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I am submitting herewith a thesis written by James John Perkowski entitled "A Compensatory Leslie Matrix Model for Two Interacting Populations." I recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Mathematics.

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A COMPENSATORY LESLIE MATRIX MODEL FOR TWO INTERACTING POPULATIONS

A Thesis

Presented for the

Master of Science

Degree

The University of Tennessee, Knoxville

James John Perkowski

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DEDICATION

To my parents

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ABSTRACT

A compensatory Leslie matrix for two-interacting populations is examined for species having density-dependent mortalities in the zero-age classes. Analytical criteria are developed to determine stability of equilibria to small perturbations for a multiple age-class model. The conditions state that each of the interacting species must be stable in the absence of the other species, and that a combination of intraspecific interactions must be stronger than a combination of interspecific interactions. The stability criterion are applied to a three-species, three-age-class model of competing fish populations, where the zero-age class of each species suffers from predation by the other species and from cannibalism and other self-regulating factors. Computer simulations supplement the analytical results developed in this thesis.

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INTRODUCTION

Leslie matrix models are used to predict the age structure of single populations in discrete time intervals. The Leslie matrix was developed to model the dynamics of populations characterized by age-specific mortality and fecundity (Lewis, 1942; Leslie, 1945, 1948). Since the development of the basic Leslie matrix, applications to single species models have been numerous (Usher, 1972).

Age-specific phenomena are prevalent in many animal communities involving interspecific and intraspecific interactions. Density-dependent, age-specific competition, predation, and self-regulation effects are commonly observed in fish communities. Although compensatory Leslie models have been developed to express the effect of density-dependent mortality and fecundity on the dynamics of single species, little work has been done to apply compensatory techniques to systems involving more than one species. Pennycuick et al. (1968) utilized computer simulations to study the dynamics of a density-dependent multispecies model, while Hassell and Comins (1976) considered some limited interactions for a system with two species.

This thesis presents a compensatory Leslie matrix model for two species and emphasizes fish populations where density-dependent mortality is believed to occur in the youngest age class. Stability criteria are developed analytically for communities of competing species to determine the effect on stability of factors related to density-dependent

mortality of the zero-age class. The criteria require that each of the interacting species be stable by itself and that intraspecific interactions dominate interspecific interactions in an inequality that will be discussed in Chapter II.

A general age-class model for two species is analyzed in Chapter I. The method employed is to linearize the compensatory Leslie matrix elements after expanding them about an equilibrium point using Taylor series. The theory of M-matrices is then used to analytically determine parameter conditions which are necessary and sufficient for local stability.

Direct application of M-matrix theory is limited, however, by the type of interactions that are modeled. A system involving cannibalism is examined in Chapter II. Although the theory does not apply directly to this system, some useful interpretations are made by examining a reduced model for the system.

CHAPTER I

A GENERAL AGE CLASS MODEL FOR TWO SPECIES

I. MODEL FORMULATION

We construct a model which predicts number and age structure of two interacting populations in discrete time intervals. For convenience we begin by dividing both populations into n age classes. The number of females alive in each age class of species x and species y at time t is given by the components of the respective column distribution vectors for each species,

$$\begin{aligned} \underline{X} &= (x_0, x_1, \ldots, x_{n-1})^T, \\ \underline{Y} &= (y_0, y_1, \ldots, y_{n-1})^T, \end{aligned} \tag{1.1}$$

where $x_i = x_i(t)$ and $y_i = y_i(t)$ for $i = 0, 1, \ldots, n-1$. Survival from age class i to age class $i + 1$ for $i = 0, 1, \ldots, n-1$ is given by

$$\begin{aligned} x_{i+1}(t+1) &= p_{x_i}\, x_i(t), \\ y_{i+1}(t+1) &= p_{y_i}\, y_i(t), \end{aligned} \tag{1.2.a}$$

while survival in the last age class is

$$\begin{aligned} x_{n-1}(t+1) &= p_{x_{n-2}}\, x_{n-2}(t) + p_{x_{n-1}}\, x_{n-1}(t), \\ y_{n-1}(t+1) &= p_{y_{n-2}}\, y_{n-2}(t) + p_{y_{n-1}}\, y_{n-1}(t), \end{aligned} \tag{1.2.b}$$

where

p_i = probability that a female in age class i at time t will survive to time t+1.

Reproduction by the sexually mature females of species x and species y are given by

$$x_0(t+1) = \sum_{i=1}^{n-1} f_{x_i} x_i(t),$$

$$y_0(t+1) = \sum_{i=1}^{n-1} f_{y_i} y_i(t), \tag{1.3}$$

where

f_i = average number of female offspring of a female in age class i born in the time interval from t to t+1 that will survive to time t+1.

Assume that the members of each age class of each species have a negative effect upon the survival of the zero-age class of the other species. Assume also that a self-regulation effect is imposed upon the zero-age classes. The survival probabilities for the zero-age class of each species will be represented here by the density dependent relations

$$p_{x_0} = r_x/[1+\alpha_{x_0} x_0+(\beta_{x_0} y_0+\beta_{x_1} y_1+ \dots +\beta_{x_{n-1}} y_{n-1})],$$

$$p_{y_0} = r_y/[1+\alpha_{y_0} y_0+(\beta_{y_0} x_0+\beta_{y_1} x_1+ \dots +\beta_{y_{n-1}} x_{n-1})], \tag{1.4}$$

where r_x, r_y, α_{x_0}, α_{y_0}, and β_{x_i}, β_{y_i}, (i=0,1, ... , n-1), are positive

constants. The magnitudes of the β's are related to the inherent degree of interspecific behavior between the two species, while intraspecific behavioral tendencies are represented by the values of the α's. The intrinsic survival probabilities r_x and r_y signify the survival rate for members of the zero-age class in the absence of interspecific and intraspecific interactions.

The system given by (1.1) to (1.4) is said to be in a state of equilibrium if

$$x_{ie} \equiv x_i(t+1) = x_i(t),$$
$$y_{ie} \equiv y_i(t+1) = y_i(t), \tag{1.5}$$

for i = 0,1, ... , n-1 and all t. Equilibrium numbers of females in each age class are given by

$$\begin{aligned}
x_{0e} &= f_{x_1} x_{1e} + f_{x_2} x_{2e} + \cdots + f_{x_{n-1}} x_{(n-1)e}, \\
x_{1e} &= \{r_x/[1+\alpha_{x_0} x_{0e} + (\beta_{x_0} y_{0e} + \beta_{x_1} y_{1e} + \cdots + \beta_{x_{n-1}} y_{(n-1)e})]\} x_{0e}, \\
x_{2e} &= p_{x_1} x_{1e}, \\
&\vdots \\
x_{(n-1)e} &= p_{x_{n-2}} x_{(n-2)e} + p_{x_{n-1}} x_{(n-1)e}, \\
y_{0e} &= f_{y_1} y_{1e} + f_{y_2} y_{2e} + \cdots + f_{y_{n-1}} y_{(n-1)e} \\
y_{1e} &= \{r_y/[1+\alpha_{y_0} y_0 + (\beta_{y_{0e}} x_{0e} + \beta_{y_1} x_{1e} + \cdots + \beta_{y_{n-1}} x_{(n-1)e})]\} y_{0e}, \\
y_{2e} &= p_{y_1} y_{1e}, \\
&\vdots \\
y_{(n-1)e} &= p_{y_{n-2}} y_{(n-2)e} + p_{y_{n-1}} y_{(n-1)e}.
\end{aligned} \tag{1.6}$$

If solutions to (1.6) exist, then expressions for equilibrium numbers of females in terms of the model parameters can be solved for algebraically or by numerical methods. The behavior of the model about an equilibrium point may be analyzed by matrix algebra techniques.

We begin by defining a Leslie matrix form for the model of two-interacting species given in (1.1) to (1.4) by adapting the techniques given by Leslie (1945) and outlined by Svoboda (1978) for single species models.

