

Stability and Harvesting of Competing Populations with Genetic Variation in Life History Strategy

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The dynamics of competing populations are investigated using discrete non-linear models with age structure. Necessary and sufficient stability conditions for the coexistence equilibrium between two competing non-interbreeding species are developed. An extension of this result shows that coexistence, which is not necessarily stable, occurs in terms of a simple geometric rule on a two dimensional phase plane, provided that each species reaches a stable equilibrium state in the absence of the other species. In the interbreeding case, analytical results are derived for a one locus, two allele model. Sufficient conditions for the stability of polymorphic equilibria are obtained. It is also shown that if both the homozygous genotypes have stable equilibria at fixation, then genetic coexistence occurs when the equilibrium heterozygous zygote production rate is overdominant. Harvesting can lead to the extinction of one of a pair of competing species, or to loss of genetic diversity in a panmictic population. When catchability increases sufficiently with body size, then harvesting preferentially removes the most productive genotypes, and this causes a reduction in the maximum sustainable yield of the population. Harvesting can also reverse the relative fitness of genotypes, since a rare inferior genotype in an unexploited population may be more fit under fishing. © 1989 Academic Press, Inc.

INTRODUCTION

In age-structured populations, genetic variation often occurs in the parameters which determine life-history strategy, such as survivorship, age

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at maturity, growth rates, and density dependent responses (Nelson and Soule, 1983). A number of resource management questions arise for such systems. These include: Can one detect changes in the stock gene pool? Can one predict such changes? Is the effect significant in terms of variables of interest to the management of the resource? The significance of genetic effects in fish population dynamics has been reported on by others (Desharnais, Foltz, and Zouros, 1985; Kincaid, 1976a, b; Kincaid, Bridges, and von Limbach, 1977; Leary, Allendorf, and Knudsen, 1983, 1984; Schaffer and Elson, 1975; Vrijenhoek and Lerman, 1982; Vrijenhoek, Douglas, and Meffe, 1985; Vuorinen, 1982). In response, there has been a recognition of the need for linking population genetics and fishery or wildlife management theory (e.g., Altukhov, 1981; Favro, Kuo, and McDonald, 1979; Favro, Kuo, McDonald, Favro, and Kuo, 1982; Nelson and Soule, 1983; Ryman, Baccus, Reuterwall, and Smith, 1981). A first step in this direction is to develop a mathematical model of the dynamics of populations exhibiting genetic variation in life history strategy. This raises more fundamental questions relating to criteria for genetic coexistence and for the existence of stable states. This paper concentrates on the fundamental mathematical issue of the existence and stability of stable states.

A logical starting point for the analysis is the density dependent age-structured model applied to fisheries management (Getz, 1980; Hightower and Grossman, 1985; Levin and Goodyear, 1980; Reed, 1980) and to other age structured renewable resources (Fowler and Smith, 1973; Getz, 1985; for a review see Getz and Haight, 1989). We extend this model to treat competing non-interbreeding populations. The necessary and sufficient Schur-Cohn stability conditions for coexistence equilibria for two competing species are developed up to a point. Beyond this point, they become too complex for useful analytical insights. Sufficient stability conditions for coexistence for m competing populations (species) are presented. Necessary and sufficient conditions for the stability of coexistence equilibria are developed for $m = 2$, subject to limited conditions on the nonlinear form of the model. These results are expressed in terms of a simple mapping of the phase plane diagram into a two dimensional aggregated-variable (summed across age class) space.

The local stability analysis is extended to a genetic model consisting of three genotypes resulting from two alleles at one locus under panmixis. Genetic polymorphisms are shown to persist if the heterozygous genotype is overdominant with respect to the equilibrium zygote production level which would be reached by each genotype in isolation from all other genotypes, subject to the condition that the homozygous equilibria are stable. This result was shown by Charlesworth (1971) for an analogous scalar model and for a more general demographic model than that considered here (Charlesworth, 1980, p. 172).

If the set of coexisting genotypes in an unexploited population have roughly the same stock values for their respective boundary equilibria, then the results presented here imply that subject to reasonable conditions, fishing reduces the fitness of the genotype that would in isolation produce the largest maximum sustainable yield (MSY). Therefore, as a fishery develops, more productive genotypes are replaced by less productive genotypes. Hence past catch statistics overestimate future sustainable yield levels. If the conditions for genetic coexistence cannot be met under fishing, then a reduction in genetic diversity must follow. This loss of genetic diversity may be irreversible, or only reversible over very long time scales. Biological studies show that loss of genetic diversity can lead to a deterioration of stock productivity via mechanisms which are not covered by our analysis (Soule, 1982; Soule and Cuzin-Roudy, 1982; Kincaid, 1976a, b; Leary *et al.*, 1984).

