributions from survival are zero because survival does not depend on κ_0 .

This decomposition requires the three sensitivities $\frac{df_j}{d\kappa_0}$ ($j > 1$), $\frac{dg_{1j}}{d\kappa_0}$ ($j > 1$), and $\frac{dg_{ij}}{d\kappa_0}$ ($i, j > 1$). These are calculated in the next section. These derivations are on the scale of demographic functions that are defined on continuous scale require that we switch to notation using continuous functions.

Analytical expression for $\frac{dg_{ij}}{d\kappa_0}$ The growth function $g(y; x)$ is assumed to be a lognormal distribution, where in our case the mean $\mu = \mu(m)$ depends on κ_0 (mean defined on the absolute scale) and the standard deviation σ depends on the mean (and thereby also on κ_0), $\sigma^2(\mu) = \beta^2 e^{-2\nu\mu}$. Note that in the above derivations g_{ij} is the discretized version of this function, where for a given bin size dy we get $g_{ij} = g(y, m)dy / \int g(y, m)dy$ (and $\sum_i g_{ij} = 1$).

To simplify calculations, we can define the following function $h(\mu)$ and its derivative:

$$h(\mu) = 1 + \frac{\sigma^2}{\mu^2} = 1 + \frac{\beta^2 e^{-2\nu\mu}}{\mu^2} = 1 + \mu^{-2} \beta^2 e^{-2\nu\mu} \quad (6)$$

$$h'(\mu) = -2\mu^{-3} \beta^2 e^{-2\nu\mu} + e^{-2\nu\mu} (-2\nu) \beta^2 \mu^2 = -2\beta^2 e^{-2\nu\mu} \mu^{-2} (\mu^{-1} + 1). \quad (7)$$

For this model we can write the lognormal distribution as a function of $\mu = \mu(m)$:

$$g(y, \mu) = \frac{1}{y} \left[2\pi \ln \left(1 + \frac{\sigma^2}{\mu^2} \right) \right]^{-\frac{1}{2}} \exp \left(- \frac{\left[\ln y - \ln \left(\mu \left[1 + \frac{\sigma^2}{\mu^2} \right]^{-\frac{1}{2}} \right) \right]^2}{2 \ln \left(1 + \frac{\sigma^2}{\mu^2} \right)} \right) \quad (8)$$

$$= \frac{1}{y} [2\pi \ln h(\mu)]^{-\frac{1}{2}} \exp \left(- \frac{\left[\ln y - \ln \left(\mu [h(\mu)]^{-\frac{1}{2}} \right) \right]^2}{2 \ln h(\mu)} \right) \quad (9)$$

$$= \frac{1}{y} g_a(\mu) \exp \left(- \frac{g_b(\mu)}{g_c(\mu)} \right), \quad (10)$$

where $g_a(\mu) = [2\pi \ln h(\mu)]^{-\frac{1}{2}}$, $g_b(\mu) = \left[\ln y - \ln \left(\mu [h(\mu)]^{-\frac{1}{2}} \right) \right]^2$, and $g_c(\mu) = 2 \ln h(\mu)$. The derivatives of these are

$$g'_a(\mu) = -\frac{1}{2} [2\pi \ln h(\mu)]^{-\frac{3}{2}} 2\pi [h(\mu)]^{-1} h'(\mu) = -\frac{\pi}{h(\mu)} [2\pi \ln h(\mu)]^{-\frac{3}{2}} h'(\mu),$$

$$\begin{aligned}
g'_b(\mu) &= 2 \left[\ln y - \ln \left(\mu [h(\mu)]^{-\frac{1}{2}} \right) \right] \frac{-1}{\mu [h(\mu)]^{-\frac{1}{2}}} \left[[h(\mu)]^{-\frac{1}{2}} - \frac{\mu}{2} [h(\mu)]^{-\frac{3}{2}} h'(\mu) \right] \\
&= 2 \left[\ln y - \ln \left(\mu [h(\mu)]^{-\frac{1}{2}} \right) \right] \left[\frac{h'(\mu)}{2h(\mu)} - \frac{1}{\mu} \right],
\end{aligned}$$

and

$$g'_c(\mu) = \frac{2h'(\mu)}{h(\mu)}.$$

Using the chain rule, the derivative of $g(y, \mu)$ with respect to κ_0 is given by

$$\frac{dg(y, \mu)}{d\kappa_0} = \frac{dg(y, \mu)}{d\mu} \frac{d\mu}{d\kappa_0} \quad (11)$$

The first term is given by

$$\frac{dg(y, \mu; \sigma)}{d\mu} = \frac{1}{y} g'_a(\mu) \exp \left(-\frac{g_b(\mu)}{g_c(\mu)} \right) + \frac{1}{y} g_a(\mu) \exp \left(-\frac{g_b(\mu)}{g_c(\mu)} \right) \left(\frac{-g'_b(\mu)g_c(\mu) + g'_c(\mu)g_b(\mu)}{g_b(\mu)^2} \right). \quad (12)$$