Let

$$W=W(t)=\begin{vmatrix} W_x & 0 \\ 0 & W_y \end{vmatrix}, \tag{1.7}$$

where the submatrices W_x and W_y are of the form

$$W_x = \begin{vmatrix} 0 & f_{x_1} & f_{x_2} & \cdots & f_{x_{n-2}} & f_{x_{n-1}} \\ p_{x_0} & 0 & 0 & \cdots & 0 & 0 \\ 0 & p_{x_1} & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & p_{x_{n-2}} & p_{x_{n-1}} \end{vmatrix},$$

$$W_y = \begin{vmatrix} 0 & f_{y_1} & f_{y_2} & \cdots & f_{y_{n-2}} & f_{y_{n-1}} \\ p_{y_0} & 0 & 0 & \cdots & 0 & 0 \\ 0 & p_{y_1} & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & p_{y_{n-2}} & p_{y_{n-1}} \end{vmatrix}$$

and

$$\underline{Z}(t)=(\underline{X},\underline{Y})^T = (z_0, z_1, \ldots, z_{2n-1})^T. \tag{1.8}$$

Here, W is a density dependent matrix since the elements p_{x_0} and p_{y_0} are density dependent, and $\underline{Z}(t)$ is the female age distribution of the entire system at any time t. Multiplication of $\underline{Z}(t)$ by the matrix W(t) will result in the female age distribution one time period later at time t+1.

$$W(t)\ \underline{Z}(t) = \begin{vmatrix} \sum_{i=1}^{n-1} f_{x_i}\, x_i(t) \\ p_{x_0}\ \ x_0(t) \\ p_{x_1}\ \ x_1(t) \\ \vdots \\ p_{x_{n-2}}\ x_{n-2}(t) \\ \sum_{i=n-2}^{n-1} p_{x_i}\, x_i(t) \\ \sum_{i=1}^{n-1} f_{y_i}\, y_i(t) \\ p_{y_0}\ \ y_0(t) \\ p_{y_1}\ \ y_1(t) \\ p_{y_{n-2}}\ y_{n-2}(t) \\ \vdots \\ \sum_{i=n-2}^{n-1} p_{y_i}\, y_i(t) \end{vmatrix} = \underline{Z}(t+1). \tag{1.9}$$

Unless the system is in a state of equilibrium the vector $\underline{Z}(t+1)$ will be different from $\underline{Z}(t)$. Conditions on the matrix W which affect the stability of the model after perturbations about the equilibrium point $\underline{Z}_e$, is the subject of the next section.

II. DEVELOPMENT OF STABILITY CRITERIA

Local stability criteria for the model presented in equations (1.1) to (1.4) can be determined by examining the behavior of the system after small displacement away from an equilibrium point $\underline{Z}_e = [z_{ie}]$. Using the procedure outlined by Svoboda (1978), we make use of a linearized expansion of the matrix W. Some special properties of the resulting matrix are used to analyze the stability of the perturbed system.

The Taylor series expansion about $\underline{Z}_e$ for the density dependent survival elements of W are

$$p_{x_0} = p_{x_{0e}} + \sum_{i=0}^{2n-1} g_i \frac{\partial p_{x_0}}{\partial z_i} + \frac{1}{2!} \sum_{i=0}^{2n-1} \sum_{j=0}^{2n-1} g_i g_j \frac{\partial^2 p_{x_0}}{\partial z_j \partial z_i} + \cdots ,$$

$$p_{y_0} = p_{y_{0e}} + \sum_{i=0}^{2n-1} g_i \frac{\partial p_{y_0}}{\partial z_i} + \frac{1}{2!} \sum_{i=0}^{2n-1} \sum_{j=0}^{2n-1} g_i g_j \frac{\partial^2 p_{y_0}}{\partial z_j z_i} + \cdots , \qquad (1.10)$$

where $p_{x_{0e}}$, $p_{y_{0e}}$, and the partial derivatives are evaluated at $\underline{Z}_e$, $z_i = z_i(t)$, and $g_i = z_i - z_{ie}$ $(i=0,1, \ldots , 2n-1)$.

Linearization of (1.10) results in approximations for p_{x_0} and p_{y_0} for small perturbations about $\underline{Z}_e$.

$$p_{x_0} \cong p_{x_{0e}} + \sum_{i=0}^{2n-1} g_i \frac{\partial p_{x_0}}{\partial z_i} \equiv p_{x_{0e}} + \overset{*}{p}_{x_0},$$

$$p_{y_0} \cong p_{y_{0e}} + \sum_{i=0}^{2n-1} g_i \frac{\partial p_{y_0}}{\partial z_i} \equiv p_{y_{0e}} + \overset{*}{p}_{y_0}. \qquad (1.11)$$

Thus an approximation for the Leslie-type matrix W may be written as

$$W = W_e + \overset{*}{W} = \begin{bmatrix} W_{xe} & 0 \\ 0 & W_{ye} \end{bmatrix} + \begin{bmatrix} \overset{*}{W}_x & 0 \\ 0 & \overset{*}{W}_y \end{bmatrix}, \qquad (1.12)$$

where the matrix W_e is given by (1.7) with the density dependent survival probabilities evaluated at $\underline{Z}_e$, and where the square submatrices $\overset{*}{W}_x$ and $\overset{*}{W}_y$ are given by

$$\overset{*}{W}_x = \begin{vmatrix} 0 & 0 & 0 & \cdots & 0 & 0 \\ \overset{*}{p}_{x_0} & 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & 0 & 0 \end{vmatrix}, \text{ and}$$

$$\overset{*}{W}_y = \begin{vmatrix} 0 & 0 & 0 & \cdots & 0 & 0 \\ \overset{*}{p}_{y_0} & 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & 0 & 0 \end{vmatrix}.$$

Next we let $\underline{G}(t) = (g_0, g_1, \ldots, g_{2n-1})^T$ and observe that

$$\underline{Z}_e + \underline{G}(t+1) = \underline{Z}(t+1) \cong (W_e + \overset{*}{\underline{W}})\, \underline{Z}_e + \underline{G}(t)). \tag{1.13}$$

The approximation in (1.13) is valid for sufficiently small elements of $\underline{G}(t)$. Thus, we may write the following linear approximation for the perturbation vector:

$$\underline{G}(t+1) \cong W_e \cdot \underline{G}(t) + (\overset{*}{\underline{W}} \cdot \underline{Z}_e)(t). \tag{1.14}$$

The second term of (1.14) may be rewritten as a product of a matrix and the vector $\underline{G}(t)$.

$$(\overset{*}{\underline{W}} \cdot Z_e)(t) = \begin{vmatrix} \overset{*}{W}_x & 0 \\ 0 & \overset{*}{W}_y \end{vmatrix} \cdot \underline{Z}_e \tag{1.15}$$

$$= \begin{vmatrix} 0 \\ z_{0_e} \sum_{i=0}^{2n-1} g_i \frac{\partial p_{x_0}}{\partial z_i} \\ 0 \\ \vdots \\ 0 \\ 0 \\ z_{ne} \sum_{i=0}^{2n-1} g_i \frac{\partial p_{y_0}}{\partial z_i} \\ 0 \\ \vdots \\ 0 \end{vmatrix}$$

$$= \begin{vmatrix} 0 & 0 & \cdots & 0 & 0 & 0 & \cdots & 0 \\ x_{0e}\frac{\partial p_{x_0}}{\partial x_0} & x_{0e}\frac{\partial p_{x_0}}{\partial x_1} & \cdots & x_0 x\frac{\partial p_{x_0}}{\partial x_{n-1}} & x_{0e}\frac{\partial p_{x_0}}{\partial y_0} & x_{0e}\frac{\partial p_{x_0}}{\partial y_1} & \cdots & x_{0e}\frac{\partial p_{x_0}}{\partial y_{n-1}} \\ 0 & 0 & \cdots & 0 & 0 & 0 & \cdots & 0 \\ \vdots & \vdots & & \vdots & \vdots & \vdots & & \\ 0 & 0 & \cdots & 0 & 0 & 0 & \cdots & 0 \\ 0 & 0 & \cdots & 0 & 0 & 0 & \cdots & 0 \\ y_{0e}\frac{\partial p_{y_0}}{\partial x_0} & y_{0e}\frac{\partial p_{y_0}}{\partial x_0} & \cdots & y_{0e}\frac{\partial p_{y_0}}{\partial x_{n-1}} & y_{0e}\frac{\partial p_{y_0}}{\partial y_0} & y_{0e}\frac{\partial p_{y_0}}{\partial y_0} & \cdots & y_{0e}\frac{\partial p_{y_0}}{\partial y_{n-1}} \\ 0 & 0 & \cdots & 0 & 0 & 0 & \cdots & 0 \\ \vdots & \vdots & & \vdots & \vdots & \vdots & & \vdots \\ 0 & 0 & \cdots & 0 & 0 & 0 & \cdots & 0 \end{vmatrix} \cdot G(t)$$

Substitution of (1.15) into (1.14) then gives

$$\underline{G}(t+1) \cong \hat{W} \cdot \underline{G}(t) \ , \tag{1.16}$$

where the interaction matrix, $\hat{W}$, has the form

$$\hat{W} = \begin{vmatrix} \hat{W}_x & Q_{xy} \\ Q_{yx} & \hat{W}_y \end{vmatrix} \ . \tag{1.17}$$

