

## **Appendix from J. Ohlberger et al., “Temperature-Driven Regime Shifts in the Dynamics of Size-Structured Populations”**

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### **Model Assumptions, Characteristics, and Equations**

A full description of the model assumptions, characteristics, and equations is given below. The model extends the size-structured consumer-resource models described by Persson et al. (1998) and Claessen et al. (2000).

#### **Growing Season**

Growing season was assumed to last for 120 days using Lake Windermere, a glacial valley lake in the English Lake District, as reference. In Windermere the growing season for perch begins when water temperature in spring rises above 13.5–14°C, and it ends when it decreases below this threshold in the fall (Le Cren 1958).

#### **Model Variables**

The model keeps track of a variable number of year classes (“cohorts”) in continuous time. Each year in spring a new cohort is created if the population contains reproducing individuals at this moment. All newborns are grouped in the same new cohort and assumed to have identical initial condition. The state of an individual is defined by two so-called  $i$ -state variables: irreversible mass ( $x$ ) and reversible mass ( $y$ ). The model defines the dynamics of  $x$  and  $y$  and also the number of individuals for each cohort. Thus, each cohort is characterized by three state variables,  $x_i$ ,  $y_i$ , and  $N_i$ , where  $i$  is the cohort index ( $i = 0, \dots, k - 1$ , where  $k$  is the current number of cohorts). The dynamics of  $x$  and  $y$  depend on the energy budget of the individual, which in turn depends on  $x$  and  $y$ , and on the environmental conditions, including the densities of potential cannibalistic prey, the alternative zooplankton resource, and temperature. The zooplankton dynamics are assumed to follow semichemostat dynamics (Persson et al. 1998).

#### **Net Energy Gain**

The amount of energy an individual can allocate to somatic or reproductive growth is its net energy gain ( $E_g$ ). It is the difference between energy acquired from food intake ( $E_a$ ) and energy required for metabolism ( $E_m$ ):

$$E_g(x, y, T) = E_a(x, T) - E_m(x, y, T). \quad (\text{A1})$$

The net energy gain is thus a function of reversible mass, irreversible mass, and environmental temperature.

#### **Temperature Dependence**

Following Karås and Thoresson (1992), the temperature-dependence term is defined by the following set of equations:

$$r(x, y, T) = V(x, y, T)^{X(x, y, T)} e^{X(x, y, T)(1 - V(x, y, T))}, \quad (\text{A2})$$

$$V(x, y, T) = \frac{(T_{\max}(x, y) - T)}{(T_{\max}(x, y) - T_{\text{opt}}(x, y))}, \quad (\text{A3})$$

$$X(x, y, T) = W^2 \left[ 1 + \left( 1 + \frac{40}{Y} \right)^{0.5} \right] \frac{1}{400}, \quad (\text{A4})$$

$$W = (T_{\max}(x, y) - T_{\text{opt}}(x, y)) \ln Q(x, y), \quad (\text{A5})$$

$$Y = (T_{\max}(x, y) - T_{\text{opt}}(x, y) + 2) \ln Q(x, y), \quad (\text{A6})$$

$$T_{\text{opt}}(x, y) = \gamma_{\text{opt}}(x + y)^{\nu_{\text{opt}}}, \quad (\text{A7})$$

$$T_{\max}(x, y) = \gamma_{\max}(x + y)^{\nu_{\max}}, \quad (\text{A8})$$

$$Q(x, y) = \vartheta(x + y)^\theta. \quad (\text{A9})$$

The variables within equations (A2)–(A6), optimum temperature ( $T_{\text{opt}}$ ), maximum temperature ( $T_{\max}$ ), and  $Q$ , are allometric functions of body mass (eqq. [A7]–[A9]). Two different parameter sets were used for scaling the metabolic and intake rates.

