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365: LESLIE MATRIX MODELS FOR FISHERIES STUDIES

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SUMMARY

Two modifications of the Leslie matrix model are developed. In the first modification the egg stage as well as the age groups of a fish population are included in the vector of state. In the second modification only the recruited members of the population are included in the vector of state.

1. INTRODUCTION

In the Leslie Matrix Model (Leslie [1945; 1948]) the vector of the number of individuals of each age at time t, $\mathbf{N}_t$, is related to the vector of the initial number of individuals of each age, $\mathbf{N}_0$, by the equation,

$$\mathbf{N}_t = \mathbf{M}^t\mathbf{N}_0 , \tag{1}$$

where $\mathbf{M}$ is the population projection matrix,

$$\mathbf{M} = \begin{bmatrix} B_0 & B_1 & B_2 & \cdots & \cdot & B_{v-1} & B_v \\ P_0 & 0 & 0 & \cdots & \cdot & 0 & 0 \\ 0 & P_1 & 0 & \cdots & \cdot & 0 & 0 \\ 0 & 0 & & & & 0 & 0 \\ \cdot & \cdot & & & & \cdot & \cdot \\ \cdot & \cdot & & & & \cdot & \cdot \\ 0 & 0 & 0 & \cdots & 0 & P_{v-1} & 0 \end{bmatrix} . \tag{2}$$

In matrix $\mathbf{M}$, B_x equals the number of females born to females of age x in one unit of time that survive to the next unit of time, P_x equals the proportion of females of age x at time t that survive to time $t + 1$, and v is the greatest age attainable. Equation (1) has frequently been applied in demographic and animal population studies (Keyfitz [1968], Pielou [1969], Usher [1971]). Jensen [1971] has applied equation (1) to a fish population.

Equation (1) is similar to the simple exponential model for population growth. Leslie [1959] proposed a modified matrix model to allow for the effect of population density on population growth. He divided each element in the population projection matrix by a quantity that depended on the size of the current population and the size of the population when the individuals were born. Several other modifications of the matrix model have been proposed. Williamson [1959] and Goodman [1968; 1969] modified the matrix model to include both sexes, and Lefkovitch [1965] developed a modification for organisms grouped

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by life stages rather than age. Goodman [1969] developed a general class of models that can be applied to organisms grouped by life stages. Usher]1969] modified the model for study of forest trees which are classified by size rather than by age.

In this note two modifications of the matrix model are proposed: (1) a model for fish populations in which individuals are grouped by a life stage as well as by age, and (2) a model for the recruited members of a fish population. Goodman's [1969] general class of models can also include both life stages and age. A fish is recruited when it becomes large enough to be vulnerable to fishing gear. This group of fish is of importance because often data are available only for the age groups captured by a fishery.

A detailed analysis of fisheries data requires separation of males and females as in actuarial science and demography, but this is not often practiced in fisheries science because the limited data do not generally allow such a detailed analysis. It will be assumed that the number of females equals the number of males and that growth and mortality rates of males and females are equal, but the models also apply to either sex alone.

2. ONE LIFE STAGE AND AGE GROUPS

It is assumed that the eggs hatch in the time period after the adults spawn. For example, if the time period is one year and the fish spawn in the fall, the eggs hatch the following spring. A similar model can be constructed for species in which the adults spawn and the eggs hatch during the same year.

The number of eggs produced at time $t - 1$ is proportional to the sizes of the age groups at time $t - 1$, i.e.,

$$E(t-1) = (h_0, h_1, \cdots, h_v)\begin{bmatrix} N(0, t-1) \\ N(1, t-1) \\ \cdot \\ \cdot \\ \cdot \\ N(v, t-1) \end{bmatrix}, \tag{3}$$

where some of the constants h_i, $i = 0, 1, 2, \cdots, v$, may be zero. The constant h_i is the number of eggs produced by the population per individual of age i. The size of the zero age group at time t is a function of the number of eggs produced at time $t - 1$, and the size of each nonzero age group at time t is a function of the size of the preceding age group at time $t - 1$, i.e.,

$$\begin{bmatrix} N(0, t) \\ N(1, t) \\ \cdot \\ \cdot \\ \cdot \\ \cdot \\ N(v, t) \end{bmatrix} = \begin{bmatrix} S_0 & 0 & \cdots & 0 & 0 & 0 \\ 0 & S_1 & & & \cdot & \cdot \\ 0 & 0 & & & \cdot & \cdot \\ \cdot & \cdot & & & \cdot & \cdot \\ \cdot & \cdot & & & \cdot & \cdot \\ 0 & 0 & & 0 & 0 & 0 \\ 0 & 0 & \cdots & 0 & S_v & 0 \end{bmatrix} \begin{bmatrix} E(t-1) \\ N(0, t-1) \\ N(1, t-1) \\ \cdot \\ \cdot \\ \cdot \\ \cdot \\ N(v, t-1) \end{bmatrix} \tag{4}$$

The survival function S_0 gives the proportion of the eggs that hatch, and the survival functions S_i, $i = 1, 2, \cdots, v$, give the proportion of individuals that survive from age

$i - 1$ to age i. The survival functions may be functions of time. Mathematical forms of these survival functions are discussed by Ricker [1954], Beverton and Holt [1957], Paulik and Greenough [1966], and Pennycuick *et al.* [1968].