DISCRETE AGE-STRUCTURED POPULATION MODELS

Single Species Review

The density dependent models which will be analysed here are all of the Leslie (1945) type in which the only non-linearities are those in the first year survivorship function (see also Getz, 1980, 1985; Getz and Haight, 1989; and Reed, 1980). We define the following state variables and model parameters:

$x_a(t)$ —the number of individuals aged exactly a years, $a = 1, 2, \dots, n$, at the beginning of year t ;

$x_0(t)$ —the total number of zygotes produced at the beginning of year t ;

s_a —the proportion of individuals aged a years at the beginning of any year which survive to the end of that year (s_0 is the density independent survivorship);

$\phi(x_0(t))$ —the first year density dependent survivorship of individuals,

b_a —the average number of zygotes produced by an a year old individual (i.e., half the number per female assuming an equal sex ratio).

With these definitions, it follows that $0 \leq s_{a-1} \leq 1$ and $b_a \geq 0$ for $a = 1, \dots, n$. We assume that $\phi(x) > 0$ for $x > 0$. Further, the zygote production level, $x_0(t)$, is given by

$$x_0(t) = \sum_{a=1}^n b_a x_a(t), \quad (1)$$

and the density dependent Leslie model is represented by the matrix-vector scheme

$$\begin{pmatrix} x_1(t+1) \\ x_2(t+1) \\ \vdots \\ x_n(t+1) \end{pmatrix} = \begin{pmatrix} s_0 b_1 \phi(x_0(t)) & s_0 b_2 \phi(x_0(t)) & \cdots & s_0 b_n \phi(x_0(t)) \\ s_1 & 0 & \cdots & 0 \\ 0 & s_2 & \cdots & 0 \\ \vdots & \vdots & \vdots & \vdots \\ 0 & \cdots & s_{n-1} & 0 \end{pmatrix} \begin{pmatrix} x_1(t) \\ x_2(t) \\ \vdots \\ x_n(t) \end{pmatrix}. \quad (2)$$

Let $l_a = s_0 s_1 s_2 \cdots s_{a-1}$, where $l_0 = 1$, so that from System (2)

$$x_a(t) = \frac{l_a}{l_1} x_1(t-a+1), \quad a = 1, 2, \dots, n, \quad (3)$$

and from Eq. (1) and System (2)

$$x_1(t) = l_1 x_0(t-1) \phi(x_0(t-1)). \quad (4)$$

Combining Eqs. (3) and (4) leads to the following algebraic delay-difference equation for the model defined in System (2):

$$x_0(t) = \sum_{a=1}^n b_a l_a x_0(t-a) \phi(x_0(t-a)). \quad (5)$$

This treatment is applicable to monoecious populations, populations with fixed sex ratio, and populations where female fecundity is independent of male density (assuming that a small number of males is always present). In the latter case, we only count females and b_a is the number of female zygotes per female.

At equilibrium, $x_0(t) = x_0^*$ for all t , and Eq. (5) reduces to

$$\sum_{a=1}^n b_a l_a \phi(x_0^*) = 1. \quad (6)$$

Define

$$R_o = \sum_{a=1}^n b_a l_a, \quad (7)$$

where R_o is commonly referred to as the net reproductive value of the population (Getz and Haight, 1989). If ϕ is an invertible function with inverse ϕ^{-1} , then x_0^* satisfies

$$x_0^* = \phi^{-1} \left(\frac{1}{R_o} \right). \quad (8)$$

In the case where the total recruitment, determined by Eq. (4), is an increasing function of x , it follows that

$$\phi(x) + x\phi'(x) > 0 \quad \text{for all } x > 0, \quad (9)$$

where $\phi'(x)$ denotes the derivative, $d\phi(x)/dx$. Condition (9) corresponds to a situation known as normal compensation with respect to the functional dependence of recruitment on the number of zygotes. If (9) is not satisfied then, for some positive x ,

$$\phi(x) + x\phi'(x) < 0, \quad (10)$$

and the relationship expressed in (4) is called overcompensatory.

