

Formulas for Daphnia model as extracted from Ando thesis

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1 Renewal equations

The model described here matches the formulation by [Ando et al. \[2020\]](#).

Dynamical variables

- resource $r(t)$
- discounted consumption

$$c_d(t) = \frac{r_{\max}}{\varphi_{\max}} \frac{c(t)}{f_r(r(t))},$$

where $c(t)$ is the consumption, and

$$f_r(r) = \frac{\sigma r}{1 + \sigma r}$$

is the Holling-type II functional response to resource.

- discounted birth rate

$$b_d(t) = \frac{b(t)}{f_r(r(t))},$$

where $b(t)$ is the birth rate,

- maturation age $\rho_A(t)$ as a quotient of maturation age $a_A(t)$ and a_{\max} ,

$$a_A(t) = \rho_A(t) a_{\max},$$

- discounted maturation size $s_{d,A}(t)$ (defined below).

Original equations Original form:

$$\text{population effect:} \quad e(t) = \int_0^{a_{\max}} f_r(r(t)) s^2(a, t) e^{-\mu a} b(t - a) da \quad (1)$$

$$\text{resource evolution:} \quad \dot{r}(t) = f_0(r(t)) - \varphi_{\max} e(t) \quad (2)$$

$$\text{size threshold:} \quad 0 = s(a_A(t), t) - s_A \quad (3)$$

$$\text{birth rate:} \quad b(t) = r_{\max} e(t), \quad \text{where} \quad (4)$$

$$\text{size } s \text{ at age } a \text{ solves} \quad s'(\alpha) = \gamma_g (s_{\max} f_r(r(t + \alpha - a)) - s(\alpha)), s(0) = s_b \text{ at } \alpha = a$$

$$\begin{aligned} \text{such that} \quad s(a, t) &= e^{-\gamma_g a} s_b + \gamma_g s_{\max} \int_0^a e^{-\gamma_g(a-\alpha)} f_r(r(t + \alpha - a)) d\alpha \\ &= e^{-\gamma_g a} s_b + \gamma_g s_{\max} \int_0^a e^{-\gamma_g \alpha} f_r(r(t - \alpha)) d\alpha, \end{aligned} \quad (5)$$

where we substituted $\alpha_{\text{new}} = a - \alpha_{\text{old}}$ in the final equation. The consumption-free resource growth rate is

$$f_0(r) = r_{\text{flow}} r(1 - r/C).$$

To reformulate this into a form where we have chains of integral delays, we introduce the purely accumulated part $s_d(a, t)$ of the individuals' size

$$s_d(a, t) = \int_0^a e^{-\gamma_g \alpha} \gamma_g s_{\text{max}} f_r(r(t - \alpha)) d\alpha, \quad \text{such that} \\ s(a, t) = e^{-\gamma_g a} s_b + s_d(a, t).$$

Replacing b with its discounted form b_d changes (4) into

$$b_d(t) = \int_{a_A(t)}^{a_{\text{max}}} r_{\text{max}} s^2(a, t) e^{-\mu a} f_r(r(t - a)) b_d(t - a) da \\ = \int_{a_A(t)}^{a_{\text{max}}} r_{\text{max}} [e^{-\gamma_g a} s_b + s_d(a, t)]^2 e^{-\mu a} f_r(r(t - a)) b_d(t - a) da. \quad (6)$$

We also note that the integrals in (2) and (6) can both be expressed using the antiderivative of the population effect density,

$$d_{\text{eff}}(a, t) = \int_0^a r_{\text{max}} s^2(\alpha, t) e^{-\mu \alpha} f_r(r(t - \alpha)) b_d(t - \alpha) d\alpha, \\ = \int_0^a r_{\text{max}} [e^{-\gamma_g \alpha} s_b + s_d(\alpha, t)]^2 e^{-\mu \alpha} f_r(r(t - \alpha)) b_d(t - \alpha) d\alpha,$$

namely through

$$c_d(t) = d_{\text{eff}}(a_{\text{max}}, t) \quad (\text{discounted consumption term}) \quad (7)$$

$$b_d(t) = d_{\text{eff}}(a_{\text{max}}, t) - d_{\text{eff}}(a_{\text{max}} \rho_A(t), t) \quad (\text{equivalent of (6)}). \quad (8)$$

Reformulated equations Thus, in the new variables, the equations are

$$\text{resource evolution:} \quad \dot{r}(t) = f_0(r(t)) - \frac{\varphi_{\text{max}}}{r_{\text{max}}} f_r(r(t)) c_d(t) \quad (9)$$

$$\text{maturation age} \quad 0 = e^{-\gamma_g a_{\text{max}} \rho_A(t)} s_b + s_{d,A}(t) - s_A \quad (10)$$

$$\text{birth rate:} \quad b_d(t) = d_{\text{eff}}(a_{\text{max}}, t) - d_{\text{eff}}(a_{\text{max}} \rho_A(t), t), \quad (11)$$

$$\text{scaled consumption:} \quad c_d(t) = d_{\text{eff}}(a_{\text{max}}, t), \quad (12)$$

$$\text{scaled maturation size:} \quad s_{d,A}(t) = s_d(a_{\text{max}} \rho_A(t), t) \quad (13)$$

where the integral chain is

$$s_d(a, t) = \int_0^a \gamma_g s_{\text{max}} e^{-\gamma_g \alpha} f_r(r(t - \alpha)) d\alpha, \quad (14)$$

$$d_{\text{eff}}(a, t) = \int_0^a r_{\text{max}} [e^{-\gamma_g \alpha} s_b + s_d(\alpha, t)]^2 e^{-\mu \alpha} f_r(r(t - \alpha)) b_d(t - \alpha) d\alpha. \quad (15)$$