The submatrices $\hat{W}_x$ and $\hat{W}_y$ indicate intraspecific behavior and are given by

$$\hat{W}_x = \hat{W}_x(t) = \begin{vmatrix} 0 & f_{x_1} & f_{x_2} & \cdots & f_{x_{n-2}} & f_{x_{n-1}} \\ (p_{x_{0e}} + v_{x_0}) & v_{x_1} & v_{x_2} & \cdots & v_{x_{n-2}} & v_{x_{n-1}} \\ 0 & p_{x_1} & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & & \vdots & \vdots \\ 0 & 0 & & \cdots & p_{x_{n-2}} & p_{x_{n-1}} \end{vmatrix}, \text{ and} \quad (1.18)$$

$$\hat{W}_y = \hat{W}_y(t) = \begin{vmatrix} 0 & f_{y_1} & f_{y_2} & \cdots & f_{y_{n-2}} & f_{y_{n-1}} \\ (p_{y_{0e}} + v_{y_0}) & v_{y_1} & v_{y_2} & \cdots & v_{y_{n-2}} & v_{y_{n-1}} \\ 0 & p_{y_1} & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & & \vdots & \vdots \\ 0 & 0 & & \cdots & p_{y_{n-2}} & p_{y_{n-2}} \end{vmatrix},$$

where

$$v_{x_i} = x_{0e} \frac{\partial p_{x_0}}{\partial x_i}, \text{ and}$$

$$v_{y_i} = y_{0e} \frac{\partial p_{y_0}}{\partial y_i}, \quad i = 0, 1, \ldots, n-1 \quad (1.19)$$

Since the survival probabilities given in (1.4) for each species are not dependent upon the density of the older age class members of that species,

the elements v_{x_i} and v_{y_i} are equal to zero for i=1, 2, ... , n-1, whereas v_{x_0} and v_{y_0} are nonzero.

The occurrence of nonzero elements in the submatrices

$$Q_{xy} = \begin{vmatrix} 0 & 0 & \cdots & 0 \\ q_{x_{21}} & q_{x_{22}} & \cdots & q_{x_{2,n}} \\ 0 & 0 & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \cdots & 0 \end{vmatrix}, \text{ and} \qquad (1.20)$$

$$Q_{yx} = \begin{vmatrix} 0 & 0 & \cdots & 0 \\ q_{y_{21}} & q_{y_{22}} & \cdots & q_{y_{2,n}} \\ 0 & 0 & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \cdots & 0 \end{vmatrix}$$

represents the effect of interspecific behavior between age classes of the two species. For example, the element $q_{x_{ij}}$ of the matrix Q_{xy} represents the effect of the j th age class of species y on the survival of the age class (i-2) of species x to the age class (i-1). This element is negative if the density of species y has a negative effect on the numbers of species x. The nonzero elements of Q_{xy} and Q_{yx} are

$$q_{x_{2j}} = x_{0e} \frac{\partial p_{x_0}}{\partial y_{j-1}}, \text{ and} \qquad (1.21)$$

$$q_{y_{2j}} = y_{0e} \frac{\partial p_{y_0}}{\partial x_{j-1}} ,$$

for $j = 2, 3, \ldots, n$.

From (1.4), (1.19), and (1.21) we get

$$\begin{aligned} v_{x_0} &= - k_x r_x x_{0e} \alpha_{x_0} < 0 , \\ v_{y_0} &= - k_y r_y y_{0e} \alpha_{y_0} < 0 , \end{aligned} \tag{1.22}$$

and for $j = 2, 3, \ldots, n$,

$$q_{x_{2j}} = - k_x r_x x_{0e} \beta_{x_j} < 0 , \text{ and}$$

$$q_{y_{2j}} = - k_y r_y y_{0e} \beta_{y_j} < 0 ,$$

where

$$k_x = 1/[1+\alpha_{x_0} x_{0e} + (\beta_{x_0} y_{0e} + \beta_{x_1} y_{1e} + \ldots + \beta_{x_{n-1}} y_{(n-1)e})]^2 , \text{ and}$$

$$k_y = 1/[1+\alpha_{y_0} y_{0e} + (\beta_{y_0} x_{0e} + \beta_{y_1} x_{1e} + \ldots + \beta_{y_{n-1}} x_{(n-1)e})]^2 .$$

Note also that the entry $(p_{x_{0e}} + v_{x_0})$ of the matrix $\hat{W}_x$ and $(p_{y_{0e}} + v_{y_0})$ of the matrix $\hat{W}_y$ are positive elements since

$$\begin{aligned} p_{x_{0e}} + v_{x_0} &= k_x r_x [1 + (\beta_{x_0} y_{0e} + \beta_{x_1} y_{1e} + \ldots + \beta_{x_{n-1}} y_{(n-1)e})] > 0 , \text{ and} \\ p_{y_{0e}} + v_{y_0} &= k_y r_y [1 + (\beta_{y_0} x_{0e} + \beta_{y_1} x_{1e} + \ldots + \beta_{y_{n-1}} x_{(n-1)e})] > 0 . \end{aligned} \tag{1.23}$$

In a stable population the perturbation vector, $\underline{G}(t)$, approaches the zero vector as t approaches infinity. Criteria for local stability about the equilibrium point $\underline{Z}_e$ may be determined by a study of some special properties of the matrix $\hat{W}$ and by estimates of the proper parameter value ranges that are necessary for stability. Stability criteria can be examined by a determination of eigenvalues of $\hat{W}$ associated with $\underline{G}$. Stability depends upon the magnitude of the dominant eigenvalue. The characterization of these eigenvalues for large matrices can be facilitated by a suitable computer program. Alternatively, some interesting relationships between stability and parameter ranges are developed for the system described in (1.1) to (1.4) by analysis of properties associated with the interaction matrix for this system. We begin by stating the following definition:

Definition 1.1. A matrix with real elements whose entries are each non-negative (non-positive) is called a non-negative (non-positive) matrix.

Interaction matrices of the type (1.17) have the following property:

Property 1.1. The nxn submatrices $\hat{W}_x$ and $\hat{W}_y$ are non-negative matrices, while Q_{xy} and Q_{yx} are non-positive matrices. Also, none of these submatrices is the zero matrix.

This form is lost if the model is modified to include such intra-specific behavior as cannibalism of the zero age class by members of the older age classes. This may impose some negative elements in either $\hat{W}_x$ or $\hat{W}_y$ or both. A case of this type does not apply directly to the theory developed

in this chapter for systems whose interaction matrices do have Property 1.1. The effect of such intraspecific behavior will be examined in Chapter II.

To continue we examine two additional properties of the matrix $\hat{W}$. The following definitions are needed:

Definition 1.2. An nxn matrix A is said to be similar to B if and only if there exists a non-singular matrix P such that $PBP^{-1} = A$.

Definition 1.3. Let U be the matrix defined by the similarity transformation $U = S\hat{W}S^{-1}$ where

$$S = \begin{bmatrix} I & 0 \\ 0 & -I \end{bmatrix},$$

and I denotes the n•n identity matrix.

The following property is verified from Definition (1.3).

Property 1.2. Any interaction matrix $\hat{W}$ having Property 1.1 is similar to a non-negative matrix

$$U = \begin{bmatrix} \hat{W}_x & -Q_{xy} \\ -Q_{yx} & -\hat{W}_y \end{bmatrix}.$$

Such a similarity transformation was performed on a Morishima matrix by Debrue and Herstein (1953). An indecomposable matrix of the type given in (1.17) is comparable to a Morishima matrix in economic literature (See Debrue and Herstein (1953), and Travis and Post (1978)).

Definition 1.4. An nxn matrix $A=[a_{ik}]$ is called reducible if the index set 1, 2, ... , n can be split into two nonempty complementary sets

$I = \{i_1, i_2, \ldots, i_\mu\}$; $K = \{k_1, k_2, \ldots, k_\nu\}$ $(\mu+\nu=n)$ such that

$$a_{i_\alpha k_\beta} = 0 \quad (\alpha=1, 2, \ldots, \mu \quad \beta=1, 2, \ldots, \nu).$$

Otherwise the matrix is called irreducible (Gantmacher, 1960).

Property 1.3. Interaction matrices $\hat{W}$ and the associated matrix U of Definition (1.3) are irreducible.

Proof. It is sufficient to show that $\hat{W}$ is irreducible since the non-zero entries of the matrices $\hat{W}$ and U are in the same position.

