Structured Models: An Introduction

Presented by:

Thomas Shores

Department of Mathematics

University of Nebraska-Lincoln

OUTLINE

1. Background and Motivation

2. Derivation of A Structured Model

3. Special Cases

4. Some Philosophy

5. Predator/Prey Systems

6. Numerics

BACKGROUND AND MOTIVATION

One of the first population models one encounters is the Malthusian model

$$\frac{dP(t)}{dt} = \alpha P(t),\ t > 0,$$

where $P(t)$ is the total population of an animal under consideration and

$$\alpha = \beta - \mu$$

is a total growth rate consisting of birth rate minus death rate. This model has the merit of simplicity. But real populations are a good deal more complex. A few key points:

- Juveniles (or eggs!) don't contribute to the birth rate in the same way as adults.
- Mortality rates vary with age or perhaps size.
- There are environmental limitations to growth.

DERIVATION OF STRUCTURED MODEL

We refine our understanding of the population by using a *maturity variable* z. Maturity could be age, weight, etc. We assume

- Population is described by density function $u(z, t)$ in units of population per maturity size, say with $0 \leq z \leq z_*$
- Maturation rate is governed by a nonnegative function $g(z, t)$ in units of maturity size per unit time.
- Mortality rate $\mu(z, t)$ is maturity and (possibly) time dependent in units of population per unit time.
- Birth rate $\beta(z, t)$ is maturity and (possibly) time dependent.
- We know the initial population distribution to be $u(z, 0) = \phi(z)$, $0 < z < z_*$.

Consider the time rate of change of the total population $\int_a^b u(s,t)\,ds$ in an interval $[a,b]$ with $0 < a < b < z_*$. The flow of population per unit time across a maturity point x at time t is $g\,(x,t)\,u\,(x,t)$. The time rate of change of the population in an interval is inflow at left minus outflow at right plus growth/decay in the interval. So a balance argument gives

$$\frac{d}{dt}\int_a^b u(s,t)\,ds = g(a,t)u(a,t) - g(b,t)u(b,t) - \int_a^b \mu(s,t)u(s,t)\,ds.$$

Thus

$$\int_a^b \frac{\partial}{\partial t}u(s,t)\,ds = -\int_a^b \left(g(s,t)u(s,t)\right)_z\,ds - \int_a^b \mu(s,t)u(s,t)\,ds$$

and

$$\int_a^b \left\{\frac{\partial}{\partial t}u(s,t)\,ds + \left(g(s,t)u(s,t)\right)_z + \mu(s,t)u(s,t)\right\}\,ds = 0.$$

Assume the integrand is continuous and we obtain from the fact that a, b are arbitrary that the integrand is identically zero. Hence, there results the classic structured population model

$$\begin{aligned} \frac{\partial u}{\partial t}+\frac{\partial}{\partial x} \quad (gu) = & \quad -\mu(z,t)u,\ t>0,\ 0<z<z_*, \\ u(z,0) \quad = & \quad \phi(z),\ 0<z<z_* \\ g(0,t)u(0,t) \quad = & \quad \int_0^{z_*} \beta(s,t)u(s,t)ds,\ t>0 \end{aligned}$$

Notice that the left boundary condition is *non-local*.

SPECIAL CASES

1. (Mc-Kendrick-von Foerster model) Maturity variable is age. In this case, the growth rate is $g(z, t) = 1$. A classic work by Nicholson (1954) studied population dynamics of sheep blowfly (*Lucilia caprina*) using what amounts to an age structured model. The laboratory results were very well approximated by mathematical solutions to the model. Note: in this case it isn't too difficult to derive explicit solutions to the model.

2. (Sinko-Streifer model) Maturity variable is size. Here the growth rate g need not be constant. Explicit solutions become a bit more difficult to obtain, but are possible in many cases. This type of model has been used to model many populations, e.g., aggregation of phytoplankton (algae) in oceans by Ackleh and Fitzpatrick (1996).

3. (Phenological models) Here the maturity variable is

$$z = \int_0^t R(\theta(s))\, ds$$

where $\theta = \theta(t)$ is temperature at time t and R is the development rate as a function of temperature. In this case the growth rate is simply

$$g(t) = \frac{dz}{dt} = R\left(\theta(t)\right).$$

This model is particularly useful in the study of insect populations such as grasshoppers, which has a good deal of local interest.

SOME PHILOSOPHY

What use do we make of these models? The answer is two-fold (well, at least!)

- *Qualitative Predictions.* Without knowing too much detail about the actual numbers we can ask questions like: will the population grow, stabilize, fall to extinction, behave periodically or even chaotically? One can recast the structured models as delay differential equations or integral equations and do mathematical analysis thereon. Monographs by Cushing, and Gurney and Nisbit address these issues in great detail and provide many interesting case studies.