Inputs for DDE-Biftool's integral chains The dynamical variables are

$$x(t) = (r(t), \rho_A(t), b_d(t), c_d(t), s_{d,A}(t)).$$

Of these, we input the variables r and b_d into the integral chain,

$$y_{0,id}(a, t) = \begin{bmatrix} r(t-a) \\ b_d(t-a) \end{bmatrix}.$$

We define the integrands for the integral chain as

$$g_1(a, y_1, p_1) = \gamma_g s_{\max} e^{-\gamma_g a} \frac{\sigma y_1}{1 + \sigma y_1}, \quad y_1 = y_{0,id,1}, \quad p_1 = (\gamma_g, s_{\max}, \sigma)$$

$$g_2(a, y_2, p_2) = r_{\max} [e^{-\gamma_g a} s_b + y_{2,3}]^2 e^{-\mu a} \frac{\sigma y_{2,1}}{1 + \sigma y_{2,1}} y_{2,2}, \quad y_2 = \begin{bmatrix} y_{0,id,1} \\ y_{0,id,2} \\ y_{1,int} \end{bmatrix}, \quad p_2 = (s_b, r_{\max}, \gamma_g, \mu, \sigma),$$

and set initial values

$$y_{1,int}(0) = 0, \quad y_{2,int}(0) = 0.$$

Finally, we extract the components

$$y_{\text{sum}}(a, t) = \begin{bmatrix} y_{1,int}(a, t) \\ y_{2,int}(a, t) \end{bmatrix}$$

from the array of integral chain results $((y_{j,id}(a, t))^2_{j=0}, (y_{j,int}(a, t))^2_{j=1})$, choose the relative (to a_{\max}) ages

$$\tau_1 = \rho_A(t), \quad \tau_2 = 1,$$

and interpolate to get

$$y_{\tau}(t) = y_{\text{sum}}([\tau_1, \tau_2]a_{\max}, t) = \begin{bmatrix} y_{1,int}(\tau_1 a_{\max}, t) \\ y_{1,int}(\tau_2 a_{\max}, t) \\ y_{2,int}(\tau_1 a_{\max}, t) \\ y_{2,int}(\tau_2 a_{\max}, t) \end{bmatrix} \in \mathbb{R}^4.$$

We then combine the results

$$\begin{bmatrix} b_d(t) \\ c_d(t) \\ s_{d,A}(t) \end{bmatrix} = M y_{\tau}(t)$$

with

$$M = \begin{bmatrix} 0 & 0 & -1 & 1 \\ 0 & 0 & 0 & 1 \\ 1 & 0 & 0 & 0 \end{bmatrix}.$$

2 Initial non-trivial equilibrium

A non-trivial equilibrium

$$x_{nt} = (r, \rho_A, b_d, c_d, s_{d,A})$$

with non-zero b_d satisfies

$$c_d = \frac{r_{\max} f_0(r)}{\varphi_{\max} f_r(r)}, \quad (16)$$

$$s_{d,A} = s_A - e^{-\gamma_g a_{\max} \rho_A} s_b. \quad (17)$$

The integral in (14) can be solved in equilibrium:

$$s_d(a) = \frac{r\sigma s_{\max}}{r\sigma + 1} (1 - e^{-\gamma_g a}) \quad (18)$$

Thus, (13) provides another relation between $s_{d,A}$ and ρ_A :

$$s_{d,A} = \frac{r\sigma}{r\sigma + 1} s_{\max} (1 - e^{-a_{\max} \gamma_g \rho_A}). \quad (19)$$

Equating (17) and (19) results in an expression for ρ_A :

$$\rho_A = \frac{1}{a_{\max} \gamma_g} \log \left(\frac{s_{\max} f_r(r) - s_b}{s_{\max} f_r(r) - s_A} \right) \quad (20)$$

The integral $d_{\text{eff}}(a, t)$ has the following form in equilibrium:

$$d_{\text{eff}}(a) = r_{\max} f_r(r) b_d \int_0^a [e^{-\gamma_g a_{\max} \alpha} s_b + s_d(\alpha)]^2 e^{-\mu \alpha} d\alpha, \quad (21)$$

where $s_d(a)$ is given by (18), such that $d_{\text{eff}}(a)$ can be calculated explicitly. Consequently, b_d is determined by the relation (12):

$$b_d = \frac{c_d}{r_{\max} f_r(r) \int_0^{a_{\max}} [e^{-\gamma_g a_{\max} \alpha} s_b + s_d(a)]^2 e^{-\mu \alpha} d\alpha} \quad (22)$$

where, again, s_d is given in (18). Finally r is determined by the balance for births, (11), divided by b_d , assuming that $b_d > 0$:

$$1 = r_{\max} f_r(r) \int_{\rho_A a_{\max}}^{a_{\max}} [e^{-\gamma_g a_{\max} \alpha} s_b + s_d(a)]^2 e^{-\mu \alpha} d\alpha, \quad (23)$$

where the value for ρ_A in the lower integration boundary is given by (20). This value depends also on r , making this equation (23) implicit in r (however, the integral in (23) is explicitly known).

References

Alessia Ando et al. *Collocation methods for complex delay models of structured populations*. PhD thesis, Università degli Studi di Udine, 2020.