

In a real fish model the calculation of the initial equilibrium population may appear to be complicated, but viewed from the right level of mathematical generality it is a trivial application of matrix algebra. In fact it will amount to simply solving the matrix equation

$$\mathbf{x} = -(\mathbf{A} - \mathbf{Id})^{-1}(\mathbf{r}) \quad (0)$$

for \mathbf{x} where \mathbf{A} is a given matrix and \mathbf{r} is a given vector

We assume that at any time the population consists of a vector where each component of the vector is the number of individuals in some category. Simple examples of categories are number at a given age or number lying in a size interval. Categories could also be separated by sex. Categories could also involve discrete spatial areas. Categories could also consist of size and age.

Each year the members of the population grow in some fashion and experience mortality. The basic assumption is that this process is a linear function of the numbers in each category. In the matrix notation of equation (0) this linear function is represented by the matrix \mathbf{A} . To make this concept precise we introduce a bit of notation.

Suppose there are n categories. We model this as an n dimensional vector space, a typical member of which is denoted by $\mathbf{v} = (v_1, v_2, \dots, v_n)$. We will assume that the process of growing and killing off the fish is linear. More specifically we assume there is a matrix \mathbf{A} so that if the population is represented by \mathbf{v} , then after growing and killing off the fish, the surviving fish size composition is equal to $\mathbf{A}\mathbf{v}$. This does not include the new recruits to the population. It is important to see that this assumption implies that the transition of the fish in a give category to new size categories depends only on the category they are in at that time period. Let $\mathbf{r} = (r_1, r_2, \dots, r_n)$ be the recruits. Then the population in the next year is equal to $\mathbf{A}\mathbf{v} + \mathbf{r}$. It is important to understand what is meant by recruitment in this context. In a simple age-structured models all the recruits enter the model in the first category and since all the individuals in that category grow a year older and leave the category, one can identify the number of individuals in the first category with the recruitment. In the more general case, not all individuals in the first category necessarily leave that category in the next year and not all individuals entering the population enter the first category so the recruitment is distinct from the vector of number of individuals in each category.

Let $\mathbf{x} = (x_1, x_2, \dots, x_n)$ be the equilibrium population when the recruitment is \mathbf{r} fish. The requirement that the population is in equilibrium is equivalent to the matrix equation

$$\mathbf{A}\mathbf{x} + \mathbf{r} = \mathbf{x} \quad (1)$$

and the equilibrium solution is given by

$$\mathbf{x} = -(\mathbf{A} - \mathbf{Id})^{-1}(\mathbf{r}) \quad (2)$$

where \mathbf{Id} is the $n \times n$ identity matrix. Note that (2) is completely general. It could apply to a multi-region model with movement between regions. In that case one could have vectors of components \mathbf{v}_j for each of the regions and the vector \mathbf{v} would be formed by concatenating the vectors \mathbf{v}_j as in $\mathbf{v} = (\mathbf{v}_1, \mathbf{v}_2, \dots, \mathbf{v}_n)$. All we need is to calculate the

matrix \mathbf{A} . The matrix is calculated by calculating what happens to the basis vectors $\mathbf{A}\mathbf{e}_j$ where $\mathbf{e}_j = (0, \dots, 1, \dots, 0)$ where the 1 is in the j' th slot, and calculating the population in the next year. The vector $\mathbf{A}\mathbf{e}_j$ forms the j' th column of \mathbf{A} . In coordinates

$$\mathbf{A}\mathbf{e}_j = (a_{1,j}, a_{2,j}, \dots, a_{n,j})$$

where $\sum_i a_{ij} < 1$ for each j since some of the fish die off. So we can think of a_{ij} as the proportion of the fish in size category i in the previous period which end up in size category j and $1 - \sum_j a_{ij}$ is the proportion of fish in size category i which do not survive.

If \mathbf{x} is a solution of (2) it follows by linearity that $\lambda\mathbf{x} = (\lambda x_1, \lambda x_2, \dots, \lambda x_n)$ is as well. So the initial equilibrium is determined only up to a scale factor without additional assumptions.

To see what sort of assumption might permit the determination of the initial recruitment assume in addition there is a stock recruitment relationship

$$R = \frac{\alpha B}{\beta + B} \quad (3)$$

where R is the recruitment in numbers of fish i.e $R = \sum_i r_i$ and B is some calculation of the reproductive potential of the population.

It turns out that (3) plus an additional assumption can be used to uniquely determine λ under some assumptions. Let $\mathbf{y} = (y_1, y_2, \dots, y_n)$ be the unique equilibrium solution corresponding to the unit recruitment (r_1, r_2, \dots, r_n) for which $\sum_i r_i = 1$. We further assume that the reproductive potential has the form

$$B(\mathbf{x}) = \sum_i c_i x_i \quad (3A)$$

The important property of (3A) is that $B(\lambda\mathbf{x}) = \lambda B(\mathbf{x})$. For the unit equilibrium recruitment \mathbf{y} let reproductive potential equal to ϕ where

$$\phi = \sum_i c_i y_i$$

The nice part about this is that if R is the equilibrium number of recruits under the stock-recruitment relationship, then because of (3A), $R\phi$ is the equilibrium reproductive potential

$$R = \frac{\alpha \phi R}{\beta + \phi R} \quad (4)$$

(4) can be solved for the equilibrium number of recruits \tilde{R} which is

$$\tilde{R} = \frac{\alpha \phi - \beta}{\phi} \quad (4)$$

So the equilibrium condition together with the stock recruitment relationship uniquely determines the initial equilibrium population. Of course this solution depends on a number of parameters including α , β , c_i etc. which are being estimated in the model.

So we have shown that under the above assumptions the initial equilibrium population is equal to $\tilde{R}\mathbf{y}$.

A Simple Example

Consider the simple age structured model where all the individuals age by one year and the annual survival rate for age class j individuals is s_j .

$$\mathbf{A} = \begin{pmatrix} 0 & 0 & 0 & \dots & 0 & 0 \\ s_1 & 0 & 0 & \dots & 0 & 0 \\ 0 & s_2 & 0 & \dots & 0 & 0 \\ 0 & 0 & s_3 & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & & \\ 0 & 0 & 0 & \dots & s_{n-1} & s_n \end{pmatrix}$$

and $\mathbf{r} = (1, 0, \dots, 0)$. If $\mathbf{y} = (y_1, y_2, \dots, y_n)$ is the equilibrium solution then $y_1 = 1$, $y_i = s_{i-1}y_{i-1}$ for $2 \leq i \leq n-1$, and $y_n = s_{n-1}y_{n-1} + s_n y_n$. Let $S_j = s_1 s_2 \dots s_j$. Then

$$\mathbf{y} = (1, S_1, S_2, \dots, S_{n-2}, \frac{S_{n-1}}{1 - s_n})$$

Note that the equilibrium solution can be calculated directly without calculating the inverse of \mathbf{A} . This tends to obscure the applicability of the general solution. In simple special cases like this it may be preferable to employ a particular solution for computational efficiency.