This can be found by plugging in the expressions defined above. The second term of eq. (11) is the derivative of the mean with respect to κ_0 , and is given by

$$\frac{d\mu}{d\kappa_0} = \frac{d}{d\kappa_0} \int_0^{t_l} [\kappa_0 e^{-\frac{m}{20000\kappa_m}} \alpha Y C(m, T) - M(m, T)] dt \quad (13)$$

$$= \int_0^{t_l} \alpha Y C(m, T) e^{-\frac{m}{18000\kappa_m}} dt. \quad (14)$$

Analytical expression for $\frac{dg_{1j}}{d\kappa_0}$ The distribution of size at age 1 follows a lognormal distribution similar to (8), but the mean and variance are defined differently for first year growth. Here the variance is a constant, and the integral defining the mean is over the interval 0 to $t_l/2$. Thus, the derivative of μ with respect to κ_0 is given by

$$\frac{d\mu(x)}{d\kappa_0} = \frac{d}{d\kappa_0} \int_0^{t_l/2} [\kappa_0 e^{-\frac{m}{18000\kappa_m}} \alpha Y C(m, T) - M(m, T)] dt \quad (15)$$

$$= \int_0^{t_l/2} \alpha Y C(m, T) e^{-\frac{m}{18000\kappa_m}} dt. \quad (16)$$

In this case we get $h(\mu) = 1 + \frac{\sigma^2}{\mu^2}$ and $h'(\mu) = -2\sigma^2\mu^{-3}$, which can be plugged into all of the above expressions calculated for the growth sensitivity (with correct values of μ and σ).

Analytical expression for $\frac{df_i}{d\kappa_0}$ Fecundity is given by (assuming enough energy available for reproduction)

$$f(x, T) = \frac{1}{2e_m} \int_0^{t_l} \frac{dR}{dt} dt = \frac{1}{2e_m} \int_0^{t_l} (1 - \kappa_0 e^{-\frac{m}{18000\kappa_m}} \alpha Y C(m, T)) dt. \quad (17)$$

The sensitivity with respect to κ_0 is thus given by

$$\frac{df(x, T)}{d\kappa_0} = -\frac{1}{2e_m} \int_0^{t_l} e^{-\frac{m}{20000\kappa_m}} \alpha Y C(m, T) dt. \quad (18)$$

S5. Growth trajectories and fecundity at for optimal allocation (κ_0^*)

Size dependent growth and fecundity for optimal allocation (κ_0^*) differs from those presented in figure 3 in the main text (i.e. with $\kappa_0 = 0.8$ which was used to tune the model). Optimal allocation in our Windermere pike DEBIPM (main text figure 2) results in increased growth (mean size at age, Fig. S5A) but decreased size specific fecundity (Fig. S5B) compared to $\kappa_0 = 0.8$) of energy to somatic growth.

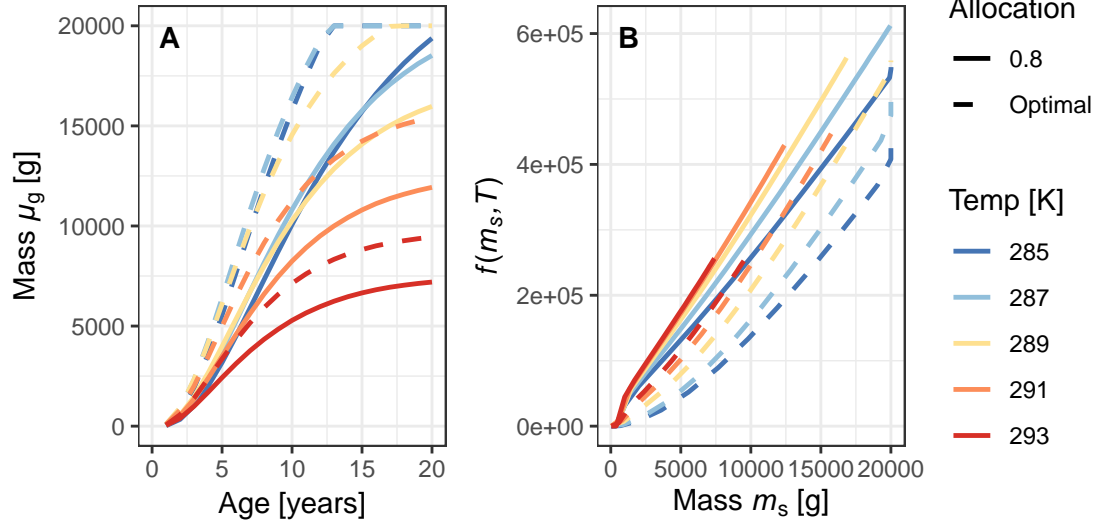


Figure S5. Mean size at age (A) and size specific fecundity (B) predicted from the optimal allocation strategy (κ_0^*), Fig. 2 main text) at five temperatures and contrasted by growth and fecundity for $\kappa_0 = 0.8$ (i.e. κ_0 used for tuning the model).