Much insight into the dynamic behaviour of the system can be gained by assessing the stability properties of x_0^* . The population may approach x_0^* asymptotically with or without damped oscillations, cycle around x_0^* in a regular fashion, or oscillate around x_0^* in a chaotic fashion (Bergh and Getz, 1988).

The next step is to extend the model to include a number of different life-history strategies. The analysis provides insight into questions of coexistence for non-interbreeding populations (e.g., competing species) and the existence of polymorphisms in genetically structured populations.

A MODEL OF m COMPETING SPECIES

Consider a system of m reproductively isolated but spatially homogeneous populations. We use the same notation as for the single population model introduced in the previous section except that there is an additional j subscript on each variable which identifies it with a specific population j . Thus, for example, Eq. (1) is more generally written as

$$x_{0j}(t) = \sum_{a=1}^n b_{aj} x_{aj}(t). \quad (11)$$

It is proposed that the dynamics of the overall population might follow the same delay-difference form shown in (1) except that now the first year density dependent survival factor is related to total adult density, or equivalently, zygote production across all j populations.

First, we define the column vector $\mathbf{x}_0(t) = (x_{01}(t), x_{02}(t), \dots, x_{0m}(t))'$ and row vectors of constants $\boldsymbol{\theta}_j = (\theta_{j1}, \theta_{j2}, \dots, \theta_{jm})$, $j = 1, \dots, m$. Then we assume that the density dependent response of the j th population is dependent on the inner product

$$\boldsymbol{\theta}_j \mathbf{x}_0(t) = \sum_{k=1}^m \theta_{jk} x_{0k}, \quad (12)$$

where $\theta_{jj} = 1$, $j = 1, 2, \dots, m$. Thus coefficients θ_{jk} of the interaction matrix Θ , where

$$\Theta = \begin{pmatrix} \theta_{11} & \cdots & \theta_{1m} \\ \vdots & \vdots & \vdots \\ \theta_{m1} & \cdots & \theta_{mm} \end{pmatrix}, \quad (13)$$

have the standard interpretation of interaction coefficients, as has been defined in the population modeling literature (e.g., May, 1973). Clearly, for $j, k = 1, \dots, m$, $\theta_{jk} \geq 0$; but if there is some partition of the resource space and competition is weak then it usually follows that $\theta_{jk} < 1$ for $j \neq k$.

For the j th population, the analogue of the delay-difference form in (5) is

$$x_{0j}(t) = \sum_{a=1}^n b_{aj} l_{aj} x_{0j}(t-a) \phi_j(\theta_j \mathbf{x}_0(t)). \quad (14)$$

The assumption that there are an equal number of age classes (n) for each species is made for notational convenience. Situations in which this is not the case can be dealt with by defining additional age classes with zero fecundity and zero survivorship until the numbers of age classes are equal for all species. The rationale for Model (14) follows from the rationale for the basic density dependent Leslie model, namely that density dependence occurs as a survivorship condition in the first year of life when individuals are most susceptible to competition and predation. The model assumes that the youngest individuals in each population compete with the youngest individuals from all other populations. We have included the possibility that the youngest individuals in some populations are better able to survive density dependence than the youngest individuals in other populations by retaining the subscript j in ϕ_j in Eq. (14).

In matrix form, the analogue of System (2) is a system of m Leslie matrices, each of which has the form shown in System (2): i.e., using population vectors $\mathbf{x}_j(t) = (x_{1j}(t), x_{2j}(t), \dots, x_{nj}(t))'$ and a matrix consisting of a series of Leslie matrices as entries along the diagonal, we have

$$\begin{pmatrix} \mathbf{x}_1(t+1) \\ \mathbf{x}_2(t+1) \\ \vdots \\ \mathbf{x}_{m-1}(t+1) \\ \mathbf{x}_m(t+1) \end{pmatrix} = \begin{pmatrix} \mathbf{L}_1 & 0 & \cdots & 0 & 0 \\ 0 & \mathbf{L}_2 & \cdots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & \mathbf{L}_{m-1} & 0 \\ 0 & 0 & \cdots & 0 & \mathbf{L}_m \end{pmatrix} \begin{pmatrix} \mathbf{x}_1(t) \\ \mathbf{x}_2(t) \\ \vdots \\ \mathbf{x}_{m-1}(t) \\ \mathbf{x}_m(t) \end{pmatrix}. \quad (15)$$

The dynamics of the j th population are given by a similar matrix relationship to that shown for the single genotype population in System (2),

except for the dependence of the first year density dependent survivorship term on the density of zeroth year cohorts in all m populations. Note that \mathbf{x}_j is an n dimensional vector denoting the age structure of the j th population, $j = 1, \dots, m$, while \mathbf{x}_0 is an m dimensional vector of the m aggregated variables x_{0j} , $j = 1, \dots, m$, defined by Relationship (11).

