Delay equation models for populations that experience competition at immature life stages

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Think of a population of insects or amphibians with distinct larval and adult life stages.

Starting point:

$$\left(\frac{\partial}{\partial t} + \frac{\partial}{\partial a}\right) u(t, a) = \begin{cases} -\mu_l\, u(t, a), & 0 < a < \tau, \\ -\mu_m\, u(t, a), & a > \tau, \end{cases}$$

subject to birth law $u(t, 0) = b(A(t))$, where τ = maturation age, and

$$A(t) = \int_\tau^\infty u(t, a)\, da = \text{number of sexually mature adults}$$

Can reformulate as a delay equation for $A(t)$:

$$\frac{dA(t)}{dt} = e^{-\mu_l \tau} b(A(t - \tau)) - \mu_m A(t)$$

- assumes competitive effects occur only among the adults, modelled solely through the way we choose $b(\cdot)$

- competition among larvae introduces nonlinearities into the age-structured equations or systems that we normally need to solve explicitly to reduce the model to ODEs with delay.

Simple delay equation for larval competition

For larval population

$$\frac{\partial u(t,a)}{\partial t} + \frac{\partial u(t,a)}{\partial a} = -\mu_l u(t,a) - k_l(u(t,a))^2, \quad 0 < a < \tau$$

For adults,

$$\frac{\partial u(t,a)}{\partial t} + \frac{\partial u(t,a)}{\partial a} = -\mu_m u(t,a), \quad a > \tau$$

Egg laying rate:

$$u(t,0) = b(A(t)) \quad \text{where} \quad A(t) = \int_\tau^\infty u(t,a)\, da$$

We have

$$\frac{dA(t)}{dt} = \underbrace{u(t,\tau)}_{\text{maturation rate}} - \mu_m A(t)$$

Calculate $u(t,\tau)$ in terms of $u(t-\tau,0)$, i.e. in terms of $A(t-\tau)$. Result:

$$\frac{dA(t)}{dt} = \frac{\mu_l e^{-\mu_l \tau} b(A(t-\tau))}{\mu_l + k_l(1 - e^{-\mu_l \tau}) b(A(t-\tau))} - \mu_m A(t)$$

- belongs to well studied class $A'(t) = F(A(t-\tau)) - \mu_m A(t)$ that includes Nicholson's blowflies equation and Mackey-Glass equation

- generates a monotone dynamical system if $b(\cdot)$ is monotone increasing

- periodic solutions exist in some situations

- if $k_l > 0$ the solution $A(t)$ is bounded for *any* egg laying rate $b(\cdot)$

- drawback: assumes a larva competes only with others of its own age.

Equation for larvae:

$$\frac{\partial u(t,a)}{\partial t} + \frac{\partial u(t,a)}{\partial a} = -\mu_l u(t,a) - \epsilon\, u(t,a) \int_0^\tau p(a,\bar{a}) u(t,\bar{a})\, d\bar{a}, \quad 0 < a < \tau$$

For adults:

$$\frac{dA(t)}{dt} = u(t,\tau) - \mu_m A(t)$$

Possibilities:

- $p(a,\bar{a}) = \text{constant}$

- $p(a,\bar{a}) = 0$ when $\bar{a} < a$ (i.e. competition only from older larvae, e.g. intimidatory tactics or cannibalism, common in amphibians)

- $p(a,\bar{a}) = \delta(a - \bar{a})$ recovers previous model
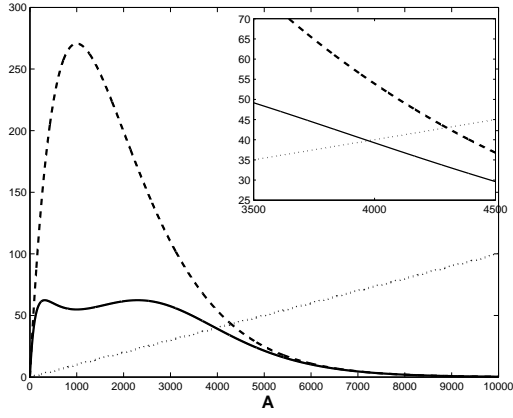
If ϵ is small, can try perturbation solution:

