1. Introduction

This chapter, originally intended for inclusion in [4], focuses on modeling issues by way of an example of a predator-prey model where the predator has a juvenile stage. A careful derivation of the model is given starting from an age-structured model for the predator population. The method of characteristics is used to reduce the partial differential equations to a system of integro-differential equations which represent delay equations with unbounded delays. The modeling assumptions of fixed maturation period and exponentially distributed death rates reduces the model to a system of familiar discrete delay equations. However, the appropriate initial data for the resulting delay equation is not what is usually assumed in the literature. Rather than analyzing the system using analytical tools, we rely on numerical simulations to suggest that the new initial conditions are superior to those commonly employed. A mathematical analysis of the equations would be quite similar to that in Chapter 8 of [4].

2. The Delay Predator-Prey Model

The focus of this chapter is on modeling issues. More specifically, we ask: how can time delays in a model be rigorously derived? We use a model, proposed by S. Gourley and Y. Kuang [2], of a predator-prey interaction where the predators are divided into immature and mature, to illustrate modeling issues. We eschew any mathematical analysis of the asymptotic behavior of solutions of the model because our primary motivation is the model construction. See [3] for a study of the model system.

If only the mature stage of the predator predates on the prey, and if the duration of the immature stage is assumed to be exactly $\tau$ time units, then Gourley and Kuang [2] obtain the following model for prey
$x$, immature predator $y_J$, and mature predator $y$:

\begin{align*}
x'(t) &= rx(t)(1 - x(t)/K) - y(t)p(x(t)) \\
y_J'(t) &= by(t)p(x(t)) - be^{-\nu t}y(t-\tau)p(x(t-\tau)) - \nu y_J(t) \\
y'(t) &= be^{-\nu t}y(t-\tau)p(x(t-\tau)) - dy(t)
\end{align*}

with initial data:

\[ x(s), y(s) \geq 0, \quad -\tau \leq s \leq 0, \quad y_J(0) > 0 \]

The predator functional response $p(x)$ can be general but is frequently taken to be either $p(x) = px$ or $p(x) = \frac{px}{1+Cx}$. The reader should note the similarity of the model to the one considered in chapter 8 of [4].

We recall the rationale for the equation for juveniles $y_J$. Because a new-born remains a juvenile for exactly $\tau$ time units by assumption, then it follows that individuals leaving the juvenile class at time $t$ due to maturation were born at time $t - \tau$. The number of these is $by(t-\tau)p(x(t-\tau))$ but some of these will have died during the time from $t - \tau$ to $t$. The fraction which survive is $e^{-\nu t}$. Therefore the loss to the juvenile class due to maturation at time $t$ is $be^{-\nu t}y(t-\tau)p(x(t-\tau))$. This loss term is precisely the rate of gain of the adult predator population at time $t$.

The equation for $y_J$ can be integrated as follows:

\[
(y_J(t)e^{\nu t})' = be^{\nu t}y(t)p(x(t)) - be^{\nu(t-\tau)}y(t-\tau)p(x(t-\tau))
\]

\[
= \frac{d}{dt} \int_{t-\tau}^{t} be^{\nu s}y(s)p(x(s))ds
\]

This leads to

\[ y_J(t) = ce^{-\nu t} + \int_{t-\tau}^{t} be^{-\nu(t-s)}y(s)p(x(s))ds \]

for some constant $c$. In fact, $c = 0$ because the integral term captures all the juveniles that were born up to time $t$ and that are still alive. Indeed, if $t - \tau \leq s \leq t$ then the number of newborns at time $s$ is $by(s)p(x(s))$ and to be alive at time $t$, this cohort must avoid death for $t - s$ time units. The latter has probability $e^{-\nu(t-s)}$.