Equilibrium, Coexistence, and Dominance

Equilibrium conditions for the m competing species model, (14) or (15), are found by setting

$$x_{0j}(t) = x_{0j}^* \quad j = 1, \dots, m \tag{16}$$

for all t in Eq. (14), giving

$$x_{0j}^* = \sum_{a=1}^n b_{aj} l_{aj} x_{0j}^* \phi_j(\boldsymbol{\theta}_j, \mathbf{x}_0^*) \quad j = 1, \dots, m. \tag{17}$$

If ϕ_j is invertible for all j , and if the inverse function is represented by ϕ_j^{-1} , then the m equations (17) become a set of m linear equations

$$\sum_{k=1}^m \theta_{jk} x_{0k}^* = \phi_j^{-1} \left[\frac{1}{R_{oj}} \right] \quad j = 1, \dots, m, \tag{18}$$

where $R_{oj} = \sum_{a=1}^n b_{aj} l_{aj}$ is the net reproductive value of the j th population (cf. Eq. (7)), and note that $\boldsymbol{\theta}_j \mathbf{x}_0^* = \sum_{k=1}^m \theta_{jk} x_{0k}^*$. This equation has a positive (biologically feasible) solution in the absence of competition ($\theta_{jk} = 0$, $j \neq k$, $j, k = 1, 2, \dots, m$) and thus, by continuity, whenever competition is insignificantly small ($0 < \theta_{jk} \ll 1$, $j \neq k$, $j, k = 1, 2, \dots, m$). Further, this equilibrium solution is unique provided that the interaction matrix Θ is non-singular. Once the existence of a coexistence equilibrium has been established, it is crucial to evaluate its stability properties if the dynamics of the system are to be understood. If \mathbf{x}_0^* is stable, coexistence of species is guaranteed in a neighbourhood of \mathbf{x}_0^* ; otherwise one or more species might become extinct even if the population system is initially arbitrarily close to \mathbf{x}_0^* . Apart from the unique coexistence equilibrium it follows from Eq. (17) that there are $\binom{m}{r}$ possible non-coexistence equilibria when any r populations are at zero population size, giving a total of p equilibria, where

$$p = \sum_{r=0}^m \binom{m}{r} = 2^m. \tag{19}$$

A special case of these equilibria is the equilibrium population size which arises for species j in the absence of all other species. For convenience, we

refer to these as the boundary equilibria (or axis equilibria in the context of a phase portrait), written x_{0j}^s , and defined for all j by

$$x_{0j}^s = \phi_j^{-1} \left(\frac{1}{R_{0j}} \right). \quad (20)$$

From Eqs. (18) and (20), $\sum_{k=1}^m \theta_{jk} x_{0k}^* = x_{0j}^s$, and it follows therefore that the argument of ϕ_j or ϕ_j' at any coexistence equilibrium state is x_{0j}^s .

Stability Results: m Competing Populations

Equilibria for the competition model are locally stable if the eigenvalues of the linearized population matrix lie within the unit circle. Necessary and sufficient conditions for this are given by the Schur–Cohn conditions (e.g., Jury, 1974). The method of application of the Schur–Cohn conditions is described for the case $m=2$ in Appendix 1. Although this approach can be used to obtain numerical results for a system with known parameter values, it does not lead to a set of general conditions that provide any analytical insights, since the algebraic complexity of the condition set is extreme. Further stability work pursued here deals with sufficient stability conditions for the general model, necessary and sufficient stability conditions for the coexistence equilibria of certain special cases for $m=2$, and necessary and sufficient stability conditions for boundary equilibria for $m=2$.

