Chapter 3: Basic Analysis : Demographic Measures and Events in the Life Cycle

Book: Data-driven Modelling of Structured Populations by Stephen P. Ellner, Dylan Z. Childs and Mark Rees

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Content

Recall

Integral Projection Models (IPMs) can be written as

$$n(z', t+1) = \int_Z K(z', z) n(z, t) dz$$

or simply

$$n(t+1) = Kn(t)$$

where

$$K(z', z) = \underbrace{s(z)G(z', z)}_{P(z',z)} + F(z', z)$$

P is the survival component
F is the reproduction component
K is the net result of survival and reproduction that projects the population size.

Goal

- Chapter 2: introduced the basic concepts underlying IPMs, and to step through the complete process of building and then using an IPM based on your population census data. The case studies illustrated how the familiar measures of population change (stable population structure, long-term growth rate, reproductive value, etc.) can be calculated from an IPM.
- Chapter 3: wants to take a closer look at population growth, and then show how a fitted IPM can be used to calculate statistics summarizing the life cycle, such as age-specific fecundity and survival probability, expected lifespan, lifetime reproductive output, and size at death.

Demographic quantities: Population growth

λ is a key demographic quantity which summarizes how all the state-dependent processes occurring in the life cycle combine to determine how rapidly a population grows.

Unstructured density independent population

$$n(t) = n(0)\lambda^t \implies \lim_{t\to\infty} \frac{n(t)}{\lambda^t} = n(0)$$

For IPMs

$$\lim_{t\to\infty} \frac{n(z,t)}{\lambda^t} = Cw(z)$$

where $w(z)$ is the stable state distribution.

An IPM typically has infinitely many eigenvalues, but the mathematical theory insures that there is a single dominant eigenvalue λ, and a nonzero gap between the magnitude of λ and that of any other eigenvalue.

Demographic quantities: R_0

R_0 is the generation-to-generation population growth rate or *Net Reproduction Rate*.

Unstructured density independent population

$$N(t+1) = (s + \underbrace{p_b p_r b}_{f})N(t)$$

so

$$R_0 = f + sf + s^2 f + ... = f(1-s)^{-1}$$

"R_0 can be defined as the average number of offspring that an individual produces over their lifetime"

Demographic quantities: R_0

In an IPM R_0: is defined as the long-term per-generation rate of increase because age-0 individuals can differ in state and therefore can differ in their expected future breeding success.

$$R_0 = \lim_{k \to \infty} \frac{g_{k+1}}{g_k}$$

where g_k is the offspring in generation k.

R_0 in IPMs

Let $n_0(z)$ be the state distribution of a cohort at birth. Then the offspring that they produce in their first year are a population with state distribution

$$Fn_0(z') = \int_Z F(z', z)n_0(z)dz$$

and the survivors to age 1 from the cohort are

$$Pn_0(z') = \int_Z P(z', z)n_0(z)dz.$$

Thus, the offspring that the focal cohort produces at age 0 is Fn_0 and the number from the cohort that survive to age 1 is Pn_0. Those survivors produce offspring which have state distribution

$$FPn_0$$

The survivors to age 2 are $P^2 n_0$, producing offspring

$$FP^2 n_0 = FP^2 n_0(z') = \int_Z F(z', z) P^2(z', z) n_0(z) dz.$$

More generally, the survivors to age k are $P^k n_0$, producing offspring

$$FP^k n_0.$$

The expected offspring from the cohort are

$$(F + FP + FP^2 + ...)n_0 = F(I - P)^{-1} n_0 = FNn_0$$

where $N = (I - P)^{-1}$ is the *fundamental operator.*

- $R = FN$ is the kernel that project the population from generation to the next. R is called the *next generation kernel*
- The long-run generation-to-generation growth rate R_0 is given by the dominant eigenvalue of R.

Demographic quantities: Age-specific vital rates

- l_a survivorship to age a
- f_a age-specific expected fecundity
- If an individual is born in state z_0, the distribution of its state next year is given by $P(z', z_0)$

So

- The probability of surviving to age a is

$$l_a(z_0) = \int_Z P^a(z', z_0)dz'$$

- The average per-capita fecundity at age a is the total reproductive output at age a of survivors, divided by the number of survivors

$$f_a(z_0) = \frac{1}{l_a(z_0)} \int_Z FP^a(z', z_0)dz'$$

Demographic quantities: Generation time

- Their definition of R_0, as per generation rate of increase, means that over one generation T the population increases by λ^T. So, $R_0 = \lambda^T$ with

$$T = \frac{\log(R_0)}{\log(\lambda)}$$

- Another measure of generation time is the mean age of mothers at offspring production. An individual is age $a+1$ when the offspring of 'last year's' a-year-olds are first censused. This measure of generation time is therefore computed

$$T = \frac{\sum(a+1)l_a(z_0)f_a(z_0)}{\sum l_a(z_0)f_a(z_0)}$$

Mortality: age and size at death

The mean lifespan can be calculated in principle as

$$\sum_{a=1}^{\infty} a(l_{a-1} - l_a)$$

Let $\eta(z)$ be the random lifespan of an individual given their initial state z. Individuals survive to age a with probability $l_a = \mathbf{e}P^a$, so

$$\begin{aligned}\bar{\eta} = E[\eta] &= \mathbf{e} + \mathbf{e}P + \mathbf{e}P^2 + \dots \\ &= \mathbf{e}(I - P)^{-1} \\ &= \mathbf{e}N\end{aligned}$$