The parameters estimated for these temperature dependence functions are  $\gamma_{\text{m, opt}}$ ,  $\nu_{\text{m, opt}}$ ,  $\gamma_{\text{m, max}}$ ,  $\nu_{\text{m, max}}$ ,  $\vartheta_{\text{m}}$ , and  $\theta_{\text{m}}$  for metabolic rate ( $r_{\text{m}}$ ) and  $\gamma_{\text{a, opt}}$ ,  $\nu_{\text{a, opt}}$ ,  $\gamma_{\text{a, max}}$ ,  $\nu_{\text{a, max}}$ ,  $\vartheta_{\text{a}}$ , and  $\theta_{\text{a}}$  for intake rate ( $r_{\text{a}}$ ). All parameter values are given in table 2 and can be found in Karås and Thoresson (1992). Both temperature terms as presented in their model are scaling functions that take values between 0 and 1. In order to adjust these relationships to the parameter values used in the previous model (Claessen et al. 2000), these functions were set to 1 at a reference temperature of 20°C (fig. 1), the experimental temperature for the determination of most physiological parameters used in the original model. The adjustment factors were 1.804 and 1.675 for the metabolic rate and intake rate relationships, respectively.

## Maintenance Requirements

Metabolic costs for maintenance are known to scale with total body mass according to an allometric power function (Peters 1983) with a scaling exponent ( $\rho_2$ ) typically close to 0.8 for fishes (Clarke and Johnston 1999). The energy expenses for maintenance in our model are given by

$$E_{\text{m}}(x, y, T) = \rho_1(x + y)^{\rho_2} r_{\text{m}}(x, y, T). \quad (\text{A10})$$

The temperature term ( $r_{\text{m}}$ ) follows the description given by equations (A2)–(A9) with the respective parameter estimates ( $\gamma_{\text{m, opt}}$ ,  $\nu_{\text{m, opt}}$ ,  $\gamma_{\text{m, max}}$ ,  $\nu_{\text{m, max}}$ ,  $\vartheta_{\text{m}}$ , and  $\theta_{\text{m}}$ ) presented in table 2. The intercept of the maximum temperature for metabolism had to be corrected from 35° to 36.5°C so that newborns at a mass of 0.0018 g had a higher maximum than optimum temperature, which was not the case in Karås and Thoresson (1992). All other parameters were adopted from their model. Since respiration costs in their model were indirectly estimated from other energetic parameters determined from feeding and growth experiments (Lessmark 1983), they can be assumed to reflect the routine metabolism of the fish including activity costs.

## Energy Acquisition

The amount of acquired energy is calculated from intake rate ( $I$ ) times assimilation efficiency ( $k_{\text{e}}$ ), which includes conversion efficiency and costs of specific dynamic action:

$$E_{\text{a}}(x, y, T) = k_{\text{e}} I(x, y, T). \quad (\text{A11})$$

The intake rate is assumed to follow a type II functional response, as observed for most planktivorous fish

(Jeschke et al. 2004). It is calculated from the total mass encounter rate ( $\eta$ ) and food handling time ( $H$ ) of an individual in cohort  $i$  according to

$$I(x_i, y_i, T) = \frac{\eta(x_i, y_i, T)}{1 + H(w_i, y_i, T)\eta(x_i, y_i, T)}. \quad (\text{A12})$$

Here, handling time limits the capacity to process and thus intake food. It is an allometric function of body mass and, since consumption scales with temperature according to the estimated hump-shaped function, handling time is inversely related to temperature:

$$H(x_i, y_i, T) = \xi_1 w_i^{\xi_2} \frac{1}{r_a(x, y, T)}. \quad (\text{A13})$$

Hence, the temperature term ( $r_a$ ) is of the same functional form as described by equations (A2)–(A9) and uses the parameter set for consumption (see table 2).