As the equations for adult predator and prey do not involve juvenile predator, the behavior of the system is determined by these two equations. The predator-prey model now becomes:
\[ x' = rx(1 - x/K) - p(x)y \]

(2) \[ y_J(t) = \int_0^t \int_0^\tau by(t - a)p(x(t - a))e^{-\nu a} da, \quad t \geq 0 \]

\[ y' = by(t - \tau)p(x(t - \tau))e^{-\nu \tau} - dy \]

with initial conditions

(3) \[ x(t) = \phi(t) \]

\[ y(t) = \psi(t), \quad -\tau \leq t \leq 0 \]

where \( \phi, \psi \) are nonnegative functions.

A further reason to prefer (2) over (1) is that (1) does not preserve positivity while (2) does. Suppose that at \( t = 0 \) there are no juvenile predators \( y_J(0) = 0 \) and note that it is quite possible that \( y(0), x(0), y(-\tau), x(-\tau) \) are nonnegative and yet \( by(0)p(x(0)) - be^{-\nu \tau}y(-\tau)p(x(-\tau)) < 0 \) so that \( y_J'(0) < 0 \). Subsequently, \( y_J(t) \) will become negative. The model (1) is flawed but (2) is not.

3. A More Flexible Model

From a biological perspective, the model (2)-(3) says that at time \( t = 0 \) we are given the past history of the prey and predators over the prior immature period \( -\tau \leq t \leq 0 \) and the initial density of immature predators is given by the integral

\[ y_J(0) = \int_0^\tau b\psi(t - a)p(\phi(t - a))e^{-\nu \tau} da \]

Therefore, this initial immature population at \( t = 0 \) is the surviving offspring of the mature predators over the prior immature period \([ -\tau, 0 ]\) resulting from consumption of the prey. To amplify this point, the model formulation (2)-(3) carries with it an assumption of the origins of the initial immature population of size \( y_J(0) \). While this may seem reasonable and natural in most settings, it is a restrictive assumption.

For example, this model does not fit the following scenario that an experimentalist might wish to consider. Suppose we assemble, at \( t = 0 \), \( x(0) \) prey and \( y(0) \) adult predators, say obtained from a certain laboratory, and from a second laboratory, we obtain \( J \) juvenile predators of various stages of maturity. Suppose, in addition, that we are given precise information about when each of the \( J \) juveniles was born. Then we should have all the information we need to calculate the future population of prey, juvenile predators, and adult predators. But our model (2)-(3) is not fit for this.
We argue here that a more natural model should not make needless assumptions linking the initial data of prey, juvenile predator, and adult predator. A flexible model should require only the following initial data at \( t = 0 \): \( x(0) \), \( y(0) \) and the age-distribution of the juveniles \( J_0(a) \) where 

\[
\int_{0}^{\tau} J_0(a) da
\]

represents the total number of juvenile predators at time \( t = 0 \) and 

\[
\int_{c}^{d} J_0(a) da
\]

represents the number of juvenile predators with ages in the interval \([c, d] \subset [0, \tau]\). Thus, \( J_0(a) da \) represents the number of juvenile predators of age in \([a, a + da]\) at \( t = 0 \). Obviously, this cohort was born at time \( t = -a \) and will mature at time \( t = \tau - a \). Note that no juvenile can be older than age \( \tau \). This implies that the initial population of juvenile predators, whose age-distribution is given by \( J_0 \), will have either died or matured to adults by time \( t = \tau \). After that time, all new juvenile predators will be offspring, or offspring of offspring, etc., of the initial adult population whose numbers are \( y(0) \).

Therefore we must describe the dynamics of the populations over the very first maturation interval \( 0 \leq t \leq \tau \) in a different way than for subsequent maturation intervals since for the former, the only maturing predators will result from the initial cohort described by \( J_0 \), whereas these will have all have died or matured by time \( t = \tau \). If \( 0 < t < \tau \), a juvenile predator from the initial cohort should have age \( a = \tau - t \) at \( t = 0 \) in order that it mature at time \( t \) when its age is \( a = \tau \). Of course, it must survive to be alive at time \( t \) and the probability for this is \( e^{-\nu t} \).