$$u(t,a) = u_0(t,a) \exp\left(-\epsilon\, u_1(t,a) + O(\epsilon^2)\right)$$
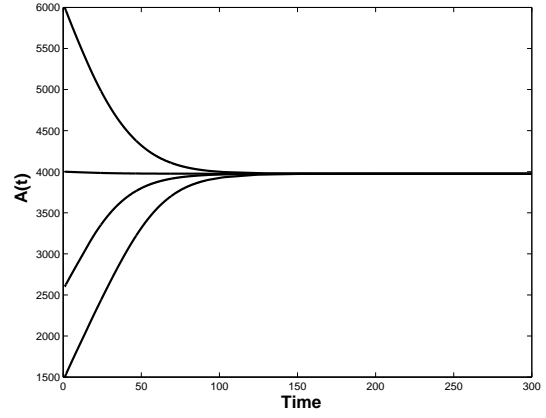
Outcome: equation for adults $A(t)$ is

$$\frac{dA(t)}{dt} = -\mu_m A(t)$$
$$+ b(A(t-\tau))e^{-\mu_l \tau} \exp\left(-\epsilon \int_0^\tau \int_0^\tau p(s,\bar{a}) b(A(s+t-\tau-\bar{a})) e^{-\mu_l \bar{a}}\, d\bar{a}\, ds\right)$$

for small ϵ. If $b(A) = rA \exp(-A/K)$, similar dynamics to spruce budworm model

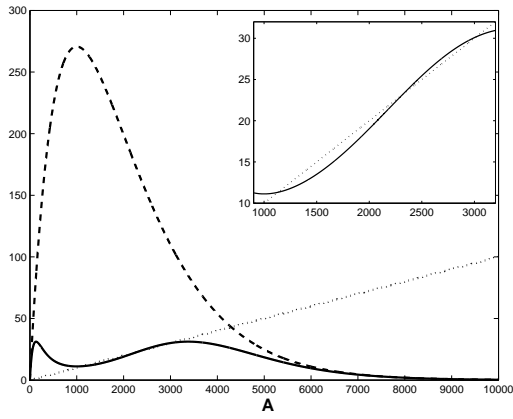$$\frac{du}{dt} = ru\left(1 - \frac{u}{q}\right) - \frac{u^2}{1+u^2}$$
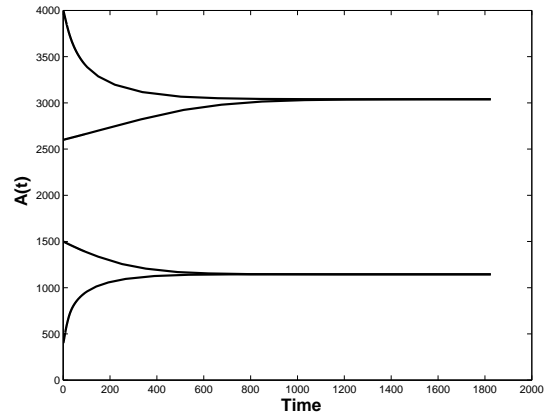
(a) The large outbreak equilibrium

(b) Evolution of $A(t)$ to the outbreak equilibrium.

Figure 1: $\boxed{\epsilon = 0.00005}$, $b(A) = rA\exp(-A/K)$, $p(s,\bar{a}) = p0 = 0.305$, $r = 2$, $K = 1000$, $\mu_M = 1/100$, $\mu_L = 1/15$, $\tau = 15$. (Dashed curve is for $\epsilon = 0$)
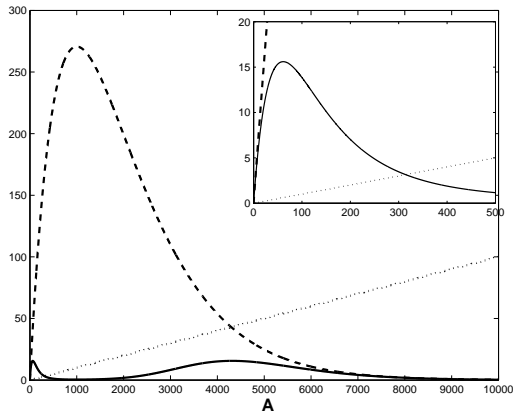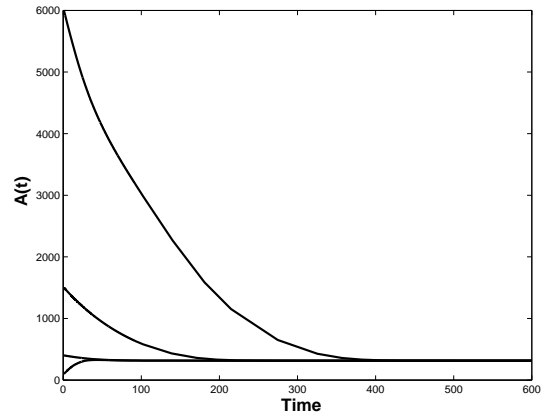

