

• insects: metamorphic moult triggered by size (not age) of a larva.

• developmental time affected by intra-specific competition.

$i(x, t)$ : density of larvae of size  $x$  at time  $t$

$$I(t) = \int_0^l i(x, t) dx$$

$l$  = threshold length.

larvae grow such that  $\frac{dx}{dt} = P(t, I(t))$  (P decreasing in I)

$$i(x + \delta x, t + \delta t) = i(x, t) - \mu_i i(x, t) \delta t$$

$$\Rightarrow \left[ \frac{\partial i}{\partial t} + P(t, I(t)) \frac{\partial i}{\partial x} = -\mu_i i(x, t) \right]$$

$x \in (0, l), t > 0.$

Also 
$$\frac{dI}{dt} = \int_0^l \left( -P(t, I(t)) \frac{\partial i}{\partial x} - \mu_i i(x, t) \right) dx$$

$$= P(t, I(t)) (i(0, t) - i(l, t)) - \mu_i I(t).$$

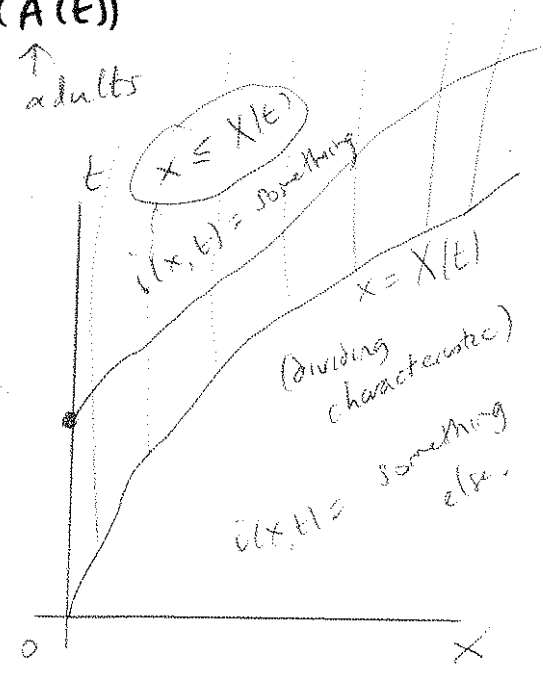
$P(t, I(t)) i(0, t)$  = birth rate  $\stackrel{\text{assume}}{=} B(A(t))$

$P(t, I(t)) i(l, t)$  = maturation rate.  
need to calculate

define 
$$X(t) = \int_0^t P(\tau, I(\tau)) d\tau$$

Can show, for  $x \leq X(t)$ , that 
$$i(x, t) = i(0, t - T(x, t)) e^{-\mu_i T(x, t)}$$

where 
$$\int_{t-T(x, t)}^t P(\tau, I(\tau)) d\tau = x.$$



larvae mature on reaching size  $l$ . Let  $\tau(t) = T(l, t)$  (2) Threshold condition.

$$\int_{t-\tau(t)}^t P(\xi, I(\xi)) d\xi = l$$

$$\begin{aligned} \frac{dI}{dt} &= B(A(t)) - P(t, I(t)) i(l, t) - \mu_i I(t) \\ &= B(A(t)) - P(t, I(t)) i(0, t - \tau(t)) e^{-\mu_i \tau(t)} - \mu_i I(t) \end{aligned}$$

$$\frac{dI(t)}{dt} = B(A(t)) - \frac{P(t, I(t)) B(A(t - \tau(t)))}{P(t - \tau(t), I(t - \tau(t)))} e^{-\mu_i \tau(t)} - \mu_i I(t)$$

$$\frac{dA(t)}{dt} = \frac{P(t, I(t)) B(A(t - \tau(t)))}{P(t - \tau(t), I(t - \tau(t)))} e^{-\mu_i \tau(t)} - \mu_a A(t)$$

Conversion to constant delay. Suppose  $P(t, I) = P_0(I)$ , & let  
 $x = \int_0^t P_0(I(\xi)) d\xi$  (new size-like indep. variable).

$x \leftrightarrow t$   
 $x - l \leftrightarrow t - \tau(t)$

Model becomes

$$\frac{dA(x)}{dx} = -\mu_a \frac{A(x)}{P_0(I(x))} + e^{-\mu_i \tau_0(I_x)} \frac{B(A(x-l))}{P_0(I(x-l))}$$

$$\frac{dI(x)}{dx} = -\mu_i \frac{I(x)}{P_0(I(x))} + \frac{B(A(x))}{P_0(I(x))} - e^{-\mu_i \tau_0(I_x)} \frac{B(A(x-l))}{P_0(I(x-l))}$$

$$\tau_0(\phi) = \int_{-l}^0 \frac{d\bar{x}}{P_0(\phi(\bar{x}))}$$

$$I_x(\bar{x}) = I(x + \bar{x})$$

Linear stability of an equilibrium

Steady state  $(A^*, I^*)$

in linearised system,  $\tau(t)$  replaced by  $\frac{l}{P_0(I^*)}$

characteristic equation:

$$\frac{P_0(I^*)}{l} (\lambda + \hat{\mu}_a) - B'(A^*) e^{-(\lambda + \hat{\mu}_i)l} = \frac{\epsilon B'(A^*) (\lambda + \hat{\mu}_i) k(\lambda) k(\lambda + \hat{\mu}_i)}{1 + \epsilon k(\lambda)}$$

homographic  
 $\rightarrow$  for  $\lambda \gg 0$   
 $\downarrow$   $\epsilon \ll 1$

$\lambda = \lambda \frac{l}{P_0(I^*)}$  ,  $(A(t), I(t)) = (A^*, I^*) + \epsilon e^{\lambda t}$

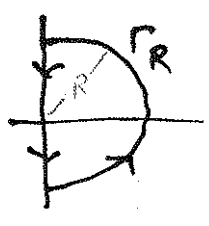
$k(x) = \frac{1 - e^{-x}}{x}$

$\epsilon = 0$  if all larvae take same time to mature.