The total encounter rate of an individual is the sum of the cannibalistic ( $\eta_c$ ) and the zooplankton ( $\eta_z$ ) encounter rates:

$$\eta(x_i, y_i, T) = \eta_z(x_i, y_i, T) + \eta_c(x_i, y_i, T). \quad (\text{A14})$$

We assume that an individual encounters zooplankton prey mass at a rate that is given by the product of its attack rate ( $A_z$ ), resource density ( $R$ ), and prey mass ( $m$ ):

$$\eta_z(x_i, y_i, T) = A_z(x_i, y_i, T)Rm. \quad (\text{A15})$$

The zooplankton attack rate increases with temperature and body mass according to a hump-shaped function. Attack rate increases as the fish grow bigger due to higher mobility, but it decreases after reaching a maximum value ( $\hat{A}$ ) at optimal body size ( $w_{\text{opt}}$ ) due to reduced ability to detect prey (Persson et al. 1998; Byström and García-Berthou 1999). The zooplankton attack rate can thus be written as

$$A_z(x, y, T) = \hat{A} \left[ \frac{w}{w_{\text{opt}}} \exp\left(1 - \frac{w}{w_{\text{opt}}}\right) \right]^\alpha r_a(x, y, T). \quad (\text{A16})$$

The exponent  $\alpha$  determines how fast the attack rate increases with body size for small individuals. As for handling time, temperature dependence is given by the same set of equations (eqq. [A2]–[A9]) with the parameter estimates for consumption ( $\gamma_{a,\text{opt}}$ ,  $\nu_{a,\text{opt}}$ ,  $\gamma_{a,\text{max}}$ ,  $\nu_{a,\text{max}}$ ,  $\vartheta_a$ , and  $\theta_a$ ) presented in table 2.

Accordingly, the planktivorous consumer imposes predation pressure on the resource population. We assume that without planktivory the resource grows following semichemostat dynamics. This might be more adequate than the commonly used logistic growth when describing the population dynamics of zooplankton that are fed on by planktivorous freshwater fish (Persson et al. 1998). The zooplankton grows at a rate  $r_z(T)$  to a maximum carrying capacity of the system, referred to as  $K$ . Its dynamics can thus be described by

$$\frac{dR}{dt} = r_z(T)(K - R) - R \sum_i \frac{A_z(x_i, y_i, T)N_i}{1 + H(x_i, y_i, T)\eta(x_i, y_i, T)}. \quad (\text{A17})$$

Here the sum represents the functional response of the consumer. The growth rate of the resource shows a temperature dependence that can be described by the same mathematical formulation as the one used for the consumers (eqq. [A2]–[A6]). However, since the zooplankton resource was modeled as an unstructured population, the variables within the temperature term were not functions of body mass in this case (table 2). Temperatures of optimum ( $T_{z,\text{opt}}$ ) and maximum ( $T_{z,\text{max}}$ ) growth as well as the slope ( $Q_z$ ) were estimated by nonlinear least squares regression on data reported in a study on temperature effects on individual and population growth rates of *Daphnia magna* (fig. 1; Mitchell et al. 2004).

In addition to consumers' predation on the zooplankton, they also prey on smaller conspecifics (eq. [A13]). Their cannibalistic encounter rate, that is, the rate at which an individual of cohort  $i$  encounters potential conspecific victims in terms of their biomass, is given by the sum over all potential victim cohorts  $j$ :

$$\eta_c(x_i, y_i, T) = \sum_j A_c(c_i, \nu_j, x_i, y_i, T)(x_j + y_j)N_j. \quad (\text{A18})$$