(a) Multiple equilibria

(b) Evolution of $A(t)$ for various initial values.

Figure 2: $\boxed{\epsilon = 0.0001}$. Dashed curve is for $\epsilon = 0$

(a) The small refuge equilibrium
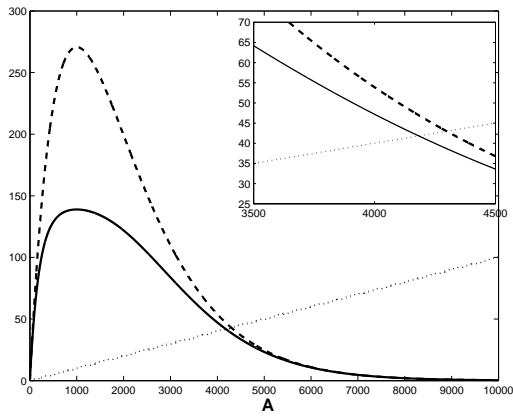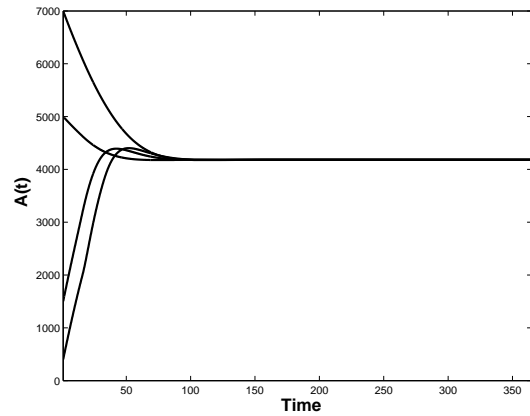

(b) Evolution of $A(t)$ to the refuge equilibrium.

Figure 3: $\boxed{\epsilon = 0.0002}$. Dashed curve is for $\epsilon = 0$

(a) The large outbreak equilibrium

(b) Evolution of $A(t)$ to the outbreak equilibrium.

Figure 4: $\epsilon = 0.00005$ and $p(s, \bar{a}) = 0$ for $\bar{a} < s$, $p(s, \bar{a}) = 0.305$ for $\bar{a} \geq s$. (Dashed curve is for $\epsilon = 0$).

$$\boxed{\text{Competition between two species } u(t,a) \text{ and } v(t,a)}$$

Assume:

- two species/strains have same maturation time τ

- larvae experience both intra- and inter-specific competition

For larvae (ages $0 < a < \tau$):

$$\frac{\partial u(t,a)}{\partial t} + \frac{\partial u(t,a)}{\partial a} = -\mu_{lu}u(t,a) - k_{lu}(u(t,a))^2 - c_{uv}u(t,a)v(t,a)$$
$$\frac{\partial v(t,a)}{\partial t} + \frac{\partial v(t,a)}{\partial a} = -\mu_{lv}v(t,a) - k_{lv}(v(t,a))^2 - c_{vu}u(t,a)v(t,a)$$

For adults (age $a > \tau$),

$$\frac{\partial u(t,a)}{\partial t} + \frac{\partial u(t,a)}{\partial a} = -\mu_{au}u(t,a), \qquad \frac{\partial v(t,a)}{\partial t} + \frac{\partial v(t,a)}{\partial a} = -\mu_{av}v(t,a).$$

Total numbers of adults:

$$U(t) = \int_\tau^\infty u(t,a)\,da \quad \text{and} \quad V(t) = \int_\tau^\infty v(t,a)\,da$$

