

**Supporting information for:**

**Individual energy dynamics reveal non-linear interaction of stressors threatening  
migratory fish populations**

P. Catalina Chaparro-Pedraza<sup>1,2\*</sup>, André M. de Roos<sup>1,3</sup>

<sup>1</sup>Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, 1090 GE Amsterdam, The Netherlands.

<sup>2</sup>Eawag—Swiss Federal Institute of Aquatic Science and Technology, Dübendorf, Switzerland.

<sup>3</sup>The Santa Fe Institute, Santa Fe, NM, USA.

\*Correspondence to: Catalina.Chaparro@eawag.ch

This supplementary note includes

1. Appendix S1. The physiologically-structured population model
2. Appendix S2. Energy allocation effects of the habitat switch explained by dynamic energy budget theory
3. Table S1
4. Figures S1 to S6

## *Appendix S1. Physiologically–structured population model*

The physiologically structured population model follows the approach introduced by Persson et al. (1998) for populations with seasonal reproduction, in which the population is represented by a dynamic set of cohorts or year classes. Since reproduction occurs as a discrete event at a specific time in the year, all individuals that are born in the same reproductive event are considered equal and hence lumped into a single cohort and assumed to grow at the same rate. Thus, we can describe the dynamics of each cohort  $i \in \mathbb{N}$  by using a system of ordinary differential equations, which keeps track of the density of individuals  $N_i$ , their age  $A_i$ , their structural mass  $W_i$  and their reversible mass  $S_i$ . Juveniles are defined as individuals with structural mass smaller than the structural mass at maturity  $W_p$  and adults as individuals with structural mass equal or larger than  $W_p$ . For each cohort  $i$ , age is monotonically increasing with time,

$$\frac{d}{dt} A_i = 1 \tag{1}$$

The age of the individuals determines the stage, which in turn, determines the differential equations that describe the variation in density of individuals, their structural mass and stored energy reserves. The number of individuals decreases due to a mortality rate specific to each stage. In addition, the presmolts and postsmolts may die due to starvation. During the egg stage the structural mass and storage does not change. The dynamics of the structural and reversible mass in presmolts and postsmolts depend on the amount of food they encounter as well as the breeding migration period if they are adults. Equations (2), (3) and (4) below define the dynamics of eggs, presmolts and postsmolts, respectively.

for  $0 \leq A_i < a_h$

$$\begin{cases} \frac{d}{dt} N_i = -\mu_e N_i \\ \frac{d}{dt} W_i = 0 \\ \frac{d}{dt} S_i = 0 \end{cases}$$

(2)

for  $a_h \leq A_i < a_s$

$$\begin{cases} \frac{d}{dt} N_i = \begin{cases} -\mu_r N_i & \text{if } \frac{S_i}{W_i} > q_s \\ -\left(\mu_r N_i + \varphi\left(q_s \frac{W_i}{S_i} - 1\right)\right) & \text{if } S_i > 0 \text{ and } \frac{S_i}{W_i} \leq q_s \\ -\infty & \text{otherwise} \end{cases} \\ \frac{d}{dt} W_i = \begin{cases} \zeta_W \left(\kappa \frac{R_r}{K + R_r} j_a W_i^{2/3} - j_m W_i\right) & \text{if } \kappa \frac{R_r}{K + R_r} j_a W_i^{2/3} > j_m W_i \\ 0 & \text{otherwise} \end{cases} \\ \frac{d}{dt} S_i = \begin{cases} (1 - \kappa) \frac{R_r}{K + R_r} j_a W_i^{2/3} & \text{if } \kappa \frac{R_r}{K + R_r} j_a W_i^{2/3} > j_m W_i \\ \frac{R_r}{K + R_r} j_a W_i^{2/3} - j_m W_i & \text{otherwise} \end{cases} \end{cases}$$

for  $a_s \leq A_i$

$$\begin{cases} \frac{d}{dt} N_i = \begin{cases} -\mu_s N_i & \text{if } \frac{S_i}{W_i} > q_s \\ -\left(\mu_s N_i + \varphi\left(q_s \frac{W_i}{S_i} - 1\right)\right) & \text{if } S_i > 0 \text{ and } \frac{S_i}{W_i} \leq q_s \\ -\infty & \text{otherwise} \end{cases} \\ \frac{d}{dt} W_i = \begin{cases} \zeta_W \left(\kappa f_s j_a W_i^{2/3} - j_m W_i\right) & \text{if } c1 \text{ and } (\sim c2 \text{ or } \sim c3) \\ 0 & \text{otherwise} \end{cases} \\ \frac{d}{dt} S_i = \begin{cases} (1 - \kappa) f_s j_a W_i^{2/3} & \text{if } c1 \text{ and } (\sim c2 \text{ or } \sim c3) \\ f_s j_a W_i^{2/3} - j_m W_i & \text{if } \sim c1 \text{ and } (\sim c2 \text{ or } \sim c3) \\ -(j_m W_i + C j'_m W_i^{\gamma}) & \text{if } c2 \text{ and } c3 \end{cases} \end{cases}$$

(4)

In this last equation  $c1$ ,  $c2$  and  $c3$  represent the conditions  $\kappa f_s j_a W_i^{2/3} > j_m W_i$ ,  $t_{um} \leq t \leq t_{dm}$ , and  $W_p \leq W_i$  respectively, while  $\sim c1$ ,  $\sim c2$  and  $\sim c3$  refer to the situation that these conditions do not hold. When the conditions are true, the  $\kappa$  fraction of the amount of assimilates necessary is sufficient to meet metabolic maintenance ( $c1$ ), the current time corresponds to the breeding migration period ( $c2$ ) and the cohort is adult ( $c3$ ).