Here,  $N_j$  is the density of the  $j$ th cohort,  $(x_j + y_j)$  is the total mass of a victim from this cohort, and  $A_c$  is the

cannibalistic attack rate. To model the consumers cannibalistic attack rate one has to account for the size structuring of the population of potential victims. It is the length ratio (victim/cannibal) that determines the outcome of an encounter, meaning that a victim has to be large enough to be detectable and small enough to be catchable (Christensen 1996; Lundvall et al. 1999). Hence, for a given cannibal length ( $c$ ), there is a range of victim lengths that are vulnerable to predation by the cannibal, referred to as the ‘‘cannibalism window.’’ It is defined by two linear functions of cannibal length,  $\delta c$  and  $\varepsilon c$ , where  $\delta$  and  $\varepsilon$  are the minimum and maximum victim/cannibal ratios, respectively. Within this region the relative attack rate resembles a tent function, which reaches its maximum at the optimal victim/cannibal ratio ( $\varphi c$ ) and decreases to 0 at the limits of the cannibalism window (for more detail see Claessen et al. 2000). The cannibalistic attack rate can thus be expressed as

$$A_c(c, v, x, y, T) = \begin{cases} \beta c^\sigma \frac{v - \delta c}{(\varphi - \delta)c} r_a(x, y, T) & \text{if } \delta c < v < \varphi c \\ \beta c^\sigma \frac{\varepsilon c - v}{(\varepsilon - \varphi)c} r_a(x, y, T) & \text{if } \varphi c < v < \varepsilon c. \\ 0 & \text{otherwise} \end{cases} \quad (\text{A19})$$

We assume that the cannibalistic attack rate scales with temperature according to the same function as the zooplankton attack rate.

## Mortality

The mortality ( $\mu_c$ ) due to cannibalism by larger conspecifics is calculated from the density of cannibals ( $N_i$ ) in cohort  $i$ , their attack rate, and their respective functional response. The per capita mortality rate in cohort  $j$  is thus given by

$$\mu_c(x_j, y_i, T) = \sum_i \frac{A_c(c_i, v_i, x_i, y_i, T) N_i}{1 + H(x_i, y_i, T) \eta(x_i, y_i, T)}. \quad (\text{A20})$$

Cannibalistic mortality directly depends on temperature, because the attack rate and handling time functions of the cannibal are temperature dependent.

Whenever the energy requirements of an individual are not met by the amount of energy intake, it starves and thus converts reversible mass into energy for maintenance. When the  $y/x$  ratio drops below a critical value ( $q_s$ ) the individual starves to death. Starvation mortality ( $\mu_s$ ) is thus given by

$$\mu_s(x, y) = \begin{cases} s(q_s x/y - 1) & \text{if } y < q_s x \\ 0 & \text{otherwise} \end{cases}. \quad (\text{A21})$$

It indirectly depends on temperature through temperature effects on energy budget. We further assume that besides mortality due to cannibalism and starvation, fish may die of other causes at a rate  $\mu_0$ , which is referred to as background mortality.

## Energy Allocation to Somatic Growth and Reproduction

Whenever the individual net energy gain ( $E_g$ ) is positive, the surplus energy is invested in growth. Since perch mature at a specific size rather than age (Thorpe 1977; Treasurer 1981), an individual in our model becomes an adult when it reaches the maturation size  $x_f$ . Energy for growth is allocated to reversible and irreversible mass during ontogeny in a manner that the  $y/x$  ratio asymptotically approaches a limit, which resembles the maximum condition that an individual can have. This ratio of reversible over irreversible mass is assumed to be larger in adults ( $q_A$ ) than in juveniles ( $q_J$ ) so that adults allocate a larger proportion of energy to reserves. The fraction ( $\kappa$ ) that is allocated to irreversible mass is given by

$$\kappa(x, y) = \begin{cases} \frac{1}{(1 + q_J)q_J} \frac{y}{x} & \text{if } x \leq x_f \\ \frac{1}{(1 + q_A)q_A} \frac{y}{x} & \text{if } x > x_f \end{cases}. \quad (\text{A22})$$