For a cohort with initial state distribution $c(z)$, the average lifespan is

$$\tilde{\eta} = \langle \mathbf{e}N, c \rangle$$

Mortality: age and size at death

Recall: $Var(\eta) = E[\eta^2] - (E[\eta])^2$

Observe that

$$\begin{aligned}
E[\eta^2] &= \sum_{a=1}^{\infty} a^2(l_{a-1} - l_a) = \sum_{a=1}^{\infty} a^2 l_{a-1} - \sum_{a=1}^{\infty} a^2 l_a \\
&= \sum_{a=0}^{\infty} (a+1)^2 l_a - \sum_{a=0}^{\infty} a^2 l_a \\
&= 2\sum_{a=0}^{\infty} a l_a + \sum_{a=0}^{\infty} l_a \\
&= \mathbf{e}(2\sum_{a=0}^{\infty} a P^a + \sum_{a=0}^{\infty} P^a) \\
&= \mathbf{e}(2\sum_{a=0}^{\infty} (a+1) P^a - \sum_{a=0}^{\infty} P^a) \\
&= \mathbf{e}(2N^2 - N)
\end{aligned}$$

Mortality: age and size at death

Thus, the lifespan variance is

$$\sigma_\eta^2 = Var(\eta) = \mathbf{e}(2N^2 - N) - (\mathbf{e}N)^2$$

The observed variance in lifespan among members of a cohort with initial state distribution $c(z)$ is

$$Var_c(\eta) = \langle \mathbf{e}(2N^2 - N), c\rangle - \langle \mathbf{e}N, c\rangle^2$$

For a fixed state z. The fundamental operator $N(z', z)$ is the distribution function for the expected total time that an individual with initial state z spends at state z' during its lifetime.

Mortality: age and size at death

In the case an individual dies, its size at death is z. If it survives, its mean size at death is the mean conditional on its new size

$$\bar{\omega}(z) = z(1 - s(z)) + \int_Z \bar{\omega}(z')P(z', z)dz' = (\mathbf{i}(z) \circ (1 - s(z))) + \bar{\omega}P.$$

After some rearrangements,

$$\bar{\omega} = (\mathbf{i} \circ (1 - s))N = \int_Z z' \underbrace{(1 - s(z'))N(z', z)}_{\Omega(z',z)} dz'$$

and the mean size at death for a cohort of newborns with size distributions c is

$$\tilde{w} = \langle \bar{\omega}, c \rangle.$$

$\Omega(z', z)$ is the probability distribution of size at death for a cohort.

Reproduction: who, when, and how much?

- Some individuals succeed in reproducing before they die. How many?
- If reproduction occurs, at what age and size does it start?*
- How often does reproduction occur?
- How much do individuals vary in reproductive output?*
- When does reproduction end?

How many individuals succeed in reproducing before they die?

The chance that an individual breeds at least once is the probability that it leaves the pre-breeding state by reproducing

$$B = p_b N_0$$

- To allow for possible costs of reproduction, we write the survival kernel P as

$$P(z', z) = p_b(z)\pi_b(z', z) + (1 - p_b(z))\pi_0(z', z).$$

- The survival and growth kernel without breeding is

$$P_0(z', z) = (1 - p_b(z))\pi_0(z', z).$$

- The fundamental operator for the modified model is

$$N_0 = (I - P_0)^{-1}.$$

How often does reproduction occur?

The expected number of times for individuals who breed at least once is

$$p_b N/B.$$

- The expected number of times an individual is size z', conditional on its initial size z, is given by $N(z', z)$
- The chance of reproducing when size z' is $p_b(z')$
- The expected number of individuals that reproduce condition to their initial size z is

$$p_b N$$

When does reproduction end?

They find the distribution for age at last breeding among those that do at least once. The mean and variance for the cohort are then

$$E_c[S] = \langle E_b[S], c_b \rangle$$
$$Var_c[S] = \langle E_b[S^2], c_b \rangle - E_c[S]^2$$

- S and S^2 are the first and second moment of age at last breeding
- $E_b[S]$ and $E_b[S^2]$ are the first and second moments of the age at last breeding among individuals that breed at least once.
- $c_b(z)$ the probability of reproducing at least once with

$$c_b(z) = \frac{c(z)B(z)}{\langle c, B \rangle}$$

THANK YOU FOR LISTENING.
ANY QUESTIONS?