Growth and development

Individual growth

x = "size"

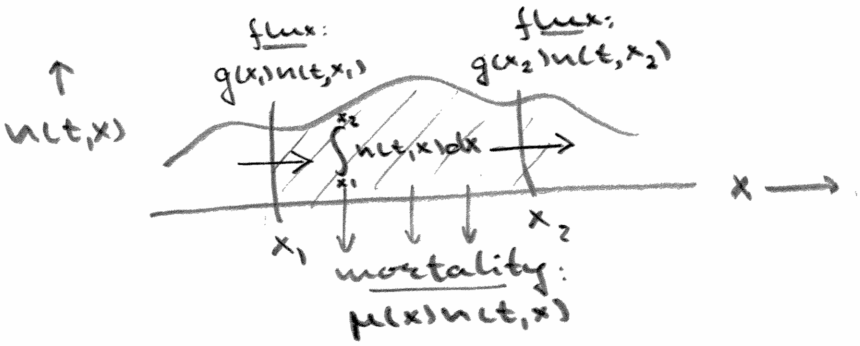
a = age

$$\frac{dx}{da} = g(x) > 0$$

$$x(0) = x_0$$

(size at birth)

Population description



$$\partial_t \underbrace{\int_{x_1}^{x_2} n(t,x)\,dx}_{\text{pop. dens. of all sizes in } [x_1,x_2)} = g(x_1)n(t,x_1) - g(x_2)n(t,x_2) - \int_{x_1}^{x_2} \mu(x)n(t,x)\,dx$$

Differentiate with respect to x_2:

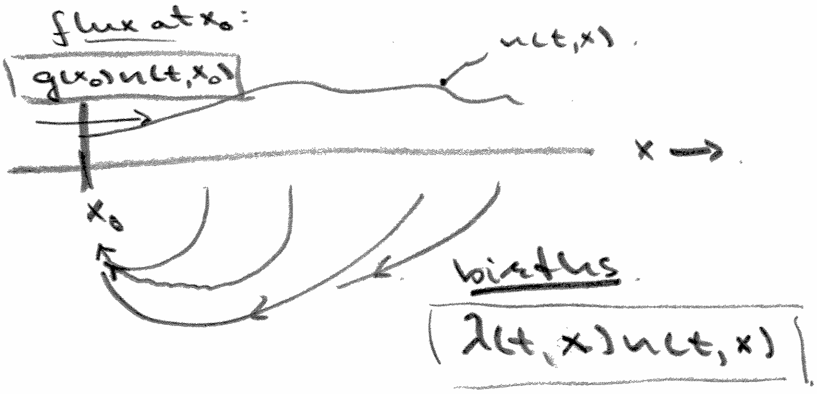
$$\partial_t n(t,x_2) = -\partial_{x_2}\big(g(x_2)n(t,x_2)\big) - \mu(x_2)n(t,x_2).$$

Write this as:

$$\boxed{\partial_t n + \partial_x (gn) + \mu n = 0}$$

(Transport equation with a loss term.)

Boundary condition



flux at $x=x_0$ must equal total birthrate:

$$\boxed{g(x_0)n(t,x_0) = \int_{x_0}^{\infty} \lambda(t,x)\,n(t,x)\,dx} \quad \forall t$$

Summary:

Transport equation & bnd. cond:

(*)
$$\boxed{\begin{aligned} &\partial_t n + \partial_x(gn) + \mu n = 0 \\ &g(x_0)n(t,x_0) = \int_{x_0}^{\infty} \lambda(t,x)\,n(t,x)\,dx . \end{aligned}}$$

size structure

Special case: $\boxed{x = a}$ ("size"=age).
and so $\boxed{g = 1}$.

$$\begin{cases} \partial_t n + \partial_a n + \mu n = 0 \\ n(t,0) = \int_{0}^{\infty} \lambda(t,a)\,n(t,a)\,da . \end{cases}$$

age structure

If individual growth $\frac{dx}{da} = g(x) > 0$ is monotonous, ⊛ (page 2) can always be rewritten as an age-structured problem:

$u(t,x)$ size distribution

$v(t,a)$ age distribution

$$\underbrace{v(t,a)\,da}_{\substack{\text{dens. of indivs.}\\ \text{with ages in } [a,a+da)}} = \underbrace{u(t,x)\,dx}_{\substack{\text{dens. of indivs.}\\ \text{with sizes in } [x,x+dx)}}$$

$$\Rightarrow \quad v(t,a) = u(t,x)\frac{dx}{da} = u(t,x)\,g(x).$$

$$\Rightarrow \quad \boxed{\partial_t v + \partial_a v + \mu v} =$$

$$= \partial_t(gu) + \partial_a(gu) + \mu g u =$$

$$= g\,\partial_t u + \partial_x(gu)\frac{dx}{da} + \mu g u = \qquad \frac{dx}{da} = g(x)$$

$$= g\underbrace{\left[\partial_t u + \partial_x(gu) + \mu u\right]}_{\text{zero (see ⊛ page 2)}} = \boxed{0}$$

transport equation

$$\boxed{v(t,0)} = g(x_0)\,u(t,x_0) \overset{⊛}{=}$$

$$= \int_{x_0}^{\infty} \lambda(t,x)\,u(t,x)\,dx \overset{\text{change of variable}}{=}$$

$x_0 < x < \infty$
$0 < a < \infty$
$dx = g\,da$

$$= \int_0^{\infty} \lambda(t,x(a))\,g(x(a))\,u(t,x(a))\,da = \boxed{\int_0^{\infty} \lambda v\,da}$$

bnd. cond.

This motivates our choice to consider only age-structured populations.