Whenever a juvenile cohort reaches the maturation size  $W_i = W_p$ , at a particular time  $t = t_p$ , a maturation event occurs. At a maturation event, the juvenile cohort becomes an adult cohort. This does not affect any cohort statistics:

$$\begin{cases} A_i(t_p) = A_i(t_p^-) \\ N_i(t_p) = N_i(t_p^-) \\ W_i(t_p) = W_i(t_p^-) \\ S_i(t_p) = S_i(t_p^-) \end{cases}$$

(5)

Reproduction occurs instantaneously at  $t_{rn} = n t_y + t_r$ , where  $n \in \mathbb{N}$ . At a reproductive event, a new cohort 0 is formed from the reversible biomass of adults, if their reversible:structural mass ratio exceeds the reversible:structural mass ratio with which the adults matured:

$$\begin{cases} A_0(t_{rn}) = 0 \\ N_0(t_{rn}) = \left( \sum_{i \in \{j \leq n | W_j \geq W_p\}} N_i \cdot \max \left( S_i - \frac{S_p}{W_p} W_i, 0 \right) \right) \frac{\zeta_e}{W_e} \\ W_0(t_{rn}) = \kappa W_b \\ S_0(t_{rn}) = (1 - \kappa) W_b \end{cases}$$

(6)

At the same time, all other cohorts are renumbered and the reversible mass of the reproducing adults is set to the amount that makes their reversible:structural mass ratio equal to their reversible:structural mass ratio at maturation.

$$\left\{ \begin{array}{l} A_{i+1}(t_{rn}) = A_i(t_{rn}^-) \\ N_{i+1}(t_{rn}) = N_i(t_{rn}^-) \\ W_{i+1}(t_{rn}) = W_i(t_{rn}^-) \\ S_{i+1}(t_{rn}) = \begin{cases} \min\left(S_i(t_{rn}^-), \frac{S_p}{W_p} W_i(t_{rn}^-)\right) & \text{if } W_i \geq W_p \\ S_i(t_{rn}^-) & \text{otherwise} \end{cases} \end{array} \right. \quad (7)$$

The resource density in the breeding habitat grows following a semi-chemostat growth and declines by foraging of presmolts (8).

$$\frac{d}{dt} R_r = \rho(R_{max} - R_r) - \frac{R_r}{K + R_r} j_a \sum_{i \in \{j \leq n | a_h < a_j < a_s\}} N_i W_i^{2/3} \quad (8)$$

*Appendix S2. Energy allocation effects of the habitat switch explained by dynamic energy budget theory*

Dynamic energy budget (DEB) theory provides a conceptual framework to describe the individual life history based on individual energetic dynamics. DEB theory describes the rules by which an individual assimilates energy and utilizes it to grow, reproduce and cover metabolic maintenance (Kooijman and Metz 1984; Kooijman 2010; Nisbet et al. 2000). It has been used to describe the life history of several species including salmonids (Pecquerie et al. 2011). In particular, the net assimilation model offers a conceptual explanation for the negative effect on fecundity caused by an increase in food abundance. This model assumes that a fraction  $\kappa$  of assimilates is allocated to first meet metabolic maintenance with the remainder of this fraction allocated to growth in structural mass, while a fraction  $1 - \kappa$  is allocated to growth in reversible mass to be used for reproduction and covering energetic deficits during starvation periods. Given the assumption that metabolic maintenance is deducted from the fraction  $\kappa$ , a change in the proportion of assimilates required to meet metabolic maintenance affects the proportion of assimilates allocated to growth in structural mass but not the fraction allocated to growth in reversible mass. When an individual experiences a step-up change in food, the amount of assimilates available for growth, reproduction and metabolic maintenance increases. However, the amount of assimilates required to meet metabolic maintenance remains constant because the somatic structure of the individual does not suddenly change. Since the amount of total assimilates increases, the proportion of assimilates to meet metabolic maintenance thus decreases with the surplus now being allocated to growth in structural mass. Therefore, the proportion of assimilates allocated to growth in structural mass increases, while the proportion of assimilates allocated to reversible mass, and thus to reproduction remains constant. The model hence predicts that an individual that experiences a step-up change in food has lower energy density (lower ratio

of reversible to structural mass) and consequently, lower mass-specific fecundity than an individual of the same size that never experiences a change in food, in line with data presented in Fig S6. Furthermore, the model predicts that this bias toward increased growth in structural mass compared to reversible mass is larger in individuals experiencing a large step-up change in food than in those experiencing a small one. Consequently, individuals that experience a large change in food grow larger (are bigger) and have a lower energy density (are leaner)