S6. Fitness landscape & stable size structure for contrasting survival scenarios

In the main analyses, we contrast the size- and temperature dependent survival used in our model using two alternative survival scenarios (Fig. 4C main text). Here we present the corresponding fitness landscape and κ_0^* (Fig S6A,B) and stable structure w at the reference temperature (287 K, Fig S6C,D) and over temperature (Fig. S6E,F) for the temperature independent survival contrast $a(m_s)$ (Fig. S6A,C,E) and constant survival $a = 0.68$ (Fig. S6B,D,F). In the first scenario, we use temperature independent survival $a(m_s)$ that correspond to survival at mean temperature (287 K) in Windermere where temperature does not affect the survival asymptote for weight ($a(m_s)$, (Fig. 4D). In the second we use constant (both size- and temperature-independent) survival that equals the this asymptote at mean temperature ($a=0.68$, Fig. 4E).

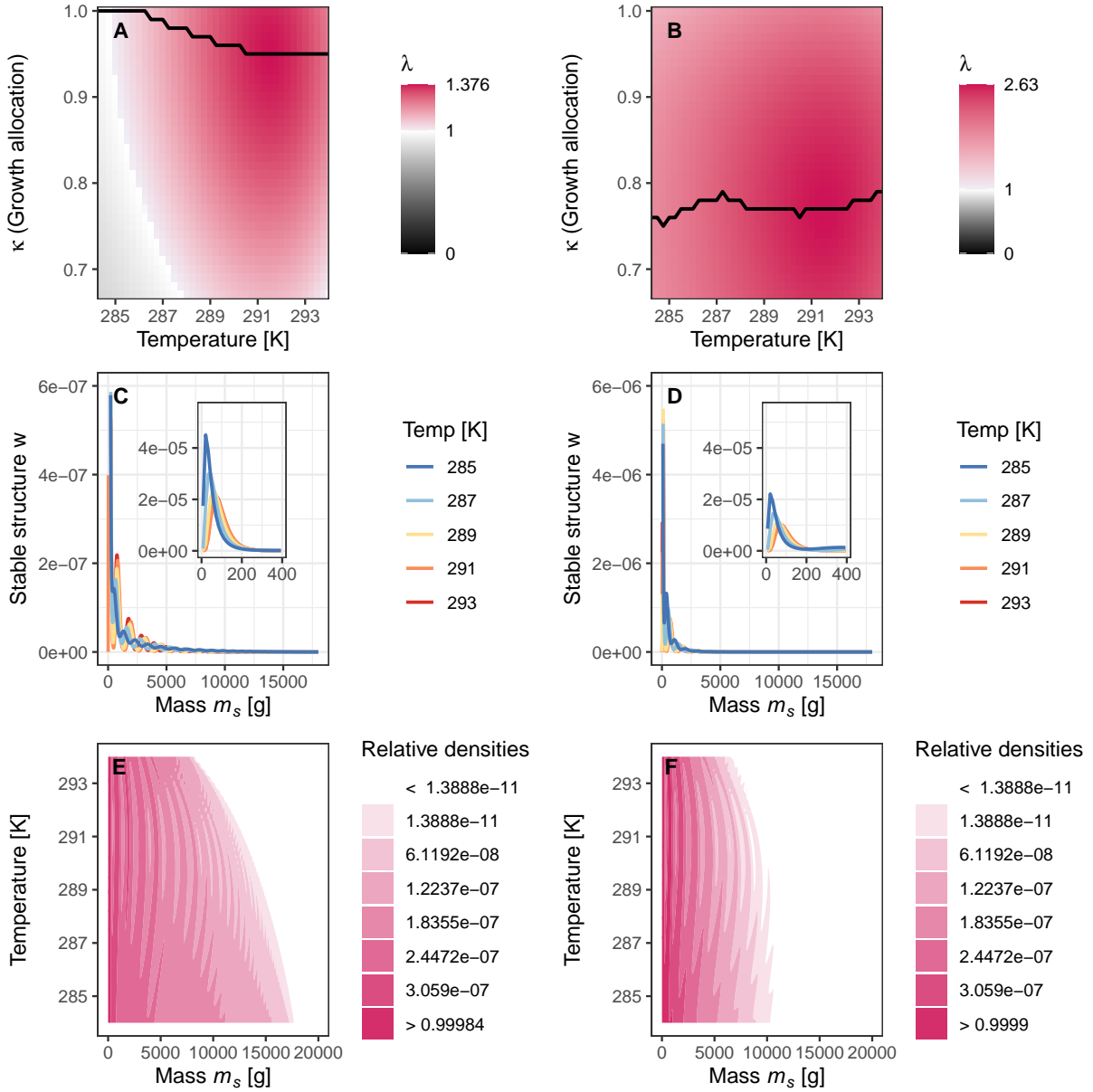


Figure S6. Fitness landscape (A,B) with solid line representing optimal allocation strategy (κ_0^*) and stable structure w for four temperatures (C,D) and over temperature (E,F) for survival contrast $a(m_s)$ (A,C,E) and $a = 0.68$ (B,D,F).