Consider the case in which only one non-zero element occurs in each of these submatrices Q_{xy} and Q_{yx}. Let $q_{x_{ij}}$ and $q_{y_{rs}}$ be those elements for a general matrix $\hat{W}$, where $1 \leq i,j,r,s, \leq n$. Assume also that the elements $p_{x_{n-1}}$ and $p_{y_{n-1}}$ are equal to zero. If in this case the matrix $\hat{W}$ is irreducible, then certainly an interaction matrix having additional nonzero entries will be irreducible.

Suppose that $\hat{W}$ is reducible. Then there exists sets I and K such that $I \cup K = \{1, 2, \ldots, n, n+1, n+2, \ldots, 2n\}$ and $I \cap K = \emptyset$.

Now suppose that $2n \in I$. Then the fact that the element $p_{y_{n-2}}$ is nonzero and appears in row 2n and column 2n-1 of $\hat{W}$ implies that $2n-1 \in I$, which implies that $2n-2 \in I$ since the element $p_{y_{n-2}}$ belonging to the row 2n-1 and column 2n-2 of the matrix $\hat{W}$ is nonzero, ... , which implies that $n+1 \in I$ since the element $p_{y_{0e}+v_{y_0}}$ of row n+2 and column n+1 is nonzero. Thus, $\{n+1, n+2, \ldots, 2n\} \subset I$. Similarly, observe that $s \in I$ since $n+r \in \{n+1, n+2, \ldots, 2n\}$ and $q_{rs} \neq 0$. This implies

that $s-1 \in I$ since $p_{x_s} \neq 0$, which implies that $s-2 \in I$ since $p_{x_{s-1}} \neq 0, \ldots$, which implies that $1 \in I$ since $p_{x_{0e}} + v_{x_0} \neq 0$. Thus we also have that $\{1, 2, \ldots, s-1, s\} \subset I$. But this implies that $n \in I$ since $1 \in I$ and $f_{x_{n-1}} \neq 0$, which implies that $n-1 \in I$ since $f_{x_{n-2}} \neq 0, \ldots,$ which implies that $s+1 \in I$ since $f_{x_s} \neq 0$. Thus, $I = \{1, 2, \ldots, n, n+1, n+2, \ldots, 2n\}$ which implies that $K = \emptyset$. This contradiction implies that $2n \notin I$.

Then suppose that $2n \in K$. This implies that $n+1 \in K$ since the element $f_{y_{n-1}}$ of row $n+1$ and column $2n$ of $\hat{W}$ is nonzero, which implies that $n+2 \in K$ since $p_{y_{0e}} + v_{y_0} \neq 0, \ldots,$ which implies that $2n-1 \in K$ since $p_{y_{n-2}} \neq 0$. Thus $\{n+1, n+2, \ldots, 2n\} \subset K$. But $n+j \in \{n+1, n+2, \ldots, 2n\}$. Thus $i \in K$ since $q_{x_{ij}} \neq 0$. This implies that $1 \in K$ since $f_{x_i} \neq 0$, which implies that $2 \in K$ since $p_{x_0} \neq 0, \ldots,$ which implies that $n \in K$ since $p_{x_{n-2}} \neq 0$. Consequently, $K = \{1, 2, \ldots, n, n+1, n+2, \ldots, 2n\}$ and $I = \emptyset$. By this contradiction, $2n \notin K$.

Therefore, the assumption that $\hat{W}$ is reducible implies that $2n \notin I \cup K$. This contradiction implies that the interaction matrix $\hat{W}$ is irreducible. Consequently, U is irreducible. This completes the proof.

Let λ denote any eigenvalue of the interaction matrix $\hat{W}$ satisfying Properties (1.1) to (1.3), and suppose the system is perturbed from an equilibrium state $\underline{Z}_e$ to the state $\underline{Z}_e + \underline{G}(0)$. If $|\lambda|<1$ for all eigenvalues

of $\hat{W}$ then the magnitude of the components of the perturbation vector decrease to zero, i.e.,

$$\lim_{t\to\infty} \underline{G}(t) = \underline{0} \tag{1.24}$$

and (1.13) becomes

$$\underline{Z}(t+1) = \underline{Z}(t) = \underline{Z}_e.$$

Definition 1.5. A system is locally stable about an equilibrium age distribution vector if, after small initial displacement, the system returns to the equilibrium state.

A system is locally stable if the interaction matrix associated with the system is stable.

Definition 1.6. W is called a stable matrix if the modulus of all the eigenvalues of $\hat{W}$ associated with the perturbation vector, $\underline{G}(t)$, are less than unity i.e., $|\lambda|<1$.

Because the matrices $\hat{W}$ and U are similar both matrices have the same eigenvalues (Noble, 1977) i.e., $\lambda \equiv \lambda_{\hat{W}} = \lambda_U$. Stability, therefore, requires that $|\lambda_U|<1$. We use the fact that U is an irreducible non-negative matrix to apply the theorem of Frobenius.

Theorem 1.1. (Frobenius Theorem). An irreducible non-negative matrix B has a positive characteristic value $\overset{*}{\lambda}$ with the property that

$$\overset{*}{\lambda} \geq |\lambda_i| \ ,$$

where λ_i denotes any other eigenvalue of B. To the maximal characteristic value $\overset{*}{\lambda}$ there corresponds a characteristic vector with positive coordinates (Debreu and Herstein (1953), Gantmacher (1960)).

We can guarantee that $|\lambda_U|<1$ and hence the system is locally stable about $\underline{Z}_e$, by criteria developed through application of the theory of M-matrices. An M-matrix may be defined as follows (Travis and Post, 1978):

Definition 1.7. An nxn matrix $A = (a_{ij})$ is said to be an M-matrix if $a_{ij} \leq 0$ for all $i \neq j$ and if any one of the following equivalent properties are true:

(a) all of the principal minors of A are positive;

(b) all of the eigenvalues of A have positive real parts;

(c) A is nonsingular and $A^{-1} > 0$;

(d) there is a vector $\underline{b} > 0$ such that $A \cdot \underline{b} > 0$;

(e) there is a vector $\underline{c} < 0$ such that $A^T \underline{c} < 0$.

The following theorem applies to interaction matrices satisfying Properties (1.1) to (1.3).

Theorem 1.2. $\hat{W}$ is stable if and only if I-U is an M-matrix.

Proof. Suppose that $\hat{W}$ is stable. Hence, the modulus of the eigenvalues of $\hat{W}$ and, therefore, of the similar matrix U given in Definition (1.4), are less than unity i.e., $|\lambda| = |\lambda_U| < 1$.

The eigenvalues of I-U are given by

$$\lambda_{I-U} = 1 - \lambda_U \ ,$$

or

$$\lambda_U = 1 - \lambda_{I-U} \ .$$

Therefore, $|\lambda_U| < 1$ implies that

$$|1-\lambda_{I-U}| < 1 \ ,$$

which implies that

$$0 < \text{Re} \ \lambda_{I-U} < 2 \ .$$

Therefore, the eigenvalues of I-U have positive real parts. Observing

that the off-diagonal elements of I-U are non-positive, it follows from part (b) of Definition (1.7) that I-U is an M-matrix.

Next, suppose that I-U is an M-matrix. Then Re $\lambda_{I-U} > 0$. But this implies that 1-Re $\lambda_U > 0$ or Re $\lambda_U < 1$. By the Frobenius theorem there exists a positive eigenvalue $\overset{*}{\lambda}_U$ with the property that $\lambda \geq |\lambda_{U_i}|$ where λ_{U_i} is any other eigenvalue of U. But since Re $\lambda_U < 1$, this implies that all of the eigenvalues of U lie in a circle of the complex plane centered at the origin and with radius less than unity. Thus, $|\lambda_U| = |\lambda| < 1$, which implies that $\hat{W}$ is stable.

This theorem establishes a technique to determine conditions for stability of the system described in equation (1.1) to (1.4). Species x and species y may coexist at an equilibrium point if and only if the matrix

$$I-U = \begin{vmatrix} \overline{W}_x & -Q_{xy} \\ -Q_{yx} & \overline{W}_y \end{vmatrix} \tag{1.25}$$

is a M-matrix, where Q_{xy} and Q_{yx} are given by (1.20, 1.21), and the submatrices $\overline{W}_x$ and $\overline{W}_y$ have the form

$$\overline{W}_x = \begin{vmatrix} 1 & -f_{x_1} & -f_{x_2} & \cdots & -f_{x_{n-2}} & -f_{x_{n-1}} \\ -(p_{x_{0e}}+v_{x_0}) & 1 & 0 & \cdots & 0 & 0 \\ 0 & -p_{x_1} & 1 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \ddots & -p_{x_{n-2}} & (1-p_{x_{n-1}}) \end{vmatrix} \text{ and}$$

$$\overline{W}_y = \begin{vmatrix} 1 & -f_{y_1} & -f_{y_2} & \cdots & -f_{y_{n-2}} & -f_{y_{n-1}} \\ -(p_{y_{0e}}+v_{y_0}) & 1 & 0 & \cdots & 0 & 0 \\ 0 & -p_{y_1} & 1 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & & \vdots & \vdots \\ 0 & 0 & & & -p_{y_{n-2}} & (1-p_{y_{n-1}}) \end{vmatrix} .$$

By Definition (1.7)(a) a necessary and sufficient condition for stability about Ze is that the principal minors of I-U be positive. The resulting inequalities can serve as stability criteria, and lend themselves to some interesting ecological interpretations which are included in this discussion of Chapter II.