Egg-laying rates:

$$u(t,0) = b_u(U(t), V(t)) \quad \text{and} \quad v(t,0) = b_v(U(t), V(t))$$

with

$$b_u(0, V) = 0 \quad \text{and} \quad b_v(U, 0) = 0$$

Adults of species u satisfy

$$\frac{dU(t)}{dt} = u(t,\tau) - \mu_{au}U(t).$$

so need $u(t, \tau)$. If $u^\xi(a) := u(a + \xi, a)$ and $v^\xi(a) := v(a + \xi, a)$ then

$$\frac{du^\xi(a)}{da} = -\mu_{lu} u^\xi(a) - k_{lu}(u^\xi(a))^2 - c_{uv} u^\xi(a) v^\xi(a),$$

$$\frac{dv^\xi(a)}{da} = -\mu_{lv} v^\xi(a) - k_{lv}(v^\xi(a))^2 - c_{vu} u^\xi(a) v^\xi(a),$$

for $0 < a < \tau$. Define $F(a, F_0, G_0)$ and $G(a, F_0, G_0)$ by

$$\frac{\partial F}{\partial a} = -\mu_{lu} F - k_{lu} F^2 - c_{uv} FG,$$

$$\frac{\partial G}{\partial a} = -\mu_{lv} G - k_{lv} G^2 - c_{vu} FG,$$

$$F(0, F_0, G_0) = F_0, \quad G(0, F_0, G_0) = G_0,$$

for arbitrary $F_0 \geq 0$, $G_0 \geq 0$. Then

$$(u^\xi(a), v^\xi(a)) = \big(F(a, u^\xi(0), v^\xi(0)), G(a, u^\xi(0), v^\xi(0))\big).$$

leading to the maturation rate for species u:

$$u(t, \tau) = F\big(\tau, b_u(U(t - \tau), V(t - \tau)), b_v(U(t - \tau), V(t - \tau))\big)$$

and similarly for $v(t, \tau)$.

Outcome: delay DEs for adult populations $U(t)$ and $V(t)$ are

$$\frac{dU(t)}{dt} = F\big(\tau, b_u(U(t - \tau), V(t - \tau)), b_v(U(t - \tau), V(t - \tau))\big) - \mu_{au} U(t)$$

$$\frac{dV(t)}{dt} = G\big(\tau, b_u(U(t - \tau), V(t - \tau)), b_v(U(t - \tau), V(t - \tau))\big) - \mu_{av} V(t)$$

Any boundary equilibrium in which $(U, V) = (U^*, 0)$ satisfies

$$F(\tau, b_u(U^*, 0), 0) = \mu_{au} U^*$$

or

$$\frac{\mu_{lu}b_u(U^*,0)e^{-\mu_{lu}\tau}}{\mu_{lu} + k_{lu}b_u(U^*,0)(1 - e^{-\mu_{lu}\tau})} = \mu_{au}U^*$$

Theorem 1 *If*

$$e^{-\mu_{lv}\tau}\left(\frac{\mu_{lu}}{\mu_{lu} + k_{lu}b_u(U^*,0)(1 - e^{-\mu_{lu}\tau})}\right)^{c_{vu}/k_{lu}}\left|\left[\frac{\partial b_v}{\partial V}\right]_{(U,V)=(U^*,0)}\right| < \mu_{av}$$

and

$$\frac{\mu_{lu}^2 e^{-\mu_{lu}\tau}}{(\mu_{lu} + k_{lu}b_u(U^*,0)(1 - e^{-\mu_{lu}\tau}))^2}\left|\left[\frac{\partial b_u}{\partial U}\right]_{(U,V)=(U^*,0)}\right| < \mu_{au}$$

then the boundary equilibrium $(U,V) = (U^*,0)$ *is locally asymptotically stable.*

Idea of proof. Coefficients in linearised system involve quantities like

$$F_2\big(\tau, b_u(U^*,0), 0\big), \quad F_3\big(\tau, b_u(U^*,0), 0\big), \quad G_3\big(\tau, b_u(U^*,0), 0\big)$$

where subscripts denote partial derivatives.