Equations (3) and (4) can be combined into a single equation. Multiplication of the matrices,

$$\begin{bmatrix} S_0 & 0 & \cdots & 0 & 0 & 0 \\ 0 & S_1 & & & 0 & 0 \\ 0 & 0 & & & 0 & 0 \\ \cdot & \cdot & & & \cdot & \cdot \\ \cdot & \cdot & & & \cdot & \cdot \\ \cdot & \cdot & & & 0 & 0 \\ 0 & 0 & \cdots & 0 & S_v & 0 \end{bmatrix} \cdot \begin{bmatrix} h_0 & h_1 & \cdots & \cdot & h_{v-1} & h_v \\ 1 & 0 & \cdots & \cdot & 0 & 0 \\ 0 & 1 & & & 0 & 0 \\ 0 & 0 & & & 0 & 0 \\ \cdot & \cdot & & & \cdot & \cdot \\ \cdot & \cdot & & & \cdot & \cdot \\ 0 & 0 & \cdots & 0 & 1 & 0 \\ 0 & 0 & \cdots & 0 & 0 & 0 \end{bmatrix} \tag{5}$$

gives the matrix,

$$\mathbf{A} = \begin{bmatrix} h_0S_0 & h_1S_0 & \cdots & h_{v-2}S_0 & h_{v-1}S_0 & h_vS_0 \\ S_1 & 0 & \cdots & 0 & 0 & 0 \\ 0 & S_2 & & 0 & 0 & 0 \\ 0 & 0 & & 0 & 0 & 0 \\ \cdot & \cdot & & \cdot & \cdot & \cdot \\ \cdot & \cdot & & \cdot & \cdot & \cdot \\ 0 & 0 & & 0 & 0 & 0 \\ 0 & 0 & & S_{v-1} & 0 & 0 \\ 0 & 0 & \cdots & 0 & S_v & 0 \end{bmatrix}. \tag{6}$$

Applying equation (6), the equation for population projection (equation 1) becomes,

$$\mathbf{N}_t = \mathbf{A}^t\mathbf{N}_0 . \tag{7}$$

The above analysis shows that the matrix for population projection, $\mathbf{A}$, is the product of: (1) a survival matrix which represents movement of individuals out of the life stage and among the age groups, and (2) a reproduction matrix which represents input of new individuals to the population.

Applying equation (7), the discrete age-discrete time equation for annual yield from a fishery (Jensen [1971]) becomes,

$$Y_t = \sum_{x=0}^{v} y_t(x), \tag{8}$$

where x is age in years, and $y_t(x)$ is the xth element in the vector $\mathbf{Y}_t$,

$$\mathbf{Y}_t = \mathbf{FWA}^t\mathbf{N}_0 . \tag{9}$$

In equation (9), $\mathbf{F}$ is a diagonal matrix with the age specific mortality rates $F(x)$ on the diagonal and $\mathbf{W}$ is a diagonal matrix with the age specific weights $W(x)$ on the diagonal.

3. THE RECRUITED POPULATION

Equation (8) is of more practical value in fisheries studies if only age groups in the recruited population are considered. The Leslie Matrix Model cannot be directly applied to only the recruited population. The number of recruits at time t depends on the number of eggs produced by the population at some previous time $t - r$, where r is the age of the recruits. The sizes of all other age groups in the recruited population depend on the sizes of the preceding age group in the previous unit of time. Hence, recruitment and mortality of the recruited population must be separated.

Both Usher [1966] and Goodman [1969] have shown that the population projection matrix is the sum of two matrices,

$$\mathbf{M} = \mathbf{R} + \mathbf{D}. \tag{10}$$

The first matrix represents input of new members to the population and the second matrix represents transition of members between the age groups. For application to a recruited fish population, the square matrices $\mathbf{R}$ and $\mathbf{D}$ can be defined as:

$$\mathbf{R} = \begin{bmatrix} h_r S_r & h_{r+1} S_r & \cdots & h_v S_r \\ 0 & 0 & \cdots & 0 \\ \cdot & \cdot & & \cdot \\ \cdot & \cdot & & \cdot \\ 0 & 0 & \cdots & 0 \end{bmatrix} \tag{11}$$

$$\mathbf{D} = \begin{bmatrix} 0 & 0 & \cdots & 0 & 0 & 0 \\ S_{r+1} & 0 & \cdots & 0 & 0 & 0 \\ 0 & S_{r+2} & & & 0 & 0 \\ 0 & 0 & & & 0 & 0 \\ \cdot & \cdot & & & \cdot & \cdot \\ \cdot & \cdot & & & \cdot & \cdot \\ 0 & 0 & & & 0 & 0 \\ 0 & 0 & \cdots & 0 & S_v & 0 \end{bmatrix}. \tag{12}$$

The function S_r gives survival from the egg to recruitment, and the functions S_{r+i} , $i = 1, 2, \cdots, v$, give survival from age $r + i - 1$ to age $r + i$. Mathematical forms of the survival function S_r are discussed by Ricker [1954], Beverton and Holt [1957], and Paulik and Greenough [1966].

Applying equations (10), (11), and (12) the vector of the number of individuals of each age at time t for the recruited population becomes,

$$\mathbf{N}_t = \mathbf{R}\mathbf{N}_{t-r} + \mathbf{D}\mathbf{N}_{t-1} . \tag{13}$$

Applying equation (13), the discrete age-discrete time equation for annual yield from a fishery becomes,

$$Y_t' = \sum_{x=r}^{v} y_t'(x) \tag{14}$$

where $y_t'(x)$ is the xth element in the vector $\mathbf{Y}_t'$,

$$\mathbf{Y}_t' = \mathbf{FW}(\mathbf{R}\mathbf{N}_{t-r} + \mathbf{D}\mathbf{N}_{t-1}). \tag{15}$$

LES MODÈLES DE MATRICE DE LESLIE POUR LES ÉTUDES DE PÊCHERIES

RESUME

On décrit deux modifications au modèle matriciel de Leslie. Dans la première on inclut dans le vecteur d'état le stade des oeufs aussi bien que les groupes d'âge de la population de poisson. Dans la seconde on n'inclut dans le vecteur d'état que les nouveaux membres de la population.

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