Thus, for \( 0 \leq t \leq \tau \):

\[
x' = rx(1 - x/K) - p(x)y
\]

\[
y'_J(t) = bp(x(t))y(t) - \nu y_J - e^{-\nu t} J_0(\tau - t), \quad t \geq 0
\]

\[
y' = e^{-\nu t} J_0(\tau - t) - dy
\]

where at \( t = 0 \), we have

\[
x(0) = x_0 \geq 0, \; y(0) = y_0 \geq 0, \; J_0(a) \geq 0, \; 0 \leq a \leq \tau,
\]

and

\[
y_J(0) = \int_{0}^{\tau} J_0(a) da < \infty.
\]
For \( t \geq \tau \), the system (1), or (2), captures the dynamics of our population keeping in mind that the delayed variables \( x(t - \tau) \) and \( y(t - \tau) \), where \( 0 \leq t - \tau \leq \tau \), are those produced by (4).

We should check that the juvenile predators cannot become negative for (4)-(6). As we noted above, this can happen for (1). If we apply the same integration steps used to pass from (1) to (2) we obtain that

\[
y_J(t) = e^{-\nu t} \int_0^{\tau-t} J_0(a)da + b \int_0^{t} e^{-\nu(t-s)}p(x(s))y(s)ds, \ 0 \leq t \leq \tau.
\]

Now we can apply the integration steps to (1) for \( t \geq \tau \), using (7), to find that

\[
y_J(t) = \int_{t-\tau}^{t} e^{-\nu(t-s)}bp(x(s))y(s)ds, \ t > \tau.
\]

Clearly then, \( y_J(t) \) is nonnegative for \( t \geq 0 \).

4. Simulations

In order to conveniently solve the system using Matlab, we must solve (4)-(6) for \( 0 \leq t < \tau \) and, for \( t \geq \tau \):

\[
x' = rx(1 - x/K) - p(x)y
\]

\[
y_J'(t) = by(t)p(x(t)) - e^{\nu t}by(t - \tau)p(x(t - \tau)) - \nu y_J(t)
\]

\[
y' = by(t - \tau)p(x(t - \tau))e^{-\nu \tau} - dy
\]

with initial data coming from the solution of (4).

In the Figures 1 and 2 we follow [2] by taking \( p(x) = px \) (i.e., \( C = 0 \)) where \( r = p = \nu = \tau = 1, d = 0.5, b = 10 \). Initial data in both cases have \( y(0) = 0 \) and \( J_0(a) = 10 \) if \( 0 < a < 0.1 \) and \( J_0(a) = 0 \) if \( a > 0.1 \). Figure 1 shows a simulation starting with only juvenile predators and no prey \( x(0) = 0 \); of course nothing interesting happens since there is no prey for predators so they are doomed. Figure 2 starts with some prey \( x(0) = 0.3 \). Retaining the same parameters, except for the maturation delay \( \tau \), the remaining figures explore the effect of an increasing maturation delay. Remarkably, the dynamics is stabilized by an increasing delay unless it gets too large in which case the predators are doomed.
Figure 1. Simulation starting with only juvenile predators, no prey

Figure 2. Simulation starting with only juvenile predators
A STAGE-STRUCTURED PREDATOR-PREY MODEL