**Table S1.** Compensatory growth studies that reported fecundity

Species	Growth	Reduced fecundity due to step-up change?	Average individual fecundity		Units	Reference
			After step-up change in food	Control		
<i>Daphnia magna</i> (Cladoceran)	Indeterminate	Yes	15.1 *	60.1 *	eggs	(Kooijman, unpublished)
<i>Poecilia reticulata</i> (Fish)	Indeterminate	Yes	40.6 *	52.3 *	eggs	(Auer et al. 2010)
<i>Phalloptycus januarius</i> (Fish)	Indeterminate	Yes	4.5 *	7.5 *	eggs/week	(Pollux and Reznick 2011)
<i>Uta stansburiana</i> (Lizard)	Indeterminate	Yes	3.53 *	5.1 *	eggs/clutch	(Sinervo and Doughty 1996)
<i>Aedes aegypti</i> (Insect)	Determinate	Yes	49 *	70 *	eggs	(Zeller and Koella 2016)
<i>Larinioides sclopetarius</i> (Arachnid)	Determinate	Yes	384 **	772 **	eggs	(Kleinteich, Wilder, and Schneider 2015)
<i>Coturnix coturnix</i> (Bird)	Determinate	No				(Hassan et al. 2003)
<i>Mus musculus</i> (Mammal)	Determinate	No				(Zamiri 1978)

\*Data digitalized from figures in the original publication

\*\*Data listed in the original publication

## References

- Auer, Sonya K., Jeffrey D. Arendt, Radhika Chandramouli, and David N. Reznick. 2010. "Juvenile Compensatory Growth Has Negative Consequences for Reproduction in Trinidadian Guppies (*Poecilia Reticulata*)."  
*Ecology Letters* 13 (8): 998–1007. <https://doi.org/10.1111/j.1461-0248.2010.01491.x>.
- Hassan, S. M., M. E. Mady, A. L. Cartwright, H. M. Sabri, and M. S. Mobarak. 2003. "Effects of Early Feed Restriction on Some Performance and Reproductive Parameters in Japanese Quail (*Coturnix Coturnix Japonica*)."  
*International Journal of Poultry Science* 13 (6): 323–28.
- Kleinteich, Anja, Shawn M. Wilder, and Jutta M. Schneider. 2015. "Contributions of Juvenile and Adult Diet to the Lifetime Reproductive Success and Lifespan of a Spider."  
*Oikos* 124 (2): 130–38. <https://doi.org/10.1111/oik.01421>.
- Kooijman, S. a. L. M. 2010. *Dynamic Energy Budget Theory for Metabolic Organisation*. Vol. 1. <https://doi.org/10.1098/rstb.2010.0167>.
- Kooijman, S. A. L. M., and J. A. J. Metz. 1984. "On the Dynamics of Chemically Stressed Populations: The Deduction of Population Consequences from Effects on Individuals."  
*Hydrobiological Bulletin* 17 (1): 88–89. <https://doi.org/10.1007/BF02255198>.
- Nisbet, R. M., E. B. Muller, K. Lika, and S. A L M Kooijman. 2000. "From Molecules to Ecosystems through Dynamic Energy Budget Models."  
*Journal of Animal Ecology* 69 (6): 913–26. <https://doi.org/10.1046/j.1365-2656.2000.00448.x>.

- Pecquerie, Laure, Leah R. Johnson, Sebastiaan A L M Kooijman, and Roger M. Nisbet. 2011. "Analyzing Variations in Life-History Traits of Pacific Salmon in the Context of Dynamic Energy Budget (DEB) Theory." *Journal of Sea Research* 66 (4): 424–33. <https://doi.org/10.1016/j.seares.2011.07.005>.
- Persson, Lennart, Kjell Leonardsson, André M. De Roos, Mats Gyllenberg, and Bent Christensen. 1998. "Ontogenetic Scaling of Foraging Rates and the Dynamics of a Size-Structured Consumer-Resource Model." *Theoretical Population Biology* 54 (3): 270–93. <https://doi.org/10.1006/tpbi.1998.1380>.
- Pollux, B. J A, and David N. Reznick. 2011. "Matrotrophy Limits a Female's Ability to Adaptively Adjust Offspring Size and Fecundity in Fluctuating Environments." *Functional Ecology* 25 (4): 747–56. <https://doi.org/10.1111/j.1365-2435.2011.01831.x>.
- Sinervo, Barry, and Paul Doughty. 1996. "Interactive Effects of Offspring Size and Timing of Reproduction on Offspring Reproduction: Experimental, Maternal, and Quantitative Genetic Aspects" 50 (3): 1314–27.
- Zamiri, M J. 1978. "Effects of Reduced Food Intake on Reproduction in Mice." *Australian Journal of Biological Sciences* 31: 629–39.
- Zeller, Michael, and Jacob C. Koella. 2016. "Effects of Food Variability on Growth and Reproduction of *Aedes Aegypti*." *Ecology and Evolution* 6 (2): 552–59. <https://doi.org/10.1002/ece3.1888>.