Techniques:

\* Rouches theorem

\*  $N_0(f) - N_p(f) = \frac{1}{2\pi} \int_{\Gamma_R} \arg f(z)$



Allée effect

If

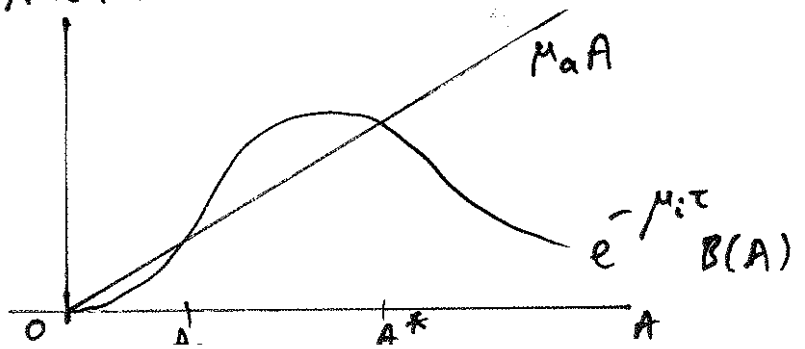
- \* Allée effect, &  $P(I) = \begin{cases} P_0 & I \leq I_c \\ 0 & I > I_c \end{cases}$  } pausing of larval development when too much competition
- \*  $\mu_i$  small,  $\mu_a$  large (+ other conds)
- \* may have  $A(t) \rightarrow 0$  even if starts off large

Starting point: constant delay case:

$\frac{dA}{dt} = -\mu_a A(t) + e^{-\mu_i \tau} B(A(t-\tau))$

with:

( $A_c =$  Allée effect threshold)



Lemma

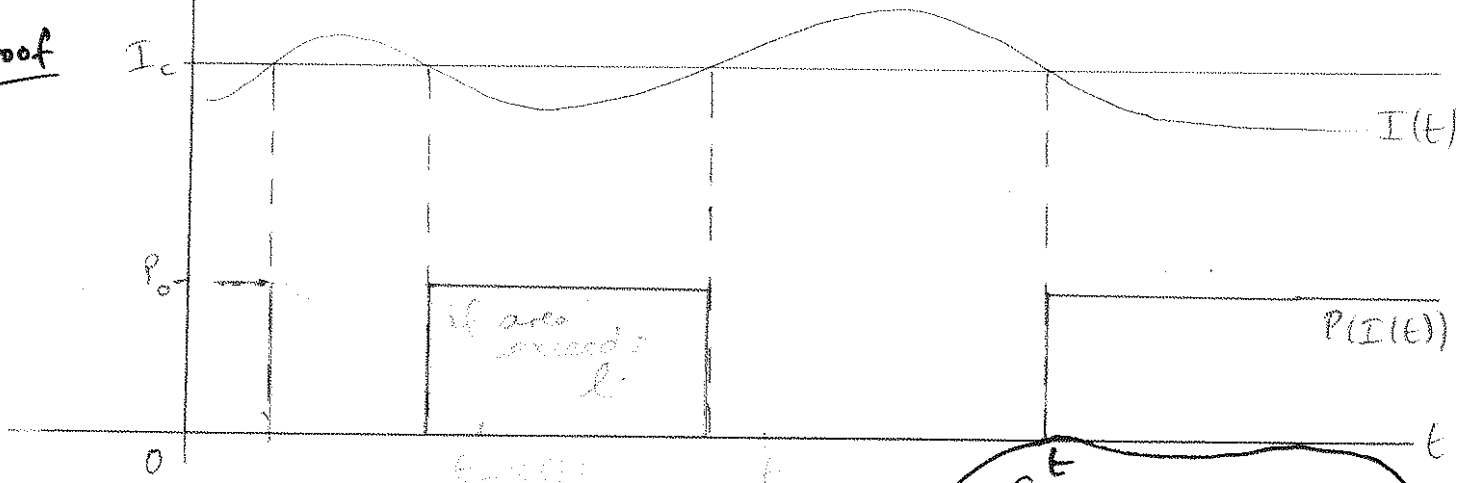
(4)

If  $\exists t^*$  s.t.  $A(t) \in [0, A_c) \quad \forall t \in [t^*, t^* + \tau]$   
 then  $A(t) \rightarrow 0$  as  $t \rightarrow \infty$ .

Lemma

$\nexists t$  s.t.  $P(I(t - \tau(t))) = 0$ .

Proof



$$\int_{t-\tau(t)}^t P(I(\tau)) d\tau = l$$

Extinction with Allee effect