The model described in equations (1.1) to (1.4) may represent portions of the dynamics of two interacting fish populations in which larger members of a species feed on smaller members of the other species. Such is the case in combinations of largemouth bass, Micropterus salmoides Lacepède, with bluegills, Leopomis macrochirus Rafinesque. The importance of self-regulating factors as stabilizing forces in this system is examined in the next chapter.

CHAPTER II

STABILITY ANALYSIS OF A TWO-POPULATION MODEL

Leslie matrix modeling techniques may be used to predict the age structure of fish communities that involve various types of age-specific interactions. Young fish are extremely vulnerable to hostile forces of their environment. In addition to the effect of physical factors such as changes in water temperature, turbidity, and water level, such factors as predation, spatial crowding, and competition for resources severely affect the number of survivors in the zero-age class. Age-specific interactions between the adults and young members of fish communities necessitate the application of a compensatory Leslie matrix model. This model should include density-dependent survival probabilities for the zero-age class of the species involved.

The stability conditions developed in the previous chapter may be applied to systems involving interspecific competition between species and intraspecies regulation within the zero-age class. The direct applicability of the theory is limited, however, by the types of interactions and self-regulating factors that are described by a particular model. For example, the phenomenon of cannibalism has been observed in many fish populations. This factor often affects the mortality of the zero-age class in a population. The importance of its effect upon the dynamics of the largemouth bass-bluegill combination in artifical lakes and ponds was stressed by Bennett (1948) and Swingle (1950). In addition to predation by bluegills cannibalism among bass appears to affect the mortality of the bass population.

The interaction matrix, $\hat{W}$, associated with a model that incorporates cannibalism does not have Property (1.1) since negative elements appear in the upper-left or lower-right submatrices of $\hat{W}$. Theoretical applications are valid, however, in a reduced model which describes a portion of the dynamics of the entire system. This reduced model includes self-regulation within the zero-age class as demonstrated in the model of Chapter I. Analytical stability criteria determined for the reduced system can be compared with stability outcome of computer runs that add varying amounts of cannibalism to the reduced model.

Consider a population model similar to that described in equations (1.1) to (1.4) with the added feature of cannibalism. Let each of the two competing species be divided into three age classes. The distribution of the system is modeled by the equation

$$\underline{Z}(t+1) = W(t) \cdot \underline{Z}(t) \ , \tag{2.1}$$

where

$$\underline{Z}(t) = (x_0, x_1, x_2, y_0, y_1, y_2)^T \ , \text{ and}$$

$$W(t) = \begin{vmatrix} 0 & f_{x_1} & f_{x_2} & 0 & 0 & 0 \\ p_{x_0} & 0 & 0 & 0 & 0 & 0 \\ 0 & p_{x_1} & p_{x_2} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & f_{y_1} & f_{y_2} \\ 0 & 0 & 0 & p_{y_0} & 0 & 0 \\ 0 & 0 & 0 & 0 & p_{y_1} & p_{y_2} \end{vmatrix} .$$

Let f_{x_i}, p_{x_i}, f_{y_i}, and p_{y_i} be constants for i=1, 2. This is justified if we assume that adult predators of the system merely supplement their diet with fish while having alternative food sources. On the other hand, let the survival probabilities for the zero-age class of each species be density dependent.

$$p_{x_0}=p_{x_0}(t)=r_x/[1+(\alpha_{x_0}x_0+\alpha_{x_1}x_1+\alpha_{x_2}x_2)+(\beta_{x_0}y_0+\beta_{x_1}y_1+\beta_{x_2}y_2)]$$

$$p_{y_0}=p_{y_0}(t)=r_y/[1+(\alpha_{y_0}y_0+\alpha_{y_1}y_1+\alpha_{y_2}y_2)+(\beta_{y_0}x_0+\beta_{y_1}x_1+\beta_{y_2}x_2)] \qquad (2.2)$$

In this model both species may coexist at one equilibrium point, $\underline{Z}_e(t) = (x_{0e}, x_{1e}, x_{2e}, y_{0e}, y_{1e}, y_{2e})^T$. This vector can be solved for algebraically and is,

$$\begin{aligned}
x_{1e} &= (c_y e_x - d_x e_y)/(c_x c_y - d_x d_y), \\
x_{2e} &= [p_{x_1}/(1 - p_{x_2})]\, x_{1e}, \\
x_{0e} &= f_{x_1} x_{1e} + f_{x_2} x_{2e}, \\
y_{1e} &= (c_x e_y - d_y e_x)/(c_x c_y - d_x d_y), \\
y_{2e} &= [p_{y_1}/(1 - p_{y_2})]\, y_{2e}, \\
y_{0e} &= f_{y_1} y_{1e} + f_{y_2} y_{2e},
\end{aligned} \qquad (2.3)$$

where

$$\begin{aligned}
c_x &= [p_{x_1}(\alpha_{x_0} f_{x_2} + \alpha_{x_2}) + (1 - p_{x_2})(\alpha_{x_0} f_{x_1} + \alpha_{x_1})], \\
d_x &= [p_{y_1}(\beta_{x_0} f_{y_2} + \beta_{x_2}) + (1 - p_{y_2})(\beta_{x_0} f_{y_1} + \beta_{x_1})],
\end{aligned}$$

$$c_y = [p_{y_1}(\alpha_{y_0} f_{y_2} + \alpha_{y_2}) + (1 - p_{y_2})(\alpha_{y_0} f_{y_1} + \alpha_{y_1})] ,$$

$$d_y = [p_{x_1}(\beta_{y_0} f_{x_2} + \beta_{y_2}) + (1 - p_{x_2})(\beta_{y_0} f_{x_1} + \beta_{y_1})] ,$$

$$e_x = r_x [p_{x_1} f_{x_2} + (1 - p_{x_2}) f_{x_1}] + (p_{x_2} - 1) , \text{ and}$$

$$e_y = r_y [p_{y_1} f_{y_2} + (1 - p_{y_2}) f_{y_1}] + (p_{y_2} - 1) .$$

Linearizing W about $\underline{Z}_e$, we get the following interaction matrix:

$$\hat{W} = \begin{vmatrix} 0 & f_{x_1} & f_{x_2} & 0 & 0 & 0 \\ (p_{x_{0e}} + v_{x_0}) & v_{x_1} & v_{x_2} & q_{x_{21}} & q_{x_{22}} & q_{x_{23}} \\ 0 & p_{x_1} & p_{x_2} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & f_{y_1} & f_{y_2} \\ q_{y_{21}} & q_{y_{22}} & q_{y_{23}} & (p_{y_{0e}} + v_{y_1}) & v_{y_1} & v_{y_2} \\ 0 & 0 & 0 & 0 & p_{y_1} & p_{y_2} \end{vmatrix} , \qquad (2.4)$$

where

$$p_{x_{0e}} + v_{x_0} = k_x r_x [1 + (\alpha_{x_1} x_{1e} + \alpha_{x_2} x_{2e}) + (\beta_{x_0} y_{0e} + \beta_{x_1} y_{1e} + \beta_{x_2} y_{2e})] ,$$

$$p_{y_{0e}} + v_{y_0} = k_y r_y [1 + (\alpha_{y_1} y_{1e} + \alpha_{y_2} y_{2e}) + (\beta_{y_0} x_{0e} + \beta_{y_1} x_{1e} + \beta_{y_2} x_{2e})] ,$$

$$v_{x_1} = -k_x r_x x_{0e} \alpha_{x_1} , \quad v_{y_1} = -k_y r_y y_{0e} \alpha_{y_1} ,$$

$$v_{x_2} = -k_x r_x x_{0e} \alpha_{x_2} , \quad v_{y_2} = -k_y r_y y_{0e} \alpha_{y_2} ,$$

$$q_{x_{21}} = -k_x r_x x_{0e} \beta_{x_0} , \quad q_{y_{21}} = -k_y r_y y_{0e} \beta_{y_0} ,$$

$$q_{x_{22}} = -k_x r_x x_{0e} \beta_{x_1} \quad , \quad q_{y_{22}} = -k_y r_y y_{0e} \beta_{y_1} \ ,$$

$$q_{x_{23}} = -k_x r_x x_{0e} \beta_{x_2} \quad , \quad q_{y_{23}} = -k_y r_y y_{0e} \beta_{y_2} \ ,$$

$$k_x = 1/[1+(\alpha_{x_0} x_{0e} + \alpha_{x_1} x_{1e} + \alpha_{x_2} x_{2e}) + (\beta_{x_0} y_{0e} + \beta_{x_1} y_{1e} + \beta_{x_2} y_{2e})]^2 \ ,$$

$$k_y = 1/[1+(\alpha_{y_0} y_{0e} + \alpha_{y_1} y_{1e} + \alpha_{y_2} y_{2e}) + (\beta_{y_0} x_{0e} + \beta_{y_1} x_{1e} + \beta_{y_2} x_{2e})]^2 \ .$$