The rest of the energy is allocated to reversible mass such as fat, muscle, and gonads. We further assume that

the maximum amount of somatic mass of an adult equals the maximum juvenile condition ( $q_j x$ ) and that the rest is gonad mass. At the end of the growing season all adults with reversible mass exceeding  $q_j x$  invest the surplus energy ( $y - q_j x$ ) in reproduction. Mature individuals with reversible mass below  $q_j x$  do not reproduce. The gonad mass is converted into eggs on the first day of the following year. A conversion factor  $k_r$  accounts for losses due to egg respiration and male gonad mass. The number of eggs ( $F$ ) with mass  $w_b$  per individual is

$$F(x, y) = \begin{cases} \frac{k_r(y - q_j x)}{w_b} & \text{if } x > x_f \text{ and } y > q_j x \\ 0 & \text{otherwise} \end{cases} \quad (\text{A23})$$

**Table A1.** Bifurcation sensitivity analysis of parameters in the temperature-dependence term for a noncannibalistic ( $\beta = 0$ ) and a cannibalistic ( $\beta = 100$ ) population

Parameter	Cannibalistic		Noncannibalistic	
	Dynamics	Onset of GCs ( $^{\circ}\text{C}$ )	Dynamics	Onset of GCs ( $^{\circ}\text{C}$ )
Nonperturbed	FP, CD, GC	$\sim 16.5$	FP, GC	$\sim 17.0$
$\vartheta_a - 10\%$	CD, GC	$\sim 15.5$	GC	$\sim 12.5$
$\vartheta_a + 10\%$	FP, CD, GC	$\sim 17.0^a$	FP, GC <sup>a</sup>	$\sim 15.5$
$\theta_a - 10\%$	FP, CD, GC	$\sim 16.0$	FP, GC	$\sim 17.0$
$\theta_a + 10\%$	FP, CD, GC	$\sim 16.5$	FP, GC	$\sim 17.0$
$\gamma_{a,\max} - 10\%$	No sensitivity analysis <sup>b</sup>			
$\gamma_{a,\max} + 10\%$	CD, GC	$\sim 17.0^c$	FP, GC <sup>c</sup>	$\sim 17.5$
$\nu_{a,\max} - 10\%$	FP, CD, GC	$\sim 16.0$	FP, GC	$\sim 13.5$
$\nu_{a,\max} + 10\%$	FP, CD, GC	$\sim 16.0$	FP, GC	$\sim 17.0$
$\gamma_{a,\text{opt}} - 10\%$	CD, GC	$\sim 14.0^d$	FP, GC	$\sim 17.5$
$\gamma_{a,\text{opt}} + 10\%$	No sensitivity analysis <sup>b</sup>			
$\nu_{a,\text{opt}} - 10\%$	FP, CD, GC	$\sim 15.5$	FP, GC	$\sim 18.0$
$\nu_{a,\text{opt}} + 10\%$	FP, CD, GC	$\sim 16.5$	FP, GC	$\sim 16.0$
$\vartheta_m - 10\%$	FP, CD, GC	$\sim 17.0$	FP, GC <sup>e</sup>	$\sim 14.5$
$\vartheta_m + 10\%$	FP, CD, GC	$\sim 16.0$	FP, GC	$\sim 15.5$
$\theta_m - 10\%$	FP, CD, GC	$\sim 16.5$	FP, GC	$\sim 16.0$
$\theta_m + 10\%$	FP, CD, GC	$\sim 16.5$	FP, GC	$\sim 17.0$
$\gamma_{m,\max} - 10\%$	No sensitivity analysis <sup>b</sup>			
$\gamma_{m,\max} + 10\%$	FP, CD, GC	$\sim 16.0$	FP, GC	$\sim 16.0$
$\nu_{m,\max} - 10\%$	FP, CD, GC	$\sim 16.5$	FP, GC	$\sim 16.5$
$\nu_{m,\max} + 10\%$	FP, CD, GC	$\sim 16.0$	FP, GC	$\sim 17.0$
$\gamma_{m,\text{opt}} - 10\%$	FP, CD, GC	$\sim 17.0^f$	FP, GC <sup>e</sup>	$\sim 13.5$
$\gamma_{m,\text{opt}} + 10\%$	No sensitivity analysis <sup>b</sup>			
$\nu_{m,\text{opt}} - 10\%$	FP, CD, GC	$\sim 16.5$	FP, GC	$\sim 16.5$
$\nu_{m,\text{opt}} + 10\%$	FP, CD, GC	$\sim 16.0$	FP, GC	$\sim 17.0$
$T_{z,\max} - 10\%$	FP, CD, GC	$\sim 16.0$	FP, GC	$\sim 16.5$
$T_{z,\max} + 10\%$	FP, CD, GC	$\sim 16.0$	FP, GC	$\sim 16.5$
$T_{z,\text{opt}} - 10\%$	FP, CD, GC	$\sim 16.0$	FP, GC	$\sim 16.5$
$T_{z,\text{opt}} + 10\%$	FP, CD, GC	$\sim 16.0$	FP, GC	$\sim 16.5$
$Q_z - 10\%$	FP, CD, GC	$\sim 16.0$	FP, GC	$\sim 16.5$
$Q_z + 10\%$	FP, CD, GC	$\sim 16.0$	FP, GC	$\sim 16.5$