- Literal Predictions. Here we want a real live model that specifically makes verifiable good predictions about a particular population. Nicholson's blowfish investigation is a good example of this (as well as qualitative prediction!) Ditto Ackleh and Fitzpatrick.

Each view has its own mathematical needs. Both need ideas from the theory of partial and ordinary differential equations. The qualitative approach involves a good deal of classical and functional analysis, as well as dynamical systems. The literal approach requires more numerical analysis and inverse theory ("here's the answer, what's the question?"). Specifically, we might attempt to make reasonable approximations to the parameters by way of population measurements. The question becomes: what measurements are needed?

Example. One can show that if g is a constant and $\mu = \mu(z)$ is known, then $\beta = \beta(z)$ is uniquely determined by the measurements $u(0,t)$, $0 \leq t \leq 2/g$.

PREDATOR/PREY SYSTEMS

If the population we are studying is a food source for another population, then these are inextricably bound together, and we must account for both. The classical model here is the famous Lotka-Volterra model for a total population $P(t)$ of predators and prey $N(t)$

$$\begin{aligned}\frac{dN}{dt} &= (r - \alpha P)\, N \\ \frac{dP}{dt} &= (\beta N - \delta)\, P.\end{aligned}$$

But we already know the situation is a good deal more complicated. Consider, e.g., grasshopper prey and spider predators. Adult grasshoppers have wings and are big. They are less likely to be successfully attacked by a spider than a wingless juvenile. Again, we see that "maturity" is an important factor. So how do we factor this into our model. There are numerous lines of thought:

1. Treat both populations as structured. For example, M. Saleem studied egg-eating age-structured predators in interaction with age-structured prey. If $u(z,t)$ is the prey density and $v(z,t)$ the predator density, then he obtains

$$\begin{aligned} u_t + u_z &= -\mu u \\ v_t + v_z &= -\eta v \\ u(0,t) &= \int_0^\infty \beta(s,t)u(s,t)ds - ku(0,t)\int_0^\infty v(s,t)\,ds, \\ v(0,t) &= \int_0^\infty \gamma(s,t)u(s,t)ds \end{aligned}$$

Now integrate these equations to obtain ordinary differential equations for $P(t)$ and $N(t)$.

2. Accept the idea that the maturity parameter is different for predator and prey. so we arrive at a system like

$$\begin{aligned} u_t + (gu)_x &= f(u,v,u(\cdot,t),v(\cdot,t)) \\ v_t + (hv)_z &= g(u,v,u(\cdot,t),v(\cdot,t)) \\ u(0,t) &= \int_0^\infty \beta(s,t)u(s,t)ds, \\ v(0,t) &= \int_0^\infty \gamma(s,t)u(s,t)ds \end{aligned}$$

3. Assume that predators are sufficiently homogeneous that a structured distinction is unnecessary. Gurtin and Levine (1980) used this approach. Now we arrive at a coupled system of PDE for prey density $u(z,t)$ and ODE for predator (total) population $P(t)$

$$\begin{aligned} u_t + (gu)_z &= -(\mu + h)\, u,\ 0 < z < z_*,\ t > 0 \\ g(0,t)u(0,t) &= \int_0^{z_*} \beta(s,t)u(s,t)\, ds, 0,\ t \geq 0 \\ u(z,0) &= \phi(z),\ 0 \leq z \leq z_* \end{aligned}$$

$$P'(t) = f(t, u, P, u(\cdot, t))$$

where f is a non-local function as is the "harvesting rate" $h = h(z, t, u, u(\cdot, t), P)$.

One example I'm currently experimenting with is

$$f = \min\left\{\left(\theta\left(G(t,F) - \delta\right) + (1-\theta)\, r\left(1 - \frac{P}{K}\right)\right), \sigma\right\} P$$

where θ is a "preference factor", r a growth rate, K a carrying capacity, δ a mortality rate and σ a maximum growth rate. Here G is a nonlocal term that determines the growth rate of the predator population (excluding mortality.) Simple choices of G: $G = cF$ for Lotka-Volterra type responses, $G = cF/\left(F_h + F\right)$ for a Holling type II response function. We can even add a time dependency to the Holling term and obtain

$$G(t,F) = \frac{c(t)F}{F_h + F}.$$

In this way, we can account for fluctuations in growth of predator due to temperature variations.

NUMERICS

Very interesting stuff!!!

REFERENCES

1. Frank Hoppensteadt, *Mathematical Theories of Population: Demographics, Genetics and Epidemics*, CBMS-NSF Conference series (20), SIAM (1975).

2. J. M. Cushing, *An Introduction to Structured Population Dynamics*, CBMS-NSF Conference series (71), SIAM (1998).

3. D. M. Auslander, G. F. Oster and C. B. Huffaker, *Dynamics of Interacting Populations*, Journal of the Franklin Institute (1974).

4. W. Gurney and R. Nisbit, *Ecological Dynamics*, Oxford U. Press (1998).