Since the elements v_{x_1}, v_{x_2}, v_{y_1}, and v_{y_2} are negative, Property (1.1) does not hold for the matrix $\hat{W}$ of (2.4), and, hence, the stability theorem does not apply. However, the strategy developed here is to first examine the reduced system which involves no cannibalism. This is equivalent to setting $\alpha_{x_1} = \alpha_{x_2} = \alpha_{y_1} = \alpha_{y_2} = 0$. The resulting interaction matrix which has Properties (1.1) to (1.3) has the form:

$$\hat{W} = \begin{vmatrix} 0 & f_{x_1} & f_{x_2} & 0 & 0 & 0 \\ (p_{x_{0e}} + v_{x_0}) & 0 & 0 & q_{x_{21}} & q_{x_{22}} & q_{x_{23}} \\ 0 & p_{x_1} & p_{x_2} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & f_{y_1} & f_{y_2} \\ q_{y_{21}} & q_{y_{22}} & q_{y_{23}} & (p_{y_{0e}} + v_{y_0}) & 0 & 0 \\ 0 & 0 & 0 & 0 & p_{y_1} & p_{y_2} \end{vmatrix} \ . \quad (2.4)'$$

By Theorem 1.2, the model associated with matrix is stable about its equilibrium, $\underline{Z}_e$, if and only if the matrix

$$I-U=\begin{vmatrix} 1 & -f_{x_1} & -f_{x_2} & 0 & 0 & 0 \\ -(p_{x_{0e}}+v_{x_0}) & 1 & 0 & q_{x_{21}} & q_{x_{22}} & q_{x_{23}} \\ 0 & -p_{x_1} & (1-p_{x_2}) & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & -f_{y_1} & -f_{y_2} \\ q_{y_{21}} & q_{y_{22}} & q_{y_{23}} & -(p_{y_{0e}}+v_{y_0}) & 1 & 0 \\ 0 & 0 & 0 & 0 & -p_{y_1} & (1-p_{y_2}) \end{vmatrix} \qquad (2.5)$$

is an M-matrix. By part (a) of Definition (1.7), this is true if and only if all the principal minors are positive. Stability exists, therefore, only if all of the following criteria are satisfied:

$$\begin{aligned} &\text{(a)} \quad 1 > R_x \ , \\ &\text{(b)} \quad 1 > R_y \ , \text{ and} \\ &\text{(c)} \quad (1-R_x)(1-R_y) > C_xC_y \ , \end{aligned} \qquad (2.6)$$

where

$$R_x = (p_{x_{0e}}+v_{x_0})[f_{x_1}+(p_{x_1}/(1-p_{x_2}))f_{x_2}] \ ,$$

$$R_y = (p_{y_{0e}}+v_{y_0})[f_{y_1}+(p_{y_1}/(1-p_{y_2}))f_{y_2}] \ ,$$

$$C_x = [p_{x_1}(q_{y_{23}}+f_{x_2}q_{y_{21}})+(1-p_{x_2})(q_{y_{22}}+f_{x_1}q_{y_{21}})] \ / \ (1-p_{x_2}) \ ,$$

$$C_y = [p_{y_1}(q_{x_{23}}+f_{y_2}q_{x_{21}})+(1-p_{y_2})(q_{x_{22}}+f_{y_1}q_{x_{21}})] \ / \ (1-p_{y_2}) \ ,$$

The terms R_x and R_y denote the net reproduction rate of each species at the equilibrium, $\underline{Z}_e$. If the net reproduction rates are too

large, condition (a) and (b) of (2.6) imply that the system will move away from the equilibrium after small perturbations. Condition (c) implies that stable behavior about $\underline{Z}_e$ can occur if and only if a combination of intraspecific interactions is stronger than a combination of interspecific competition coefficients.

It is of interest to determine stability ranges for the model under various combinations of the intraspecific parameters α_{x_0} and α_{y_0}. By substitution of the equilibrium numbers of each age class determined by (2.3) into the inequalities of (2.6), the following equivalent stability criteria are obtained:

$$\text{(a)}\quad \alpha_{x_0} > 0 \,, \tag{2.7}$$

$$\text{(b)}\quad \alpha_{y_0} > 0 \,, \text{ and}$$

$$\text{(c)}\quad \alpha_{x_0}\,\alpha_{y_0} > K_x\,K_y \,,$$

where

$$K_x = \{[p_{x_1} f_{x_2} + (1-p_{x_2}) f_{x_1}]\beta_{y_0} + (1-p_{x_2})\beta_{y_1} + p_{x_1}\beta_{y_2}\}/[f_{x_1}(1-p_{x_2}) + p_{x_1} f_{x_2}] \,, \text{ and}$$

$$K_y = \{[p_{y_1} f_{y_2} + (1-p_{y_2}) f_{y_1}]\beta_{x_0} + (1-p_{y_2})\beta_{x_1} + p_{y_1}\beta_{x_2}\}/[f_{y_1}(1-p_{y_2}) + p_{y_1} f_{y_2}] \,.$$

Conditions (2.7) (a), (b) require that the zero-age class of each species have a negative effect upon its own survival rate. The inequality (2.7) (c) shows that a combination of self-regulation effects must be stronger than a combination of interspecific interactions.

To examine the effect of the self-regulating factors, we vary α_{x_0} and α_{y_0}, while holding all other parameters constant. A stable

region can be pictured as an area above a hyperbola in the $\alpha_{x_0} - \alpha_{y_0}$ plane (Figure 1). Feasible equilibria are obtained in two regions of the parameter space. One of these regions lies above the hyperbola where the stable equilibrium exists and the self-regulatory parameters α_{x_0} and α_{y_0} are large. The other region, containing equilibria that are locally unstable, lies below the hyperbola. The parameters α_{x_0} and α_{y_0} are also related to the relative abundance of each species during equilibrium. Consider a simplified case in which both species have the same parameter values except for α_{x_0} and α_{y_0} (Figure 2). If the point $(\alpha_{x_0}, \alpha_{y_0})$ lies above the line $\alpha_{x_0} = \alpha_{y_0}$ in the stable region, i.e., $\alpha_{y_0} > \alpha_{x_0}$, it can be shown that species x will dominate species y during equilibrium. (See Appendix.) However, if $\alpha_{x_0} > \alpha_{y_0}$, species y will dominate. Thus, relative strengths of self-regulating factors within the zero-age class help determine species dominance.

Computer simulations reveal that one species survives and the other goes to extinction after small perturbations from an unstable equilib-

Figure 2 summarizes these results. If $\alpha_{x_0} > \alpha_{y_0}$ species x goes extinct and species y increases with damped oscillation. Species y goes extinct if $\alpha_{y_0} > \alpha_{x_0}$.