Figure 3. $\tau = 0.1$

Figure 4. $\tau = 0.6$
Figure 5. $\tau = 1.8$

Figure 6. $\tau = 3.5$
4.1. **MATLAB Code.** The code is given below. As usual in MATLAB, any text following a % is ignored by MATLAB. The first file is called "predpreydelay.m":

```matlab
function Ydot=predpreydelay(t,Y,Z,j,r,K,nu,d,b,p,C,D,tau)
% this file contains the differential equation
% here are the parameters appearing in it

% D=exp(-nu*tau);
Ylag=Z(:,1);
Ydot=zeros(3,1);

% Here is \( J(t-tau) \) where \( J(a)=j*10*tau*(1-H(a-tau/10)) \)
% where H is heaviside function
if t <= 0.9 * tau
    J=0;
else
    J=j*10*tau;
end

% here are the delay differential equations dy/dt=Ydot
if t <= tau
    Ydot(1) = r * Y(1) * (1 - Y(1)/K) - p * Y(3) * Y(1)/(1 + C * Y(1));
    Ydot(2) = b * p * Y(1) * Y(3)/(1 + C * Y(1)) - nu * Y(2) - exp(-nu * t) * J;
    Ydot(3) = exp(-nu * t) * J - d * Y(3);
else
    Ydot(1) = r * Y(1) * (1 - Y(1)/K) - p * Y(1) * Y(3)/(1 + C * Y(1));
    Ydot(2) = b * p * Y(1) * Y(3)/(1 + C * Y(1)) -
               D * b * p * Ylag(1) * Ylag(3)/(1 + C * Ylag(1)) - nu * Y(2)
    Ydot(3) = D * b * p * Ylag(1) * Ylag(3)/(1 + C * Ylag(1)) - d * Y(3);
end
```

The function "predpreydelay.m" above is called by the following MATLAB file called "predpreydelaygraph.m":

```matlab
% Ydot=predpreydelay(t,Y,Z,j,r,K,nu,d,b,p,C,D,tau)
r=1;
K=1;
p=1;
nu=1;
d=0.5;
b=10;
C=0;
tau=3.5;
D=exp(-nu*tau);

% initial
x=0.3;
j=1; % j= total initial juvenile population
z=1.0;

history = [x;j;z];
tspan = [0,200];
opts = ddeset('Jumps',tau,'RelTol',1e-7,'AbsTol',1e-9);
sol=dde23('predpreydelay',tau,history,tspan,opts,j,r,K,nu,d,b,p,C,D,tau);

plot(sol.x,sol.y);
legend('x','y','J','y',1);
```

An Age Structured Model of the Juveniles

We are motivated to consider a more general modeling approach which accounts for the age (maturity level) of a juvenile and allows the possibility to relax the assumption that all juveniles mature on their $\tau$-th birthday.

Let $J(a, t)$ be the juvenile predator age-distribution, defined for age $a \geq 0$ and $t \geq 0$ such that

$$\int_c^b J(a, t) da = \text{juveniles of age between } c \text{ and } b$$
Let $\nu(a)$ denote the juvenile death rate and $m(a)$ denote the maturation rate. Then $J(a,t)$ satisfies
\[
\frac{d}{dt} \int_c^b J(a,t) \, da = J(c,t) - J(b,t) - \int_c^b (m(a) + \nu(a))J(a,t) \, da
\]
This just says that the number of juveniles of age between $c$ and $b$ increases by juveniles of age $c$ entering the age window, and decreases by juveniles aging out of the window, or by maturing to adults, or by death. Differentiating both sides with respect to $b$ and setting $b = a$ results in
\[
\frac{\partial J(a,t)}{\partial t} = -\frac{\partial J(a,t)}{\partial a} - (m(a) + \nu(a))J(a,t)
\]
If $x$ denotes prey density and $y$ denotes mature predator density, then the age-structured model becomes:
\[
\begin{align*}
x' &= r x(1 - x/K) - p(x)y \quad x(0) = x_0 \\
\frac{\partial J(a,t)}{\partial t} + \frac{\partial J(a,t)}{\partial a} &= - (m(a) + \nu(a))J(a,t) \\
J(0,t) &= by(t)p(x(t)) \quad \text{new-born juveniles} \\
J(a,0) &= J_0(a) \quad \text{initial juvenile age-distribution} \\
y' &= \int_0^\infty m(a)J(a,t) \, da - dy, \quad y(0) = y_0
\end{align*}
\]
Notice that the gain to the juvenile population comes from births by adults and since births enter the juvenile population with age zero, this gain term appears in the boundary condition at $a = 0$. An initial juvenile distribution $J_0(a)$ at times $t = 0$ must also be prescribed. The first term in the equation for adults reflects the rate of maturation of juveniles.