Sufficient stability conditions for equilibria of the general model are given (Appendix 1) by

$$\sum_{a=1}^n |l_{aj} b_{aj} \phi_j(x_{0j}^s) + l_{aj} b_{aj} x_{0j}^* \phi_j'(x_{0j}^s)| + \sum_{\substack{k=1 \\ k \neq j}}^m \sum_{a=1}^n |l_{ak} b_{ak} \theta_{jk} x_{0j}^* \phi_j'(x_{0j}^s)| < 1. \quad (21)$$

Because these conditions are sufficient but not necessary, they cannot be used to define the precise point at which stability is lost (i.e., the point of bifurcation).

The precise point of bifurcation is now given for a *special form* of the general model.

Two Competing Species Subject to Special Conditions

Consider the case $m=2$ and suppose at the coexistence equilibrium that the inequality (cf. Inequality (9))

$$\phi_j(x_{0j}^s) + x_{0j}^* \phi_j'(x_{0j}^s) > 0, \quad j = 1, 2, \quad (22)$$

is satisfied. Stability results for this case have been reported by Travis, Post, DeAngelis, and Perkowski (1980) with respect to a more general model that allows the survival parameters s_{aj} to be functions of the state

variables. Here we derive sharper results for the case of constant adult survivorship. Under (22) the linearized population matrix, \mathbf{M} , can be expressed in terms of submatrices (see Appendix 1) as

$$\mathbf{M} = \begin{pmatrix} \mathbf{M}_{11} & \mathbf{M}_{12} \\ \mathbf{M}_{21} & \mathbf{M}_{22} \end{pmatrix}. \quad (23)$$

The matrices \mathbf{M}_{11} and \mathbf{M}_{22} contain intra-species effects terms, and \mathbf{M}_{21} and \mathbf{M}_{12} contain the inter-species terms. The matrix \mathbf{S} , where

$$\mathbf{S} = \begin{pmatrix} \mathbf{M}_{11} & -\mathbf{M}_{12} \\ -\mathbf{M}_{21} & \mathbf{M}_{22} \end{pmatrix}, \quad (24)$$

is similar to \mathbf{M} , since

$$\begin{aligned} \mathbf{S} &= \begin{pmatrix} \mathbf{I} & \mathbf{0} \\ \mathbf{0} & -\mathbf{I} \end{pmatrix} \begin{pmatrix} \mathbf{M}_{11} & \mathbf{M}_{22} \\ \mathbf{M}_{21} & \mathbf{M}_{22} \end{pmatrix} \begin{pmatrix} \mathbf{I} & \mathbf{0} \\ \mathbf{0} & -\mathbf{I} \end{pmatrix} \\ &= \begin{pmatrix} \mathbf{M}_{11} & -\mathbf{M}_{12} \\ -\mathbf{M}_{21} & \mathbf{M}_{22} \end{pmatrix}, \end{aligned} \quad (25)$$

and therefore \mathbf{S} has the same eigenvalues as \mathbf{M} and the original Jacobian \mathbf{A} . \mathbf{S} is a non-negative matrix, so from the Perron Frobenius Theorem, the dominant eigenvalue λ_0 is real and positive. The upper and lower bounds on λ_0 are given by the largest and smallest of the row sums of \mathbf{S} (see Luenberger, 1979). All row sums of \mathbf{S} are equal to one, except for the first and the $(n+1)$ st row sums, σ_1 and σ_{n+1} , which are given (Appendix 1) by

$$\sigma_1 = \sum_{a=1}^n (l_{a1} b_{a1} [\phi_1(x_{01}^s) + x_{01}^* \phi_1'(x_{01}^s)] - l_{a2} b_{a2} \theta_{12} x_{01}^* \phi_1'(x_{01}^s)) \quad (26)$$

and

$$\sigma_{n+1} = \sum_{a=1}^n (l_{a2} b_{a2} [\phi_2(x_{02}^s) + x_{02}^* \phi_2'(x_{02}^s)] - l_{a1} b_{a1} \theta_{21} x_{02}^* \phi_2'(x_{02}^s)). \quad (27)$$

If $\sigma_1 > 1$ and $\sigma_{n+1} > 1$, then $\lambda_0 > 1$ and \mathbf{x}_0^* is unstable. However, if $\sigma_1 < 1$ and $\sigma_{n+1} < 1$, then $\lambda_0 < 1$ and \mathbf{x}_0^* is stable. When $\sigma_1 > 1$ and $\sigma_{n+1} < 1$ or vice versa, then the stability properties of \mathbf{x}_0^* cannot be determined without further analysis. A point of bifurcation occurs when $\sigma_1 = \sigma_{n+1} = 1$.