Alternative formulation.

$$(**)\quad \begin{cases} n(t,a) = \underbrace{B(t-a)}_{\substack{\text{total birth} \\ \text{rate at} \\ \text{time } t-a}} \cdot \underbrace{\mathcal{F}(a)}_{\substack{\text{survival probability} \\ \text{from birth till age } a.}} & \text{if } \boxed{0 \leq a < t} \\[2ex] n(t,a) = \underbrace{n_0(a-t)}_{\substack{\text{pop. dens. of} \\ \text{indivs. of} \\ \text{age } a-t \text{ at} \\ \text{time zero.}}} \underbrace{\dfrac{\mathcal{F}(a)}{\mathcal{F}(a-t)}}_{\substack{\text{survival probability} \\ \text{from age } a-t \text{ to age } a.}} & \text{if } \boxed{t \leq a} \end{cases}$$

where

$$\begin{cases} B(t) = \displaystyle\int_0^\infty \lambda(t,a)\, n(t,a)\, da \\[2ex] \mathcal{F}(a) = \exp\left\{-\displaystyle\int_0^a \mu(x)\,dx\right\}. \end{cases}$$

The delay-differential equation (**) is also called a <u>renewal equ.</u>

The second equation in (**) gives the <u>transient part</u> of the solution $n(t,a)$.

We show that the transport equ. with boundary condition

$$(*)\quad \boxed{\begin{aligned} &\partial_t u + \partial_a u + \mu u = 0 \\ &u(t,0) = B(t) \end{aligned}}$$

is equivalent to the renewal equ.

$$(**)\quad \boxed{u(t,a) = B(t-a)\,F(a)}$$

if $u(t,a)/F(a)$ is differentiable with respect to both t and a:

From (**) we have

$$\frac{u(t,a)}{F(a)} = B(t-a).$$

$$\Longrightarrow \quad \partial_t\left(\frac{u(t,a)}{F(a)}\right) = \partial_t B(t-a) = -\partial_a B(t-a)$$

$$= -\partial_a\left(\frac{u(t,a)}{F(a)}\right).$$

$$\Longleftrightarrow \quad \frac{1}{\cancel{F}}\partial_t u = -\frac{\partial_a u \cdot F - u\,F'}{F^{\cancel{2}}}$$

$$\Longleftrightarrow \quad \partial_t u = -\partial_a u + \frac{F'}{F}\,u$$

$F(a) = \exp\{-\int_0^a \mu(\alpha)d\alpha\}$ which satisfies $\Big\} \Rightarrow$

$$\frac{F'(a)}{F(a)} = -\mu(a)$$

$$\Rightarrow \quad \boxed{\partial_t u = -\partial_a u - \mu u}$$

which satisfies the transport equ.

The bnd. cond. of the PDE system ⊛ follows directly from the renewal equ. ⊛⊛ with $a=0$.

Notice that in the renewal equation ⊛⊛ we don't make assumptions about differentiability. So, the renewal equ. is, after all, more general.

<u>Example</u> (resource consumer)

$$\left\{\begin{aligned} \frac{dR}{dt} &= f(R) - \underbrace{\int_0^\infty \frac{\beta(a)\, R(t)\, n(t,a)}{1+\beta(a)T(a)R(t)}\, da}_{\text{Holling-II funct. resp.}} \\ n(t,a) &= B(t-a)\, F(a) \\ B(t) &= \int_0^\infty \frac{\gamma(\alpha)\beta(\alpha)R(t)\, n(t,\alpha)}{1+\beta(\alpha)T(\alpha)R(t)}\, d\alpha . \end{aligned}\right.$$

$$F(a) = \exp\left\{-\int_0^a \mu(\alpha)\, d\alpha\right\} \quad \text{(known function)}$$

Equilibrium $R(t) = \bar{R}$, $n(t,a) = \bar{n}(a)$:

$$\boxed{\begin{aligned} &\text{(i)} \quad 0 = f(\bar{R}) - \int_0^\infty \frac{\beta(a)\bar{R}\,\bar{n}(a)}{1+\beta(a)T(a)\bar{R}}\,da \\ &\text{(ii)} \quad \bar{n}(a) = \bar{B}\,F(a) > 0 \\ &\text{(iii)} \quad \bar{B} = \int_0^\infty \frac{\gamma(a)\beta(a)\bar{R}\,\bar{n}(a)}{1+\beta(a)T(a)\bar{R}}\,da . \end{aligned}}$$

- Substitute (ii) into (iii):

$$\text{(iv)} \qquad 1 = \int_0^\infty \frac{\gamma(a)\beta(a)\bar{R}\,F(a)}{1+\beta(a)T(a)\bar{R}}\,da$$

which is a scalar equation in $\bar{R}$ which (at least in principle) can be solved

- Substitute (ii) into (i):

$$\text{(v)} \qquad \bar{B} = f(\bar{R})\left[\int_0^\infty \frac{\beta(a)\bar{R}\,F(a)}{1+\beta(a)T(a)\bar{R}}\,da\right]^{-1}$$

- Substitute $\bar{B}$ into (ii) and the equilibrium equation is solved for $(\bar{R}, \bar{n})$.

Special case previous example:

Suppose $T(a) = 0 \quad \forall a$

(i.e., we have Holling-I instead of Holling-II).

Then, from (iv) (on page 7) we get:

$$\bar{R} = \left[\int_0^\infty \gamma(a)\beta(a)\mathcal{F}(a)\,da \right]^{-1}$$

and from (v) (on page 7) we get:

$$\bar{B} = f(\bar{R}) \left[\int_0^\infty \beta(a)\bar{R}\,\mathcal{F}(a)\,da \right]^{-1}$$

and

$$\bar{n}(a) = \bar{B}\,\mathcal{F}(a) \quad \forall a.$$

Which explicitly solves the equilibrium equation (i),(ii),(iii) on page 7.