In addition to far greater generality relative to the delay differential equation model (2), the issue of initial conditions is more transparent for (10) from a biological perspective: one gives the initial number of predator and prey and the initial age distribution of the juvenile predators.

6. Method of Characteristics

An explicit expression for the juvenile age-distribution in terms of the other variables may be obtained by solving the PDE by the method of characteristics [5]. $J(a,t)$ is known at the boundary of the first quadrant by virtue of the boundary conditions. Our task is to determine $J(a,t)$ at an interior point. The cohort of juveniles of age $a$ at time $t$, born after $t = 0$, were born at time $t - a \geq 0$. Their path
through age and time space is described by the characteristic curve $s \rightarrow (s, t - a + s), \ 0 \leq s \leq a$. From the equation for juveniles:

$$\frac{d}{ds} J(s, t - a + s) = \frac{\partial J(s, t - a + s)}{\partial t} + \frac{\partial J(s, t - a + s)}{\partial a}$$

$$= -(m(s) + \nu(s))J(s, t - a + s)$$

with

$$J(0, t - a) = by(t - a)p(x(t - a))$$

The solution of this initial value problem for $J(s) = J(s, t - a + s)$ is given by

$$J(s) = J(s, t - a + s) = by(t - a)p(x(t - a)) \exp \left( - \int_0^s m(u) + \nu(u)du \right)$$

Setting $s = a$ in this expression we find that

$$J(a, t) = by(t - a)p(x(t - a)) \exp \left( - \int_0^a m(s) + \nu(s)ds \right), \ t \geq a$$

The cohort of juveniles of age $a$ at time $t$ which were born before $t = 0$ are derived from the initial cohort $J_0(a-t)$. Their path through age and time space is described by the characteristic curve $s \rightarrow (a - t + s), \ 0 \leq s \leq t$. From the equation for juveniles:

$$\frac{d}{ds} J(a - t + s, s) = \frac{\partial J(a - t + s, s)}{\partial t} + \frac{\partial J(a - t + s, s)}{\partial a}$$

$$= -(m(a - t + s) + \nu(a - t + s))J(a - t + s, s)$$

and integrating this equation gives

$$J(a - t + s, s) = J_0(t - a) \exp \left( \int_0^s m(a - t + u) + \nu(a - t + u)du \right)$$

Setting $s = t$ results in

$$J(a, t) = J_0(t - a) \exp \left( \int_0^t m(a - t + u) + \nu(a - t + u)du \right)$$

$$= J_0(t - a) \exp \left( \int_{a-t}^t m(r) + \nu(r)dr \right)$$

In summary, after a change of integration variable, we have expressed the juvenile predator age distribution in terms of the initial data and the adult predator and prey population densities:

$$J(a, t) = \begin{cases} 
by(t - a)p(x(t - a))\tilde{f}(a), & t > a \\
J_0(a-t)\frac{\tilde{f}(a)}{\tilde{f}(a-t)}, & t < a 
\end{cases}$$
where

\[
\mathcal{F}(a) = e^{-\int_0^a \nu(u) + m(u) \, du}
\]

The total juvenile population \( y_J(t) = \int_0^\infty J(a, t) \, da \) is

\[
y_J(t) = \int_0^t J(a, t) \, da + \int_t^\infty J(a, t) \, da \\
= \int_0^t by(t - a)p(x(t - a))\mathcal{F}(a) \, da \\
+ \int_t^\infty J_0(a - t) \frac{\mathcal{F}(a)}{\mathcal{F}(a - t)} \, da \\
= \int_0^t by(t - a)p(x(t - a))\mathcal{F}(a) \, da \\
+ \int_0^\infty J_0(r) \frac{\mathcal{F}(r + t)}{\mathcal{F}(r)} \, dr
\]