Recall that at the boundary equilibria, $\sum_{a=1}^n b_{aj} l_{aj} \phi_j(x_{0j}^s) = 1$ for $j = 1, 2$ (cf. Identities (6) and (17)). Hence $\sum_{a=1}^n b_{aj} l_{aj} = 1/\phi_j(x_{0j}^s)$ for $j = 1, 2$, and it follows from Eqs. (26) and (27) that the stability conditions are

$$1 + x_{01}^* \phi_1'(x_{01}^s) \left[\frac{1}{\phi_1(x_{01}^s)} - \theta_{12} \frac{1}{\phi_2(x_{02}^s)} \right] < 1 \quad (28)$$

and

$$1 + x_{02}^* \phi_2'(x_{02}^s) \left[\frac{1}{\phi_2(x_{02}^s)} - \theta_{21} \frac{1}{\phi_1(x_{02}^s)} \right] < 1. \quad (29)$$

Since ϕ_j' is strictly negative when ϕ_j is a strictly monotonically decreasing function, stability is guaranteed when both

$$\frac{1}{\phi_1(x_{01}^s)} > \theta_{12} \frac{1}{\phi_2(x_{02}^s)} \quad (30)$$

and

$$\frac{1}{\phi_2(x_{02}^s)} > \theta_{21} \frac{1}{\phi_1(x_{01}^s)}. \quad (31)$$

Instability is certain if Inequalities (30) and (31) are both violated.

A phase plane representation is a useful aid here (Figs. 1 and 2). Equilibrium isoclines in the x_{01} - x_{02} plane can be obtained from Eqs. (18) and (20); i.e.,

$$x_{01} + \theta_{12} x_{02} = x_{01}^s \quad \text{and} \quad x_{02} + \theta_{21} x_{01} = x_{02}^s, \quad (32)$$

or alternatively

$$x_{02} = -\frac{x_{01}}{\theta_{12}} + \frac{x_{01}^s}{\theta_{12}} \quad \text{and} \quad x_{02} = -\theta_{21} x_{01} + x_{02}^s. \quad (33)$$

If these two lines intersect in the positive quadrant of the x_{01} - x_{02} plane, and if $\theta_{12}\theta_{21} \neq 1$, then there exists a unique biologically meaningful coexistence equilibrium given by

$$x_{01}^* = \frac{x_{01}^s - \theta_{12} x_{02}^s}{1 - \theta_{12}\theta_{21}} \quad (34)$$

and

$$x_{02}^* = \frac{x_{02}^s - \theta_{21} x_{01}^s}{1 - \theta_{21}\theta_{12}}. \quad (35)$$

If $\theta_{12}\theta_{21} = 1$, then the two lines coincide when $x_{02}^s = x_{01}^s/\theta_{12}$ and so $(x_{01}^*, x_{02}^*) \in X^s$, where

$$X^s = \left\{ (x_{01}, x_{02}) \mid x_{01} \geq 0 \quad x_{02} \geq 0 \quad \text{and} \quad \frac{x_{01}}{x_{01}^s} + \frac{x_{02}}{x_{02}^s} = 1 \right\}. \quad (36)$$

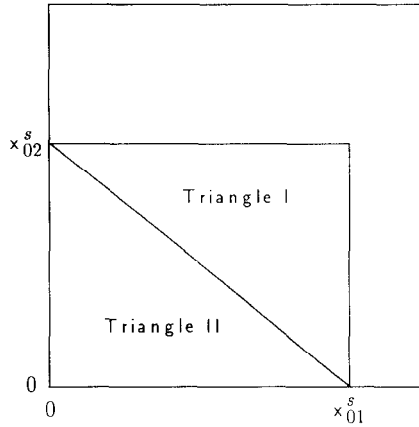


FIG. 1. The two dimensional aggregated-variable phase plane for two competing, age-structured populations. The rectangle contains all biologically meaningful coexistence equilibria (x_{01}^s, x_{02}^s) for the model of two competing species when $0 < \theta_{12} < 1$ and $0 < \theta_{21} < 1$. If Condition (22) is met everywhere in the rectangle, then equilibria inside I are stable, and those inside II are unstable.

