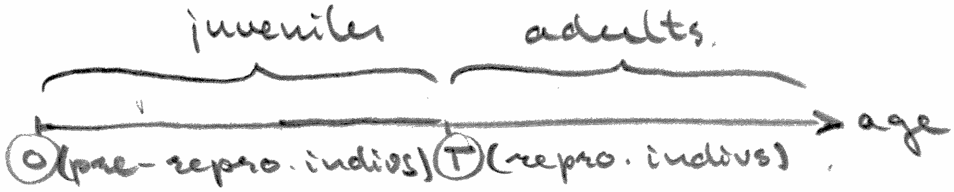
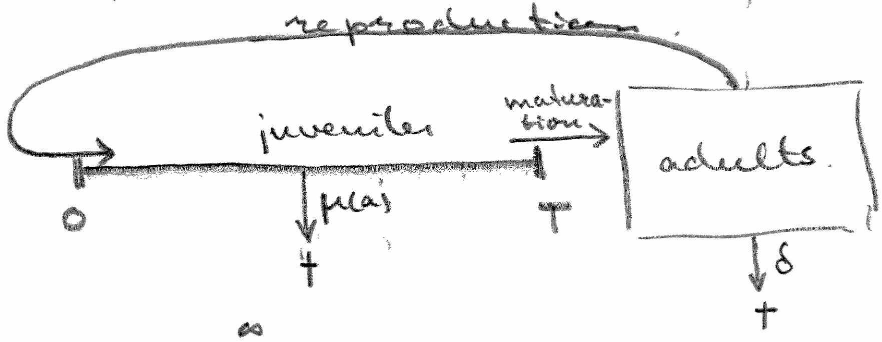
Delay differential equations



Reproduction : $\lambda(a) = \begin{cases} 0 & \text{for } a \leq T \\ \gamma & \text{for } a > T \end{cases}$

mortality : $\mu(a) = \delta$ for $a > T$

(Effectively, we've removed any age-structure among adults.)



$$\begin{cases} N(t) := \int_T^\infty n(t,a)\,da & \text{(pop. dens. adults)} \\ B(t) = \gamma N(t) & \text{(pop. birth rate)} \\ F(a) = \exp\left\{-\int_0^a \mu(x)\,dx\right\} & \text{for } 0 \leq a \leq T \end{cases}$$

Integrate transport equation over $[T,\infty)$:

$\Rightarrow \quad \dot{N}(t) - n(t,T) + \delta N(t) = 0$

From renewal equation:

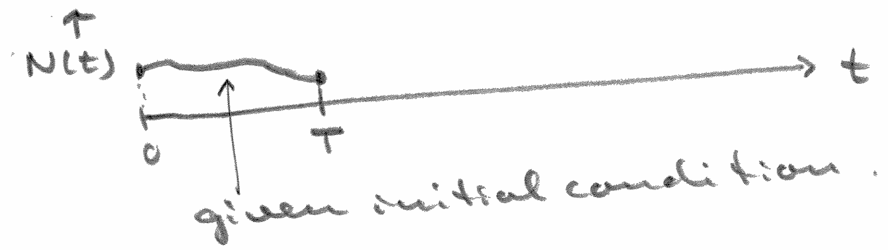
$\Rightarrow \quad n(t,T) = B(t-T)F(T) \quad (t \geq T)$

$$\Rightarrow \quad \boxed{\dot{N}(t) = \gamma F(T)\, N(t-T) - \delta N(t)}$$

(Delay differential equation)

$$(*) \quad \dot{N}(t) = \underbrace{\underbrace{\gamma N(t-T)}_{\substack{\text{birth rate} \\ \text{T time} \\ \text{units ago}}} \; \underbrace{F(T)}_{\substack{\text{survival} \\ \text{probability} \\ \text{till present} \\ \text{time } t}}}_{\substack{\text{recruitment rate} \\ \text{at presen time } t.}} \; \underbrace{-\, \delta N(t)}_{\text{deaths.}}$$

