Age and Size Structured Models: A Survey

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

4. A. Acleh and B. Fitzpatrick, Modeling aggregation and growth processes in an algal population model: analysis and computation, J. of Math. Biology, 481-502 (1997).

OUTLINE

1. Review of Background
2. McKendrick-von Foerster Model
3. Sinko-Streifer Model
4. Nicholson Blowfly Experiment
5. Numerical methods

BACKGROUND

The problem is to determine a population density function $u(x,t)$, $0 \leq x \leq L$, $t > 0$, where t is time and x a continuous "tag" variable, like age or size. We assume that u has units of population/tag and that all newborns (recruits) come into existence with tag 0. Consequently,

$$\int_0^1 u(x,t)dx = U(t),\ t \geq 0,\ 0 \leq x \leq L$$

the total population at time t and

$$u(0,t) = \int_0^L \beta(x,t)u(x,t)dx$$

is the population of newborns, where β is a fecundity function.

A balance argument leads us to the model differential equation

$$\frac{\partial u}{\partial t} + \frac{\partial \Phi}{\partial x} = f(x,t),\ t > 0,\ 0 < x < L$$

where we understand that Φ is a flux function with units of population/time and $f(x,t)$ is a source or sink term with units of density/time.

Mc-KENDRICK-von FOERSTER MODEL

In this model the tag x is age, which is measured in the same units as time. Thus L represents the maximum life span. The flux term is given by

$$\Phi = u$$

and the source term is

$$f(x,t) = -\mu(x,t)u(x,t),$$

where μ is a mortality rate. The fecundity function is β. The resulting system (limits on variables as above) is

$$\begin{aligned} \frac{\partial u}{\partial t} + \frac{\partial \Phi}{\partial x} &= -\mu(x,t)u \\ u(x,0) &= \phi(x) \\ u(0,t) &= \int_0^L \beta(x,t)u(x,t)dx \end{aligned}$$

SINKO-STREIFER MODEL

In this model the tag x is size. The flux term is given by

$$\Phi = g(x,t)u$$

where g is a growth term and the source term is

$$f(x,t) = -\mu(x,t)u(x,t),$$

where μ is a mortality rate. The fecundity function is β. The resulting system is

$$\begin{aligned} u_t + (gu)_x &= -\mu(x,t)u(x,t) \\ u(x,0) &= \phi(x) \\ g(0,t)u(0,t) &= \int_0^L \beta(x,t)u(x,t)dx. \end{aligned}$$

A standard assumption in this model is that $g > 0$ for $0 \leq x < L$.

Case Study: Sheep Blowflies

Experiments by A. Nicholson (1954) studied population dynamics of sheep blowfly (*Lucilia caprina*). Background facts:

- Blowfly has four life stages: egg (day 0), larvae (day 1), pupae (day <11), immature adult (day 11) and mature adult (15 onward). Mature adult stage is the reproducing stage.

- Larvae had unlimited food supply.

- Adults had unlimited sugar and water, but limited protein (ground liver). This limits egg production.

Data:

- Survival rate to mature adult stage is about 91%.

- Per capita death rate beyond day 15 is about 27%.

- Peak adult populations fluctuate between about 5K and 10K, with troughs around 150-300 adults.

- Egg production depends on available protein. Nicholson used 500 mg. per day.

Modeling the Experiment

The units of time and age are clearly days.

Gurney et al. argue that if f mg. of protein per day is consumed by an adult, then reproductive rate per adult is $\beta = 8.5e^{-5/(6f)}$, so if available protein is equally divided, each adult gets $f = 500/F(u(\cdot,t))$ mg. daily, where $F(u(\cdot,t)) = \int_{15}^{45} u(x,t)dx$.

Since the survival to mature adult is 91% likely, we assume a daily pre-adult survival rate of

$$(0.91)^{1/15} \approx 0.9937.$$

It follows that the pre-adult mortality rate is 0.0063.

The daily mortality rate is 0.27, so that in 30 days a peak population of 10K shrinks to $10000 \cdot (0.73)^{30} \approx 0.8$. So it is reasonable to take the maximum life span to be $L = 45$

In summary, our model takes this form:

- Population density is $u(x,t)$, x age, t time.

- Age x has the range $0 \leq x \leq L = 45$

- Mortality rate

$$\mu(x) = \begin{cases} 0.0063, \; x < 15 \\ 0.27, \; x \geq 15. \end{cases}$$

- Reproductive rate ($F(u(\cdot,t)) = \int_{15}^{45} u(x,t)dx.$)

$$\beta(x,t,u(\cdot,t)) = \begin{cases} 0, \; x < 15 \\ 8.5e^{-F(u(\cdot,t))/600}, \; x \geq 15. \end{cases}$$

Model Equations (a souped-up McKendrick-von Foerster model):

$$\begin{aligned} u_t + u_x &= -\mu(x,t)u \\ u(x,0) &= \phi(x) \\ u(0,t) &= \int_0^L \beta(x,t,u(\cdot,t))u(x,t)dx. \end{aligned}$$

A Simple Numerical Scheme for McK-vF

We are going to develop a simple intuitive scheme for solving the McKendrick-von Foerster model, even in its souped up form.

The idea: break the interval $0 \leq x \leq L$ up into subintervals of uniform size so that the population represented in that subinterval becomes a "cohort" that we will track through time.

We shall assume, for simplicity, that there is at most one point in the interval $(0, L)$ at which μ or ϕ suffers a discontinuity. We always use a subdivision that puts this point of discontinuity at the boundary of our subintervals.

We use the midpoint values of μ and ϕ in each subinterval where a cohort resides.

Finally, we assume a suitable approximation (e.g., a midpoint method for integrals) to the functional in $\beta(x, t, u(\cdot, t))$ can be obtained by the cohort values.

The Boxcar Method

The method we have just described is a very simple discretization into a non-stationary Leslie model. There is a more sophisticated version of the method we have described, called the *escalator boxcar train*. The idea is to descretize the population into “cohorts” exactly as we did above. Let N_i be the population of the ith cohort and $R(t)$ the total number of recruits at time t. Now we allow the population to vary *continuously* in time, which results in the system of differential equations

$$\frac{dN_i}{dt} = \begin{cases} R(t) - \mu(\overline{a}_i, t)N_i, \text{ if } i\,dx \leq t < (i+1)dx \\ -\mu(\overline{a}_i, t)N_i, \text{ otherwise} \end{cases}$$

where $\overline{a}_i$ is the average age in the ith cohort. This is essentially a “method of lines” that moves along characteristics.