Similarly, the integral source term in the adult predator equation is given by

\[
\int_0^\infty m(a)J(a, t) \, da = \int_0^t m(a)J(a, t) \, da + \int_t^\infty m(a)J(a, t) \, da \\
= \int_0^t by(t - a)p(x(t - a))\mathcal{F}(a)m(a) \, da \\
+ \int_t^\infty m(a)J_0(a - t) \frac{\mathcal{F}(a)}{\mathcal{F}(a - t)} \, da \\
= \int_0^t by(t - a)p(x(t - a))\mathcal{F}(a)m(a) \, da \\
+ \int_0^\infty m(r + t)J_0(r) \frac{\mathcal{F}(r + t)}{\mathcal{F}(r)} \, dr
\]
System (10) becomes:

\[
x' = rx(1 - x/K) - p(x)y
\]

\[
y_J(t) = \int_0^t by(t - a)p(x(t - a))\mathcal{F}(a)da
\]

\[
+ \int_0^\infty J_0(r)\frac{\mathcal{F}(r + t)}{\mathcal{F}(r)}dr
\]

\[
y' = \int_0^t by(t - a)p(x(t - a))\mathcal{F}(a)m(a)da
\]

\[
+ \int_0^\infty m(r + t)J_0(r)\frac{\mathcal{F}(r + t)}{\mathcal{F}(r)}dr - dy
\]

(13) is a delay differential equation, sometimes called an integro-differential equation. The delay is effectively unbounded.

7. Fixed Maturation Time, Constant Death Rate

Now we specialize our model in order derive a model similar to (2). Assume that the maturation rate \(m(a)\) satisfies

\[
m(a) = MH(a - \tau)
\]

where \(M \gg 1\) and \(H(t)\) is the Heaviside function. Then the probability of being in the juvenile class at age \(a\), given alive, is

\[
e^{-\int_0^a m(u)du} = \begin{cases} 1, & a < \tau \\ e^{-M(a - \tau)}, & a > \tau \end{cases} \rightarrow 1 - H(a - \tau), \ M \rightarrow \infty
\]

The maturation rate (14) captures the idealized situation where an individual remains a juvenile for precisely \(\tau\) units of time, if it remains alive. Formally, this corresponds to \(M = \infty\) in (14). As juvenile ages are now restricted to be less than \(\tau\), we assume hereafter that:

\[J_0(a) = 0, \ a > \tau\]

For simplicity, lets also assume that the juvenile death rate is constant

\[
\nu(s) \equiv \nu > 0.
\]

Now,

\[
e^{-\int_0^a m(u)da}m(a) = \begin{cases} 0, & a < \tau \\ Me^{-M(a - \tau)}, & a > \tau \end{cases} \rightarrow \delta_\tau(a), \ M \rightarrow \infty
\]

where \(\delta_\tau\) is the unit impulse function centered at \(\tau\) in the sense that

\[
\int_0^\infty F(a)MH(a - \tau)e^{-M(a - \tau)}da \rightarrow F(\tau), \ M \rightarrow \infty
\]
for every bounded continuous function $F$. Also,

\begin{equation}
(17) \quad e^{-\int_{r+t}^{r+t} m(u) du} \rightarrow \begin{cases} 
1, & r + t < \tau \\
0, & r + t > \tau 
\end{cases}, \quad M \rightarrow \infty
\end{equation}

Using (16)-(17), we may compute the limiting values of the four integral terms in (13) as $M \to \infty$. The first is:

\[ \int_0^t by(t-a)p(x(t-a)) \mathcal{F}(a) da \rightarrow \left\{ \begin{array}{ll}
\int_0^t by(t-a)p(x(t-a))e^{-\nu a} da, & t < \tau \\
\int_0^\infty by(t-a)p(x(t-a))e^{-\nu a} da, & t > \tau 
\end{array} \right. \]