The rectangle in the plane defined by the corners $(0, 0)$, $(0, x_{02}^s)$, $(x_{01}^s, 0)$, and (x_{01}^s, x_{02}^s) (Fig. 1) contains all possible equilibria. The boundary equilibria defined in (20) correspond to the two equilibria $(0, x_{02}^s)$ and $(x_{01}^s, 0)$ on the axes of the coordinate system and are therefore sometimes referred to as axis equilibria in the context of the phase plane.

From Eq. (33) and Fig. 2, the x_{01} isocline intersects the x_{02} axis at the point $(0, x_{01}^s/\theta_{12})$ while the x_{02} isocline intersects the x_{01} axis at the point $(x_{02}^s/\theta_{21}, 0)$. Hence, provided $0 < \theta_{12} < 1$ and $0 < \theta_{21} < 1$, the isoclines intersect in Triangle I when

$$x_{01}^s \leq \frac{x_{02}^s}{\theta_{21}} \quad \text{and} \quad x_{02}^s \leq \frac{x_{01}^s}{\theta_{12}} \quad (\text{i.e., } \theta_{12}\theta_{21} < 1), \quad (37)$$

and in Triangle II when

$$x_{01}^s \geq \frac{x_{02}^s}{\theta_{21}} \quad \text{and} \quad x_{02}^s \geq \frac{x_{01}^s}{\theta_{12}} \quad (\text{i.e., } \theta_{12}\theta_{21} > 1). \quad (38)$$

It is easily shown, as presented below, that the equilibrium $(0, 0)$ is unstable, that the equilibrium (x_{01}^s, x_{02}^s) is stable in the absence of competition ($\theta_{12} = \theta_{21} = 0$), and that equilibria lying on the diagonal joining the points $(0, x_{02}^s)$ and $(x_{01}^s, 0)$ are marginally stable. Therefore, using a continuity argument, it follows that Triangles I and II, respectively, define regions of locally stable and unstable coexistence equilibria, depending on where the equilibrium is located as a function of the values of θ_{12} and θ_{21} .