Figure 3 shows that changing the value of other parameters may affect the product $K_x K_y$ in (2.7) (c). An increase in the interspecific competition parameters β_{x_i} and β_{y_i} (i=0, 1, 2) will have the effect of

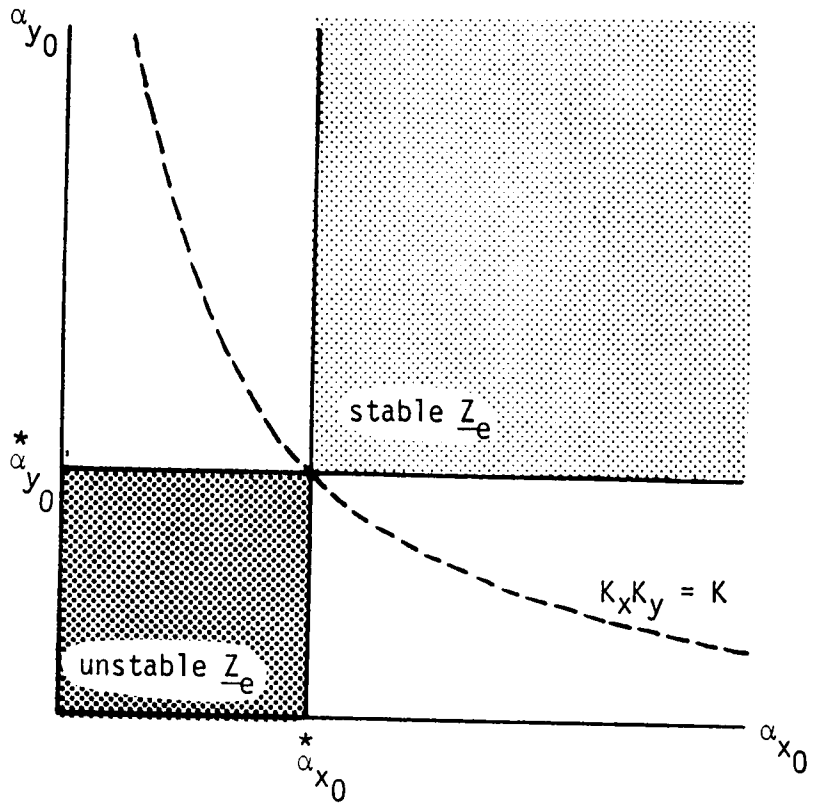


Figure 1. Stable-unstable range for feasible equilibrium in α_{x_0}-α_{y_0} parameter space under simplified parameter set; all other parameters of (2.1) to (2.2) are given the same values for each species (i.e., $K_x = K_y$) and $K_xK_y = K$ for some positive constant constant K. Feasible equilibria, $\underline{Z}_e$ are determined by the lines $\alpha_{x_0} = \overset{*}{\alpha}_{x_0}$ and $\alpha_{y_0} = \overset{*}{\alpha}_{y_0}$ where $\overset{*}{\alpha}_{x_0} = d_y/[p_{x_1}f_{x_2} - (1-p_{x_2})f_{x_1}]$ and $\overset{*}{\alpha}_{y_0} = d_x/[p_{y_1}f_{y_2}+(1-p_{y_2})f_{y_1}]$. If the point $(\alpha_{x_0}, \alpha_{y_0})$ lies in the shaded region above the hyperbola, stability criteria (2.7) are satisfied.

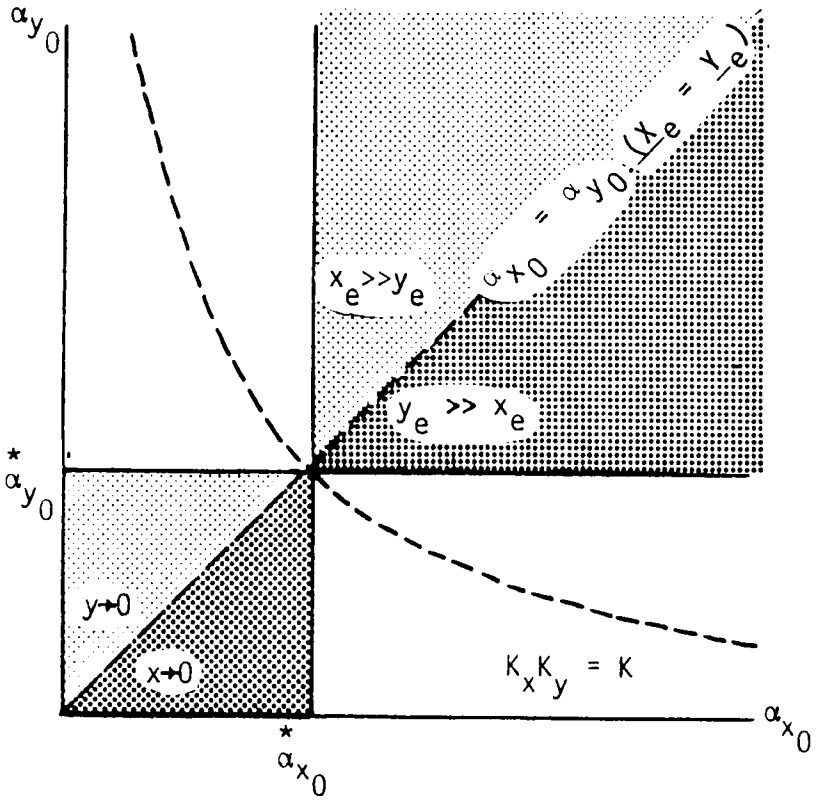


Figure 2. Relative abundance of species at equilibrium; all conditions are the same as in Figure 1. If $\alpha_{x_0}/\alpha_{y_0} > 1$ then a stable coexistence will favor species x. If $\alpha_{x_0} = \alpha_{y_0}$ then $\underline{X}_e = \underline{Y}_e$. (See Appendix.) Computer simulations for various points $(\alpha_{x_0}, \alpha_{y_0})$ in the unstable range show that after small perturbations from $\underline{Z}_e$, species x goes to extinction and species y survives with damped oscillation if $\alpha_{x_0}/\alpha_{y_0} < 1$ and species y goes to extinction if $\alpha_{y_0}/\alpha_{y_0} > 1$.

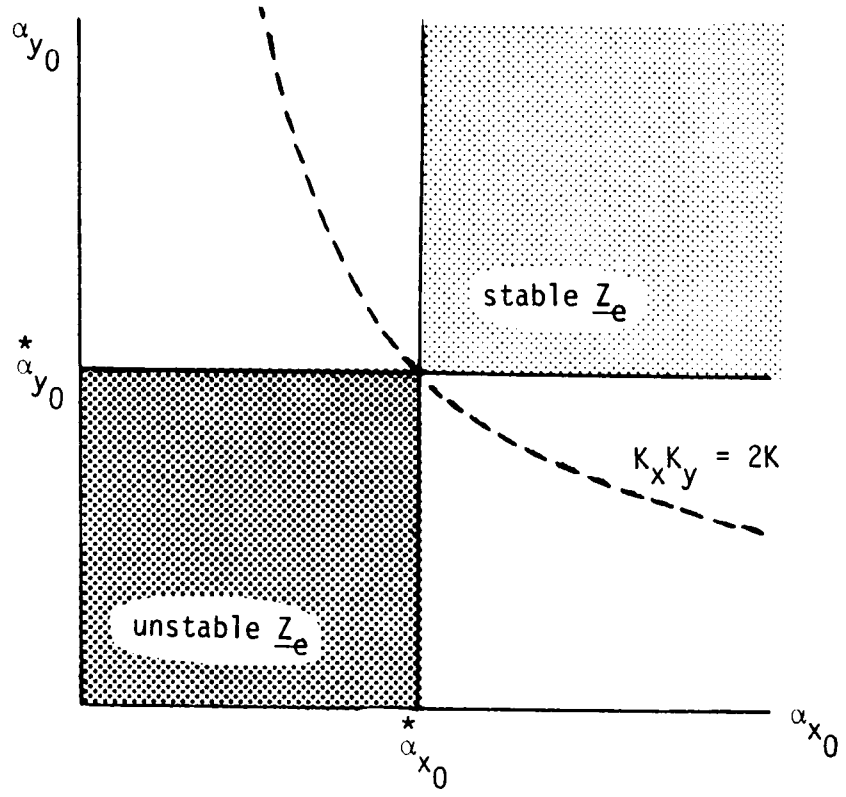


Figure 3. Effect of increasing K_xK_y; if the parameters are changed from those of Figure 1 such that $K_xK_y = 2K$ where $K_x = K_y$, then the hyperbola associated with stability is raised. This increases the unstable range.

raising the hyperbola associated with stability, thus decreasing the area of species coexistence in the parameter space of α_{x_0} and α_{y_0}. This illustrates that relatively strong interspecific phenomena may induce unstable behavior in the system. Figure 4 illustrates the relationships between relative strength of the competition parameters and species dominance For example, if $\beta_{x_i} = k\beta_{y_i}$ where k is some constant greater than 1, the area of stability is shifted upwards and to the left. Thus, if species y increases the predation rate on species x, a balance of the population at equilibrium (i.e., $\underline{X}_e = \underline{Y}_e$) would require either less self-regulation of species x or more self-regulation of species y.