The delay differential equation $(*)$ is complemented by an initial cond which gives N over an interval of lengt T:



How to "put" a delay in a given ODE like, e.g.,

$$\dot{N} = rN\left(1 - \frac{N}{K}\right). \qquad \text{(logistic)}$$

Example (Hutchinton 1948; May 1972)

$$\dot{N} = rN\left(1 - \frac{N_T}{K}\right) \qquad \text{(delayed logistic)}$$

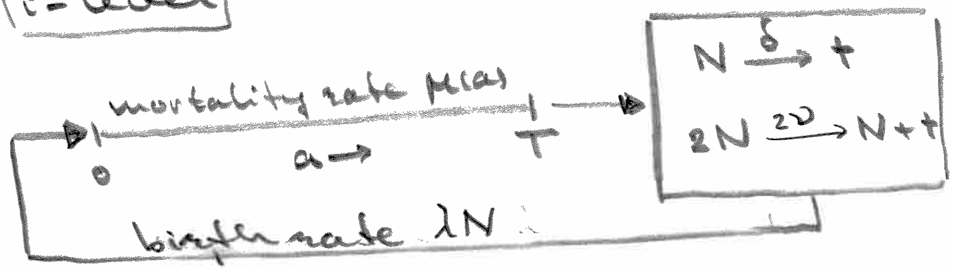
with $N_T(t) := N(t-T)$. Where does the Hutchinton-May equation come from? What are the underlying i-level processes?

The Hutchinson-May equation is of the form

(1) $$\boxed{\dot{N} = aN - bNN_T} \quad (a, b > 0 \text{ constant})$$

First mechanism:

i-level



p-level

(2) $$\boxed{\dot{N} = \lambda F(T)\, N_T - \delta N - \nu N^2}$$

Although this mechanism gives a delay-differential equation, it is not of the form of the Hutchinson-May equation (1).

Note, however, that without the delay (or $T=0$) both (1) and (2) become the logistic ODE.

Second mechanism.

i-states

N : territory owner (adult)

Y : adult without territory.

X_a : juvenile of age $a \in [0,T]$.

S : free territory.

i-processes

$N \xrightarrow{\lambda} N + X_0$ (reproduction).

$S + Y \xrightarrow{\beta} N$ (finding territory)

$$\left.\begin{array}{l} N \xrightarrow{\delta} S \\ Y \xrightarrow{\gamma} \dagger \\ X_a \xrightarrow{\mu(a)} \dagger \end{array}\right\} \text{(death)}$$

$X_0 \xrightarrow{\text{delay } T} Y$ (maturation)

p-equations

$$\begin{cases} \dot{N} = \beta S Y - \delta N \\ \dot{Y} = -\beta S Y - \gamma Y + \lambda N_T F(T) \\ \dot{S} = -\beta S Y + \delta N \end{cases}$$

with $F(T) = \exp\left\{-\int_0^T \mu(a)\,da\right\}$.

Note that $\boxed{S_0 := S + N}$ is constant.
Use this to eliminate S from the equations:

$$\begin{cases} \dot{N} = \beta(S_0 - N)Y - \delta N \\ \dot{Y} = -\beta(S_0 - N)Y - \gamma Y + \lambda N_T F(T) \end{cases}$$

Assume that λ and γ are large compared with other parameters.
$\Rightarrow$ Y fast variable ; N slow variable.

Fast Y-dynamics:

QSS $\quad Y = \frac{\lambda}{\gamma} F(T) \cdot N_T$.

Slow N-dynamics:

$$③ \quad \boxed{\dot{N} = \frac{\lambda \beta F(T)}{\gamma} (S_0 - N) N_T - \delta N}$$

Note that this equation is also not the Hutchinson-May equation ①, although without delay (i.e, $T=0$) both ① and ③ give the ordinary logistic equation

Third mechanism

|i-states|

N : territory owner who has sufficiently settled down to start reproducing.