Note: The population dynamics are referred to as fixed point (FP), cannibal driven (CD), and generation cycle (GC). Threshold values for the onset temperatures, where the dynamics shift to generation cycles, were estimated by eye from the bifurcation plot to the nearest half-degree Celsius.

<sup>a</sup>Population extinct below  $13.5^{\circ}\text{C}$ .

<sup>b</sup> $T_{\text{opt}} \geq T_{\text{max}}$  for recruit consumption or metabolism.

<sup>c</sup>Population extinct below  $15.0^{\circ}\text{C}$ .

<sup>d</sup>Population extinct below  $13.0^{\circ}\text{C}$ .

<sup>e</sup>Population extinct below  $12.5^{\circ}\text{C}$ .

<sup>f</sup>Population extinct below  $12.0^{\circ}\text{C}$ .

**Table A2.** Bifurcation sensitivity analysis of the size scaling of resource attack rate ( $\alpha$ ) for a non-cannibalistic population and the “cannibalism window” ( $\delta$ ,  $\epsilon$ ) for a cannibalistic population

Parameter	Value	Species	Dynamics	Onset of GCs (°C)	Reference
$\alpha$	.47	Pikeperch	FP, GC	~14.0	Persson and Brönmark 2002b
$\alpha$	.62	Eurasian perch	FP, GC	~17.0	
$\alpha$	.65	Arctic char	FP, GC	~18.0	Byström and Andersson 2005
$\alpha$	.66	Bluegill sunfish	FP, GC	~18.5	Mittelbach 1981
$\alpha$	.67	Bream	FP, GC <sup>a</sup>	~19.0	Persson and Brönmark 2002a
$\alpha$	.68	Roach	FP, GC <sup>b</sup>	~19.5	Hjelm and Persson 2001
$\delta$ , $\epsilon$	.08, .4	Yellow perch	FP, CD, GC	~15.0	Persson et al. 2004
$\delta$ , $\epsilon$	.06, .45	Eurasian perch	FP, CD, GC	~16.5	
$\delta$ , $\epsilon$	.03, .7	Northern pike	FP, CD	...	Persson et al. 2004

Note: The population dynamics are referred to as fixed point (FP), cannibal driven (CD), and generation cycles (GCs). Threshold values for the onset temperatures, where the dynamics shift to generation cycles, were estimated by eye from the bifurcation plot to the nearest half-degree Celsius.

<sup>a</sup>The FP dynamics destabilize transiently to GCs within the temperature range 12.5°–14°C.

<sup>b</sup>The FP dynamics destabilize to multicohort (small-amplitude) GCs at 12.5°C, then to single-cohort GCs at 14°C. The FP and GCs are bistable in the range 12.5°–19.5°C.

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