

Supplementary materials for "The consequences of density-dependent individual growth for sustainable harvesting and management of fish stocks"

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Underlying equations of the dynamic energy budget model

In the underlying Dynamic Energy Budget (DEB) model, individuals are characterized by the energy stored in lean, or irreversible mass (E_m). In DEB theory, it is assumed that energy in lean mass scales with the mass of an individual through the mass specific energy density (d_m). Likewise, the mass is assumed to scale with the volume through the mass density (d_v) and the volume can be related to the length cubed using a shape coefficient (δ_m) (Kooijman, 2010).

All life history processes are expressed in terms of the energy stored in the lean mass of an individual. Energy ingestion is assumed to scale with the surface area of an individual, and thus with lean mass to the power two-third ($E_m^{2/3}$). In addition, the ingestion rate scales with the resource density following a scaled type II functional response ($f(R) = \frac{R}{R_h + R}$), with a half saturation constant R_H . The ingestion rate furthermore scales with the maximum ingestion rate scalar I_{max} , which represents the maximum ingestion rate per unit surface area. If we assume assimilation efficiency is constant, we can express the total assimilated energy as $\alpha f(R) E_m^{2/3}$, in which α represents the maximum ingestion rate per unit surface area times the assimilation efficiency, which is the efficiency of taking up energy in the body.

The energy dynamics of individuals with plastic growth are based on the DEB model specified by Jager et al. (2013). This model assumes that a fraction κ of the assimilated energy is used for somatic processes, while the remainder of the energy is used for maturation in juveniles and reproduction in adults (E_r). The energy allocated to somatic processes is first used to cover maintenance costs, which scale with the energy stored in lean mass through the energy specific

maintenance costs (b). The remainder of the energy allocated to somatic processes is converted to lean mass with conversion efficiency y_m . Likewise, the conversion efficiency of ingested energy to reproductive energy is y_r . These conversion efficiencies represent the efficiency of converting energy present in the body to tissue after allocation. This results in the following model for energy usage within an individual with plastic growth:

$$\frac{dE_m}{dt} = y_m(\kappa\alpha f(R)E_m^{2/3} - bE_m) \quad (\text{S1a})$$

$$\frac{dE_r}{dt} = y_r(1 - \kappa)\alpha f(R)E_m^{2/3} \quad (\text{S1b})$$

The growth dynamics from this model is density-dependent, because the growth in lean mass depends on the energy consumption of the individual and hence on the resource density R , which might be depressed by population foraging (De Roos & Persson, 2002; De Roos et al., 2003). To obtain the growth equation for an individual with density-independent growth, we decouple the energy allocation to somatic processes from energy assimilation, by scaling energy allocation to somatic processes with a constant value (ζ) instead of the scaled resource density. As in the model with density-dependent growth, we assume that all energy not used for somatic growth and maintenance is used for reproduction. This results in the following equation for the growth in lean mass for individuals with density-independent growth:

$$\frac{dE_m}{dt} = y_m(\kappa\alpha\zeta E_m^{2/3} - bE_m) \quad (\text{S2a})$$

$$\frac{dE_r}{dt} = y_r(\alpha f(R)E_m^{2/3} - \kappa\alpha\zeta E_m^{2/3}) = y_r\alpha(f(R) - \kappa\zeta)E_m^{2/3} \quad (\text{S2b})$$

We combine the equation for the energy dynamic with and without density dependence in growth. To do so, we assume that the level of plasticity in individual growth is given by a separate parameter (ϕ). This resulted in our final formulation of the individual energetic model:

$$\frac{dE_m}{dt} = y_m \left(\phi\kappa\alpha f(R)E_m^{2/3} + (1 - \phi)\kappa\alpha\zeta E_m^{2/3} - bE_m \right) \quad (\text{S3a})$$

$$\frac{dE_r}{dt} = y_r \left(\alpha f(R)E_m^{2/3} - \left(\phi\kappa\alpha f(R)E_m^{2/3} + (1 - \phi)\kappa\alpha\zeta E_m^{2/3} \right) \right) \quad (\text{S3b})$$

To convert the energy dynamics of a single individual to the dynamics of the entire population, we follow allometric scaling from dynamic energy budget theory (Kooijman, 2000). We assume

that the energy stored in lean mass scales with the mass of an individual through the mass-specific energy density (d_m) and likewise the mass scales with the volume through the mass density (d_v) and the volume can be related to the length cubed using a shape coefficient (δ_m).

$$\ell = \frac{V^{1/3}}{\delta_m} = \frac{W^{1/3}}{d_v^{1/3} \delta_m} = \frac{E_m^{1/3}}{d_m^{1/3} d_v^{1/3} \delta_m} \quad (\text{S4})$$

By using these rules, the equations for the individual energy dynamics can be rewritten for individual growth in length ($g(\ell, R)$). To derive the individual fecundity ($\beta(\ell, R)$) from the energy equations we need to know the energy per egg which we estimated by van der Veer et al. (2001). In addition, we use some composite parameters representing the asymptotic size under unlimited food conditions (ℓ_∞), the Von Bertalanffy growth rate scalar (r_B) and the individual fecundity scalar (r_F):

$$\ell_\infty = \frac{\alpha \kappa}{b d_m^{1/3} d_v^{1/3} \delta_m} \quad (\text{S5a})$$

$$r_B = \frac{\gamma_m b}{3} \quad (\text{S5b})$$

$$r_F = \frac{b \gamma_r}{\ell_b^3} \quad (\text{S5c})$$

This eventually results in the model described in table ??.

References for supplementary information

- De Roos, A. M., & Persson, L. (2002). Size-dependent life-history traits promote catastrophic collapses of top predators. *Proceedings of the National Academy of Sciences*, *99*(20), 12907–12912. doi: 10.1073/pnas.192174199
- De Roos, A. M., Persson, L., & McCauley, E. (2003). The influence of size-dependent life-history traits on the structure and dynamics of populations and communities. *Ecology Letters*, *6*(5), 473–487. doi: 10.1046/j.1461-0248.2003.00458.x
- Jager, T., Martin, B. T., & Zimmer, E. I. (2013). DEBkiss or the quest for the simplest generic model of animal life history. *Journal of theoretical biology*, *328*, 9–18. doi: 10.1016/j.jtbi.2013.03.011

Kooijman, S. A. L. M. (2000). *Dynamic energy and mass budgets in biological systems*. Cambridge university press.

Kooijman, S. A. L. M. (2010). *Dynamic energy budget theory for metabolic organisation*. Cambridge university press.

van der Veer, H. W., Kooijman, S. A. L. M., & van der Meer, J. (2001). Intra- and interspecies comparison of energy flow in North Atlantic flatfish species by means of dynamic energy budgets. *Journal of Sea Research*, 45(3-4), 303–320. doi: 10.1016/S1385-1101(01)00061-2