If G_0 is very small (but F_0 is not),

$$\frac{\partial F}{\partial a} \approx -\mu_{lu}F - k_{lu}F^2, \quad \frac{\partial G}{\partial a} \approx -(\mu_{lv} + c_{vu}F)G,$$
$$F(0, F_0, G_0) = F_0, \quad G(0, F_0, G_0) = G_0.$$

so that, for small G_0,

$$F(a, F_0, G_0) \approx \frac{\mu_{lu}F_0 e^{-\mu_{lu}a}}{\mu_{lu} + k_{lu}F_0(1 - e^{-\mu_{lu}a})}$$

and

$$G(a, F_0, G_0) \approx G_0 e^{-\mu_{lv}a} \exp\left\{-c_{vu} \int_0^a \frac{\mu_{lu}F_0 e^{-\mu_{lu}\eta}}{\mu_{lu} + k_{lu}F_0(1 - e^{-\mu_{lu}\eta})} d\eta\right\}$$

$$= G_0 e^{-\mu_{lv}a} \left(\frac{\mu_{lu}}{\mu_{lu} + k_{lu}F_0(1 - e^{-\mu_{lu}a})}\right)^{c_{vu}/k_{lu}}$$

Differentiating, and letting $G_0 \to 0$,

$$G_3\big(\tau, b_u(U^*, 0), 0\big) = e^{-\mu_{lv}\tau} \left(\frac{\mu_{lu}}{\mu_{lu} + k_{lu}b_u(U^*, 0)(1 - e^{-\mu_{lu}\tau})}\right)^{c_{vu}/k_{lu}}$$

Global dynamics

Lemma 2 *For a fixed $a > 0$, and for positive F_0, G_0,*

(i) $F(a, F_0, G_0)$ increases with respect to F_0 and decreases with respect to G_0,

(ii) $G(a, F_0, G_0)$ increases with respect to G_0 and decreases with respect to F_0,

Theorem 3 *Suppose*

(i) $b_u(U, V)$ is strictly increasing in U and strictly decreasing in V, $b_v(U, V)$ is strictly decreasing in U and strictly increasing in V;

(ii) the equilibrium $(0, 0)$ is unstable;

(iii) there exists an equilibrium $(U, V) = (U^*, 0)$ which globally attracts all solutions with $V \equiv 0$ and $U_0(\theta) \geq 0$, $U_0(\theta) \not\equiv 0$ for $\theta \in [-\tau, 0]$. Also there exists an equilibrium $(U, V) = (0, V^*)$ which globally attracts all solutions with $U \equiv 0$ and $V_0(\theta) \geq 0$, $V_0(\theta) \not\equiv 0$ for $\theta \in [-\tau, 0]$.

Then precisely one of the following holds:

(a) there is an equilibrium with both U and V strictly positive;

(b) all non-negative solutions with $U_0(\theta) \not\equiv 0$ and $V_0(\theta) \not\equiv 0$ on $[-\tau, 0]$ approach $(U^*, 0)$ as $t \to \infty$;

(c) all non-negative solutions with $U_0(\theta) \not\equiv 0$ and $V_0(\theta) \not\equiv 0$ on $[-\tau, 0]$ approach $(0, V^*)$ as $t \to \infty$.

Summary

- Immature competition makes it harder (or impossible) to solve the age-structured model equations that determine maturation rates at time t in terms of birth rates at time $t - \tau$

- in scalar case we have the simple reasonable model

$$\frac{dA(t)}{dt} = \frac{\mu_l e^{-\mu_l \tau} b(A(t-\tau))}{\mu_l + k_l(1 - e^{-\mu_l \tau})b(A(t-\tau))} - \mu_m A(t)$$

or more complex model

$$\frac{dA(t)}{dt} = -\mu_m A(t)$$
$$+ b(A(t-\tau))e^{-\mu_l \tau} \exp\left(-\epsilon \int_0^\tau \int_0^\tau p(s,\bar{a})b(A(s+t-\tau-\bar{a}))e^{-\mu_l \bar{a}} \, d\bar{a} \, ds\right)$$

- with competition between two strains or species, we cannot reformulate as delay differential equations in which the right hand sides are explicitly known functions or functionals of the state variables ...

- ... but important monotonicity properties of the unknown right hand sides of those delay equations can be worked out, and the linearisation of the model near to a boundary equilibrium can be tackled leading to verifiable and interpretable conditions for stability of such an equilibrium.