Supplementary Material

DEB-IPM Model Description

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Energetics of individuals

The energetics of individuals in the model follows the Kooijman-Metz model (Kooijman & Metz, 1984), containing several assumptions on individual body shape, energy acquisition, energy allocation, growth and reproduction.

(1) Individuals in the model are isomorphic, meaning that body surface area and volume are proportional to body length L^2 and L^3.

(2) Individual food ingestion rate I, is assumed to be proportional to the product of the maximum ingestion rate I_{max}, experienced feeding level Y, and body surface area L^2.

$$I = I_{max} Y L^2$$

(3) Food ingested by individuals is assimilated with a constant efficiency ϵ.

$$\epsilon I$$

(4) A constant fraction of assimilated energy κ is allocated to metabolic maintenance and growth.

$$\kappa \epsilon I$$

4.1 Metabolic maintenance take precedence over growth, and is proportional to body volume following ξL^3.

4.2 The amount of assimilated energy in an individual that is allocated to maintenance therefore equals $\xi \mathrm{L}^3 \kappa \epsilon I$.

4.3 and the amount of assimilated energy in an individual that is allocated to growth: $\kappa \epsilon I - \xi \mathrm{L}^3 \kappa \epsilon I$

(5) The remaining assimilated energy after allocation to maintenance and growth is allocated to reproduction in mature individuals and gonad development in immature individuals. It can be expressed as:

$$(1 - k)\epsilon I$$

(6) Individual growth over time follows a von Bertallanfy growth curve with parameters growth rate $\dot{r_B}$ and maximum length L_m.

$$\frac{dL}{dt} = \dot{r_B}(L_m \cdot Y - L)$$

6.1 Maximum body size under conditions of unlimited resources depends on food ingestion and the scaling of energy maintenance costs with volume: $L_m = \frac{\kappa\epsilon I_{max}}{\xi}$

(7) Reproduction scales hyperallometrically with body size and depends on the current length L, maximum length L_m, maximum number of offspring by an individual of maximum length R_m, and food conditions Y.

$$YR_m \frac{L^2}{L_m^2}$$

7.1 Maximum reproduction rate depends on the allocated energy, food ingestion rate, maximum size, and the energy investment per single offspring β that is of length at birth L_b.

$$R_m = \frac{(1-k)\epsilon I_{max} L_m^2}{\beta L_b^3}.$$

(8) Maximum length L_m is proportional to κ (6.1), and the maximum reproduction rate R_m is proportional to $(1-k)$(7.1). This controls for the law of energy conservation in the model.

These assumptions are incorporated in the four fundamental functions that describe population dynamics in the DEB-IPM.

Environmental conditions

Individuals in the model can experience either unfavourable or favourable environmental conditions at every time step. This is translated in the model as experiencing low feeding levels $E(Y)_{low}$, or high feeding levels $E(Y)_{high}$. These feeding levels provide important conditional statements on individual development in the DEB-IPM depending on the reproduction strategy.

Basic Fish model

Here we continue with a case by case description of the fundamental functions included in the DEB-IPM, starting with the basic adaptations for fish, and continuing with separate models for different reproductive strategies.

Survival function

The survival of fish over the course of individual development follows two main processes (1) a decrease in natural predation with increased body size, and (2) an increase in sensitivity to anthropogenic fishing pressure with increased body size. These processes, which can both be modelled with exponential functions, are acting upon the individual simultaneous. Survival can therefore be modelled using a single additive exponential (eqn. x), similar to that of Heppel et al. (1999).

$$S(L(t)) = \begin{cases} e^{-\left(\mu_P \frac{L_m}{L(t)}\right)-\left(\mu_F \frac{L(t)}{L_m}\right)}, & \text{if } L \leq \frac{L_m E(Y)}{k} \\ 0, & \text{otherwise.} \end{cases} \tag{1}$$

Where μ_P and μ_F are the background mortality rates of individuals of size L_m to predation and fishing respectively. The condition $L \leq \frac{L_m E(Y)}{k}$ accounts for death from starvation. Individuals die from starvation when they reach a body length at which maintenance requirements exceeds the total amount of assimilated energy.

Growth function

Fish typically show an indeterminate and food supply driven growth in body size from larval size at hatching L_b, to a maximum size L_m, over multiple orders of magnitude (Ref.). The underlying growth function in the standard Kooijman and Metz model already adequately captures this process based on the von Bertallanfy growth curve (see Energetic conditions assumption 6). We therefore do not change the fundamental growth function in the DEB-IPM.