The second integral term becomes:

\[ \int_0^\infty J_0(r) \frac{\mathcal{F}(r+t)}{\mathcal{F}(r)} dr \rightarrow \left\{ \begin{array}{ll}
e^{-\nu t} \int_0^{\tau-t} J_0(r) dr, & t < \tau \\
0, & t > \tau \end{array} \right. \]

The third becomes:

\[ \int_0^t by(t-a)p(x(t-a))m(a) da \rightarrow \left\{ \begin{array}{ll}
0, & t < \tau \\
by(t-\tau)p(x(t-\tau))e^{-\nu t}, & t > \tau \end{array} \right. \]

The final integral is trickier. Ignoring the factor $e^{-\nu t}$ in the integrand, we rewrite the integral as:

\[ \int_0^\infty m(r+t)J_0(r)e^{-\int_{r+t}^{r+t} m(u) du} dr = \int_0^\tau m(r+t)J_0(r)e^{-\int_{r+t}^{r+t} m(u) du} dr \\
= \int_0^{t+\tau} m(s)e^{-\int_0^s m(u) du} J_0(s-t) ds \\
\rightarrow \int_t^{t+\tau} \delta_r(s) J_0(s-t) ds \]

where we used that $e^{-\int_0^a m(u) du} = 1$, $a < \tau$ in the second line. Therefore

\[ \int_0^\infty m(r+t)J_0(r)e^{-\nu t} e^{-\int_{r+t}^{r+t} m(u) du} dr \rightarrow \left\{ \begin{array}{ll}
e^{-\nu t} J_0(\tau - t), & t < \tau \\
0, & t > \tau \end{array} \right. \]

Finally, we arrive at the model equations.

For $0 \leq t < \tau$:

\begin{align*}
x' & = rx(1-x/K) - p(x)y, \quad x(0) = x_0 \\
y_1(t) & = \int_0^t by(t-a)p(x(t-a))e^{-\nu a} da + e^{-\nu t} \int_0^{\tau-t} J_0(r) dr \\
y' & = e^{-\nu t} J_0(\tau - t) - dy, \quad y(0) = y_0
\end{align*}
For $t \geq \tau$:

\begin{align*}
x' &= rx(1 - x/K) - p(x)y \\
y_J(t) &= \int_0^\tau by(t - a)p(x(t - a))e^{-\nu a}da \\
y' &= by(t - \tau)p(x(t - \tau))e^{-\nu \tau} - dy
\end{align*}

These equations are exactly (4) derived earlier. Basically, (18) gives the dynamics before the initial juvenile cohort $J_0$ has matured while (19) describes the subsequent dynamics.

The first integral term in (18) represents new juvenile predators produced by predation since time $t = 0$ and which survive to be alive at time $t$. The second integral term represents the survivors from the initial cohort $J_0$. They must be the survivors among that cohort with age less than $\tau - t$ in order to be age less than $\tau$ at time $t$. Finally, the integral term is the $y$ equation of (18) represents the rate at which juveniles in the initial cohort $J_0$ mature at time $t$.

Although the structured model takes a long road to the final equations, it is more flexible (allowing for different death and maturation rates) and there is less chance for modeling errors.

8. Exercises

(1) Verify (7) and (8). Can you give a biological interpretation of it?

(2) Show that a positive equilibrium exists for ((2)) with $p(x) = px$ if and only if $be^{-\nu \tau}p(K) > d$. Does this hold if $p(x) = \frac{px}{1+Cx}$?

(3) Compute the predator reproductive number in the prey-only equilibrium state.

(4) Show that $y(t) \to 0$ if $be^{-\nu \tau}p(K) < d$. Hint: estimate $p(x(t-\tau))$ from above and use Theorem 3.6 of [4].

(5) Compute the characteristic equation corresponding to the linearization about the positive equilibrium of (2), ignoring the equation for juvenile predators. Note its similarity to (8.19) in [4]. Can the analysis of the latter be carried over?

(6) Verify the limiting values of the three integral terms below (17).

(7) Verify (16).

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References