Y : free individuals (i.e., without a territory)

S : unoccupied territory.

Z_a : territory owner who is still in the phase of preparing herself and the territory for reproduction. ($a \in [0,T]$)

|i-processes|

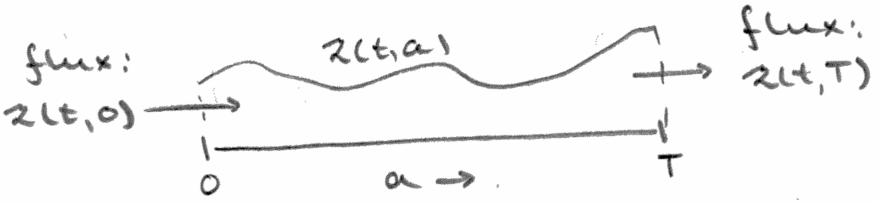
$$N \xrightarrow{\lambda} N + Y \qquad \text{(reproduction)}$$

$$S + Y \xrightarrow{\beta} Z_0 \qquad \text{(occupying territory)}$$

$$Z_0 \xmapsto{\text{delay } T} N \qquad \text{(preparing for repro)}$$

$$\left.\begin{array}{l} N \xrightarrow{\delta} S \\ Z_a \xrightarrow{\mu} S \\ Y \xrightarrow{\gamma} \dagger \end{array}\right\} \begin{array}{l}\text{death} \\ \text{(notice } \mu \text{ is now} \\ \text{age-}\underline{\text{in}}\text{dependent)}.\end{array}$$

p-equations



$$\begin{cases} \dot N = z(t,T) - \delta N \\ \dot Y = \lambda N - \beta S Y - \gamma Y \\ z(t,a) = B(t-a)\,F(a) \\ B(t) = \beta S Y \\ F(a) = e^{-\mu a} \\ \dot S = -\beta S Y + \delta N + \mu \int_0^T z(t,a)\,da \end{cases}$$

renewal equation

Note that $\boxed{S_0 := N(t) + \int_0^T z(t,a)\,da}$ is constant.

Also define $\boxed{Z(t) := \int_0^T z(t,a)\,da}$

$$\Rightarrow \begin{cases} \dot N = \beta(S_0 - N_T - Z_T)\,Y_T\,F(T) - \delta N \\ \dot Y = \lambda N - \beta(S_0 - N - Z)\,Y - \gamma Y \end{cases}$$

From the transport equation:

$$\Rightarrow \quad \dot Z(t) + z(t,a)\Big|_0^T + \mu Z = 0$$

$$\Leftrightarrow \quad \dot Z(t) + \beta(S_0 - N_T - Z_T)\,Y_T\,F(T) - \beta(S_0 - N - Z)\,Y + \mu Z = 0$$

Assume that λ and γ are large compared with the other parameters. (Interpret γ)

Fast Y-dynamics

QSS: $Y = \frac{\lambda}{\gamma} N$.

Slow (N, Z)-dynamics.

$$\boxed{\begin{aligned} \dot N &= \beta(S_0 - N_T - Z_T)\frac{\lambda}{\gamma} N_T F(T) - \delta N \\ \dot Z &= -\beta(S_0 - N_T - Z_T)\frac{\lambda}{\gamma} N_T F(T) + \beta(S_0 - N - Z)\frac{\lambda}{\gamma} N - \mu Z \end{aligned}} \quad (4)$$

There are two equations in an essential way, i.e., we cannot eliminate one or the other by separation of time scales.

Without delay ($T=0$ and hence $Z=0$) system (4) becomes the ordinary logistic equation.

But *with* the delay, we still don't have recovered the Hutchinson-May equation (1).

(I don't know, and I've never seen a mechanistic derivation of the H-M eqn.)

But we've had some practice with deriving delay diff. equations.