The fundamental growth function in the DEB-IPM is conditional on survival and describes the probability that an individual of length L at time t, grows to length L' at $t+1$. Following IPM literature, we use a Gaussian distribution (REFs).

$$G(L', L(t)) = \frac{1}{\sqrt{2\pi\sigma_L^2(L(t+1))}} e^{\frac{-(L'-E(L(t+1))^2}{2\sigma_L^2(L(t+1))}} \tag{2}$$

Where $E(L(t+1))$ is the expected growth of individuals of length L, and σ_L^2 individual variance in length at $t+1$, itself dependent on the standard deviation of expected feeding level $\sigma(Y)$.

$$E(L(t+1)) = \begin{cases} L(t)e^{-\dot{r_B}} + (1-e^{-\dot{r_B}})L_m E(Y), & \text{if } L \leq L_m E(Y), \\ 0, & \text{otherwise.} \end{cases} \tag{3}$$

$$\sigma^2(L(+1)) = \begin{cases} (1-e^{-\dot{r_B}})L_m^2\sigma^2(Y), & \text{if } L \leq L_m E(Y), \\ 0, & \text{otherwise.} \end{cases} \tag{4}$$

Reproduction function

Fish widely differ widely in their reproductive strategies in terms of the timing and the number of breeding events over the life cycle. However, across species they are also very similar in terms of hyperallometric scaling of reproductive output with body size (Barneche et al. 2018). This means that large females contribute disproportionally to the reproductive output of a population. The standard DEB-IPM already accounts for this by assuming a quadratic scaling of reproductive output with body size.

$$R(L(t)) = \begin{cases} 0, & \text{if } L_b < L < L_p, \\ \phi\left(E(Y)R_m\dfrac{L(t)^2}{L_m^2}\right), & \text{if } L_p < L < L_m E(Y) \\ \phi\left(\dfrac{R_m}{1-k}\left[E(Y)L(t)^2 - \dfrac{kL(t)^3}{L_m}\right]\right), & \text{if } L_m < L \leq \frac{L_m E(Y)}{k} \end{cases} \tag{5}$$

In which reproduction occurs in individuals that have reached maturation length Lp, and energy is allocated from reproduction to maintenance if maintenance costs cannot be covered due to starvation, i.e. $L > L_m E(Y)$. R_m refers to the maximum number of eggs produced by a female of size L_m. The output of the function therefore expresses the number of eggs produced. However, the model model tracks the growth and survival individuals starting from hatching. Therefore, we multiply the outcome of the reproduction function by a parameter ϕ that expresses the background mortality during the egg phase.

Parent - offspring function

The number of breeding events during a single breeding season differs between fish species and impacts the variation in offspring size $\sigma^2_{L_b}$, as measured at the next population census in the model at $t+1$. There is a gradient from income breeders, that will reproduce small batches of offspring daily during an extended breeding period, to total spawners releasing all eggs at a single event.

The variation in offspring size is a part of the fundamental parent-offspring function in the DEB-IPM. This Gaussian function describes the probability that the offspring of an individual of length L is of length L' at $t+1$.

$$D(L', L(t)) = \begin{cases} 0, & \text{if } L < L_p, \\ \dfrac{1}{\sqrt{2\pi\sigma^2_{L_b}(L(t)}} e^{\frac{-(L'-E_{L_b}(L(t))^2}{2\sigma^2_{L_b}(L(t))}}, & \text{otherwise.} \end{cases} \tag{6}$$

Semelparous breeders

Survival function

Semelparous species have a single reproductive event in their life cycle, after which they die. In the model, semelparous species reproduce if they have reached maturation length and environmental conditions are favourable. If conditions are unfavourable, individuals will skip breeding for that season and instead allocate the energy to further growth. This translates into a conditional statement on the survival function at time t, based on the body size, and on the environmental conditions at $t-1$. The survival function for semelparous species therefore becomes:

$$S(L(t)) = \begin{cases} e^{-\left(\mu_P \frac{L_m}{L(t)}\right)-\left(\mu_F \frac{L(t)}{L_m}\right)}, & \text{if } L \leq L_p \;\&\; L \leq \frac{L_m E(Y)}{\kappa}, \\ e^{-\left(\mu_P \frac{L_m}{L(t)}\right)-\left(\mu_F \frac{L(t)}{L_m}\right)}, & \text{if } L > L_p \;\&\; L \leq \frac{L_m E(Y)}{\kappa} \;\&\; E(Y)_{t-1} = E(Y)_{low}, \\ 0, & \text{if } L > L_p \;\&\; L \leq \frac{L_m E(Y)}{\kappa} \;\&\; E(Y)_{t-1} = E(Y)_{high}, \\ 0, & \text{otherwise.} \end{cases} \tag{7}$$

Growth function

Semelparity does not impose additional conditions on the fundamental growth function in the model.

$$G(L', L(t)) = \frac{1}{\sqrt{2\pi\sigma_L^2(L(t+1))}} e^{\frac{-(L'-E(L(t+1))^2}{2\sigma_L^2(L(t+1))}} \tag{8}$$

Reproduction function

Semelparous species will pass up on the opportunity to breed in times of unfavourable environmental conditions. This translates into a conditional statement on the reproduction function of these species.