Cumputer results agree with the predictions of the stability criterion, Moreover, if cannibalism is added to the model, computer simulations reveal similar relationships between the model parameters and stability. If α_{x_1}, α_{x_2}, α_{y_1} and α_{y_2} are made nonzero as in (2.1) to (2.4) the effect is to intensify species self-regulation.

The results of the stability analysis need to be validated with data from a real-life system. It would seem that cannibalism does indeed play a significant role in the equilibrium outcome of systems. In many bass-bluegill combinations, stunted bluegill overrun the bass population, creating a rather undesirable condition for fishermen (Bennett, 1971). Although many factors contribute to this behavior it seems that the commonly observed phenomenon of cannibalism among the bass population significantly influences the outcome. A more detailed analysis of the bass-bluegill system is needed. Application of the compensatory matrix model to this and other systems requires an estimation of the parameters

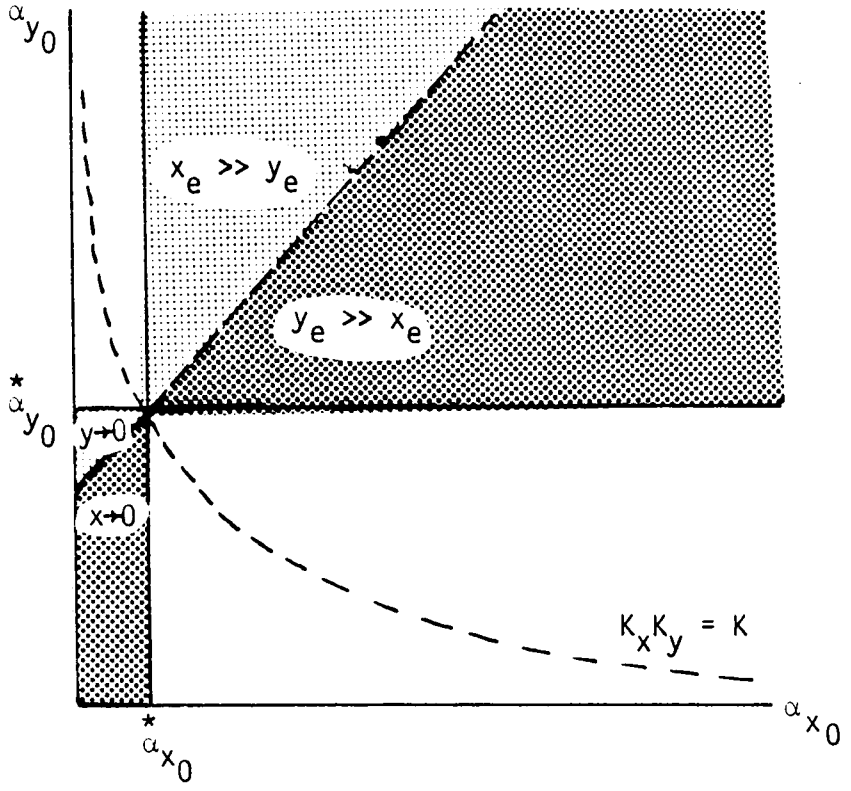


Figure 4. Relative effect of β_{x_i} and β_{y_i} (i=0, 1, 2); the graph shows the effect of increasing the ratio β_{x_i}/β_{y_i}. In Figure 1 $\beta_{x_i}/\beta_{y_i} = 1$, whereas $\beta_{x_i}/\beta_{y_i} = k = 4$ in Figure 2.

of the model. Various methodology have been developed to determine natural mortality rates in single species (Ricker, 1945; Paloheimo, 1959; and Vaughan and Saila, 1976). The model of this paper, however, requires estimates of the intrinsic survival rates r_x and r_y for the zero-age class. These parameters are related to the survival capacity of young fish in the absence of self-crowding effects, cannibalism, competition and predation. A parameter space can be determined for the self-regulatory parameters, α, and the competition parameters, β, if the value of r_x, r_y, $p_{x_{0e}}$, $p_{y_{0e}}$, and $\underline{Z}_e$ are known. However, estimates of these parameters are not available for a suitable system at this time.

In conclusion, we emphasize that stability of multispecies compensatory matrix models depends highly upon the degree of intraspecific behavior of the modeled species. The M-matrix theory can be extended to systems involving n interacting species. The results show that all interacting species must be stable in the absence of other species and that a combination of intraspecific interactions must be stronger than a combination of interspecific interactions.

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APPENDIX

APPENDIX

Feasible equilibrium ranges in the parameter space of α_{x_0} and α_{y_0} are given in Figure 1, page 32, where all other parameters are the same for each species and $\alpha_{x_i} = \alpha_{y_i} = 0$ for $i = 1, 2$, and $K_x K_y = K$ for same positive constant K. These conditions imply that $d_x = d_y$ and $e_x = e_y$ where these expressions are given by (2.3). Feasible equilibrium (i.e., $x_e > 0$, $y_e > 0$) result from two cases:

Case 1. Each of the following must hold

(a) $c_x c_y - d_x d_y < 0$,

(b) $c_y e_x - d_x e_y < 0$,

(c) $c_x e_y - d_y e_x < 0$.

Case 2. The inequality sign < is replaced by > in (a), (b), and (c) of Case 1.

From condition (a) of Case 1 we have

$$\alpha_{x_0}\,\alpha_{y_0} < \{d_y/p_{x_1} f_{y_2} + (1-p_{x_2}) f_{x_1})\} \cdot \{d_x/(p_{y_1} f_{y_2} + (1-p_{y_2}) f_{y_1})\}.$$

Using the fact that

$$r_x = [1+(\alpha_{x_0} x_{0e} + \beta_{x_0} y_{0e} + \beta_{x_1} y_{1_e} + \beta_{x_2} y_{2e})]/[f_{x_1} + p_{x_1}\, f_{x_2}/(1-p_{x_2})],$$

it can be shown that $e_x > 0$. Hence condition (b) implies that $c_y < d_x$ since $e_x = e_y$. That is,

$$\alpha_{y_0} < d_x/[p_{y_1} f_{y_2} + (1-p_{y_2}) f_{y_1}] \equiv \overset{*}{\alpha}_{y_0}$$

Similarly, condition (c) implies that

$$\alpha_{x_0} > d_y/[p_{x_1} f_{x_2} + (1-p_{x_2}) f_{x_1}] \equiv \overset{*}{\alpha}_{x_0}$$

The inequality signs are reversed for Case 2.

To derive the conditions necessary for relative abundance of each species note that $x_e >> y_e$ if and only if

$$c_y e_x - d_x c_y > c_x e_y - d_y e_x.$$

But since $d_x = d_y$ and $e_x = e_y$, this implies that $c_y > c_x$ or $\alpha_{y_0} > \alpha_{x_0}$. Similarly, $x_e = y_e$ and $x_e << y_e$ implies that $\alpha_{x_0} = \alpha_{y_0}$ and $\alpha_{x_0} > \alpha_{y_0}$, respectively.

In Figure 4, page 36, note that if $\beta_{x_i} = k\beta_{y_i}$ for i=0, 1, 2 and some positive constant k, then the assumption that all parameters are the same for each species (except α_{x_0} and α_{y_0}) implies that $d_x = 4d_y$. Hence, $\overset{*}{\alpha}_{y_0} = 4\,\overset{*}{\alpha}_{x_0}$ and $x_e > y_e$ implies that $c_y > c_x + 3d_y$ or $\alpha_{y_0} > \alpha_{x_0} + 3\overset{*}{\alpha}_{x_0}$.

Computer simulations support the analytical results summarized in Figures 1 through 4, pages 32, 33, 34, and 36, respectively. A variety of values were chosen representing 20 points in each shaded region, while the other parameter values in Figure 1 were $f_{x_1} = f_{y_1} = 5{,}000$; $f_{x_2} = f_{y_2} = 10{,}000$, $r_x = r_y = 0.3$; $p_{x_1} = p_{y_1} = 0.5$; $p_{x_2} = p_{y_2} = 0.9$; $\beta_{x_i} = \beta_{y_i} = 100.$, i = 0, 1, 2; $\alpha_{x_i} = \alpha_{y_i} = 0.0$, i = 1, 2.

VITA

James John Perkowski was born in Erie, Pennsylvania on November 14, 1954. He attended Allegheny College in Meadville, Pennsylvania from September 1972 to June 1976, and received a Bachelor of Science degree with majors in Mathematics and Biology. The following September he accepted a teaching assistantship and began graduate studies in Mathematics at The University of Tennessee, Knoxville. In June 1979 he was awarded a Master of Science degree in Mathematics. During the period from July 1978 to October 1978, he was employed as a technical assistant at the Environmental Science Division of Oak Ridge National Laboratory, Oak Ridge, Tennessee.