$$R(L(t)) = \begin{cases} 0, & \text{if } L_b < L < L_p, \\ 0, & \text{if } L_p < L < L_m E(Y) \;\&\; E(Y) = E(Y)_{low}, \\ \phi\left(E(Y) R_m \dfrac{L(t)^2}{L_m^2}\right), & \text{if } L_p < L < L_m E(Y) \;\&\; E(Y) = E(Y)_{high}, \\ \phi\left(\dfrac{R_m}{1-k}\left[E(Y) L(t)^2 - \dfrac{k L(t)^3}{L_m}\right]\right), & \text{if } L_m < L \leq \frac{L_m E(Y)}{k} \end{cases} \tag{9}$$

Parent-offspring function

Semelparity does not impose additional conditions on the fundamental parent-offspring function in the model.

$$D(L', L(t)) = \begin{cases} 0, & \text{if } L < L_p, \\ \frac{1}{\sqrt{2\pi\sigma^2_{L_b}(L(t)}} e^{\frac{-(L' - E_{L_b}(L(t))^2}{2\sigma^2_{L_b}(L(t))}}, & \text{otherwise.} \end{cases} \tag{10}$$

Species list and parameters

Table 1

Iteroparous obligate breeders

Iteroparous obligate breeders have multiple reproductive events over their life cycle. They reproduce every season regardless of environmental conditions. Their fundamental functions follow the basic fish model.

Survival function

$$S(L(t)) = \begin{cases} e^{-\left(\mu_P \frac{L_m}{L(t)}\right) - \left(\mu_F \frac{L(t)}{L_m}\right)}, & \text{if } L \leq \frac{L_m E(Y)}{k} \\ 0, & \text{otherwise.} \end{cases} \tag{11}$$

Growth function

$$G(L', L(t)) = \frac{1}{\sqrt{2\pi\sigma^2_L(L(t+1))}} e^{\frac{-(L' - E(L(t+1))^2}{2\sigma^2_L(L(t+1))}} \tag{12}$$

Reproduction function

$$R(L(t)) = \begin{cases} 0, & \text{if } L_b < L < L_p, \\ \phi\left(E(Y) R_m \frac{L(t)^2}{L_m^2}\right), & \text{if } L_p < L < L_m E(Y) \\ \phi\left(\frac{R_m}{1-k}\left[E(Y) L(t)^2 - \frac{k L(t)^3}{L_m}\right]\right), & \text{if } L_m < L \leq \frac{L_m E(Y)}{k} \end{cases} \tag{13}$$

Parent-offspring function

$$D(L', L(t)) = \begin{cases} 0, & \text{if } L < L_p, \\ \frac{1}{\sqrt{2\pi\sigma^2_{L_b}(L(t)}} e^{\frac{-(L' - E_{L_b}(L(t))^2}{2\sigma^2_{L_b}(L(t))}}, & \text{otherwise.} \end{cases} \tag{14}$$

Species list and parameters

Table 2

Iteroparous skip breeders

Iteroparous skip breeders have multiple reproductive events over their life cycle. They can pass up on the opportunity to breed under unfavourable environmental conditions. This imposes additional restrictions on the fundamental reproductive function. Apart from this, the functions are the same as in the basic fish model.

Survival function

$$S(L(t)) = \begin{cases} e^{-\left(\mu_P \frac{L_m}{L(t)}\right)-\left(\mu_F \frac{L(t)}{L_m}\right)}, & \text{if } L \leq \frac{L_m E(Y)}{k} \\ 0, & \text{otherwise.} \end{cases} \tag{15}$$

Growth function

$$G(L', L(t)) = \frac{1}{\sqrt{2\pi\sigma_L^2(L(t+1))}} e^{\frac{-(L'-E(L(t+1))^2}{2\sigma_L^2(L(t+1))}} \tag{16}$$

$$R(L(t)) = \begin{cases} 0, & \text{if } L_b < L < L_p, \\ 0, & \text{if } L_p < L < L_m E(Y) \text{ \& } E(Y) = E(Y)_{low}, \\ \phi\left((E(Y) R_m \frac{L(t)^2}{L_m^2}\right), & \text{if } L_p < L < L_m E(Y) \text{ \& } E(Y) = E(Y)_{high}, \\ \phi\left(\frac{R_m}{1-k}\left[E(Y)L(t)^2 - \frac{kL(t)^3}{L_m}\right]\right), & \text{if } L_m < L \leq \frac{L_m E(Y)}{k} \end{cases} \tag{17}$$

Parent-offspring function

$$D(L', L(t)) = \begin{cases} 0, & \text{if } L < L_p, \\ \frac{1}{\sqrt{2\pi\sigma_{L_b}^2(L(t)}} e^{\frac{-(L'-E_{L_b}(L(t))^2}{2\sigma_{L_b}^2(L(t))}}, & \text{otherwise.} \end{cases} \tag{18}$$

Species list and parameters

Table 3