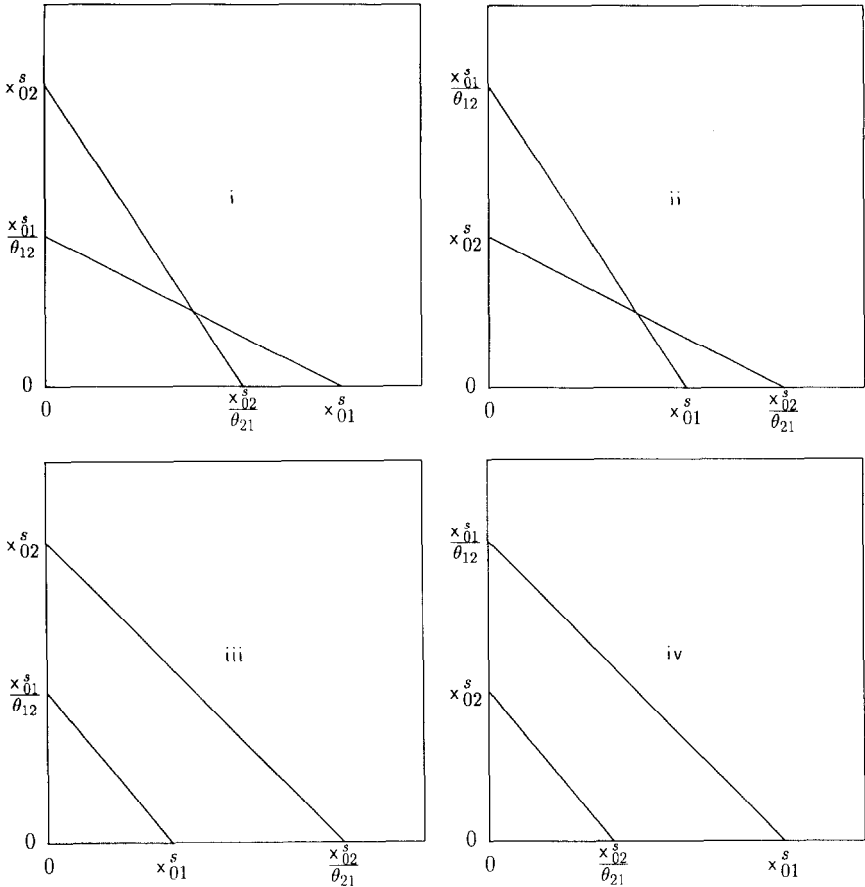


FIG. 2 (i-iv). The phase plane, presented in Fig. 1, with isoclines corresponding to the four cases (i) $x_{01}^s/\theta_{12} < x_{02}^s$, $x_{02}^s/\theta_{21} < x_{01}^s$; (ii) $x_{01}^s/\theta_{12} > x_{02}^s$, $x_{02}^s/\theta_{21} > x_{01}^s$; (iii) $x_{01}^s/\theta_{12} < x_{02}^s$, $x_{02}^s/\theta_{21} > x_{01}^s$; (iv) $x_{01}^s/\theta_{12} > x_{02}^s$, $x_{02}^s/\theta_{21} < x_{01}^s$.

When $\theta_{12} = \theta_{21} = 0$, the coexistence equilibrium $\mathbf{x}_0^* = (x_{01}^s, x_{02}^s)$ is stable provided that (from (26) and (27))

$$\sum_{a=1}^n l_{aj} b_{aj} [\phi_j(x_{0j}^s) + x_{0j}^s \phi_j'(x_{0j}^s)] < 1, \quad j = 1, 2. \quad (39)$$

Reed (1980) and Bergh and Getz (1988) have shown that Inequality (39) is always satisfied when (22) holds at both single species equilibria, and when there is a single unique biologically meaningful and non-trivial (i.e., positive and non-zero) equilibrium point for both species.

When $\theta_{12} \rightarrow \infty$ and $\theta_{21} \rightarrow \infty$ the isoclines approach the axes and the coexistence equilibrium approaches the point (0, 0) which is the origin of

the coordinates in Figs. 1 and 2. From (30) and (31), stability of the origin depends on the signs of $1/\phi_1(x_{01}^s) - \theta_{12}/\phi_2(x_{02}^s)$ and $1/\phi_2(x_{02}^s) - \theta_{21}/\phi_1(x_{01}^s)$ in the limit as $\theta_{12} \rightarrow \infty$ and $\theta_{21} \rightarrow \infty$. Since the sign is negative for both terms, a coexistence equilibrium at the origin is unstable.

The general form of any eigenvector \mathbf{x} of \mathbf{M} or \mathbf{S} is (see Appendix 1)

$$\mathbf{x} = \left(1, \frac{1}{\lambda}, \frac{1}{\lambda^2}, \dots, \frac{1}{\lambda^{n-1}}; c, \frac{c}{\lambda}, \frac{c}{\lambda^2}, \dots, \frac{c}{\lambda^{n-1}} \right), \tag{40}$$

where the value of c depends on the value of λ and on the elements in the first and $(n + 1)$ st rows of \mathbf{M} or \mathbf{S} .

Under (22), if $\lambda = 1$ in $\mathbf{S}\mathbf{x} = \lambda\mathbf{x}$, then the first and $(n + 1)$ st spectral equations are

$$x_{01}^* \phi_1'(x_{01}^s) \left(\frac{1}{\phi_1(x_{01}^s)} - c \frac{\theta_{12}}{\phi_2(x_{02}^s)} \right) = 0 \tag{41}$$

and

$$x_{02}^* \phi_2'(x_{02}^s) \left(\frac{1}{\phi_2(x_{01}^s)} - \frac{\theta_{21}}{c\phi_1(x_{01}^s)} \right) = 0. \tag{42}$$

For $x_{0j}^* \neq 0, j = 1, 2$, these equations reduce to

$$c = \frac{1}{\theta_{12}} \frac{\phi_2(x_{02}^s)}{\phi_1(x_{01}^s)} \tag{43}$$

and

$$c = \theta_{21} \frac{\phi_2(x_{02}^s)}{\phi_1(x_{01}^s)}, \tag{44}$$

i.e., $\theta_{12}\theta_{21} = 1$. This is the condition under which the isoclines are parallel (see Eq. (33)), which includes the special case of coincidence for which there are an infinite number of coexistence equilibria, $\mathbf{x}_0^* \in X^s$ (see Identity (36)).

Thus, if both boundary equilibria $x_{0j}^s; j = 1, 2$, are stable then the equilibrium state $\mathbf{x}_0^* = (x_{01}^s, x_{02}^s)$ (i.e., when $\theta_{12} = 0, \theta_{21} = 0$) is stable, which implies $\lambda_0 < 1$. The equilibrium state $\mathbf{x}_0^* = (0, 0)$ (this occurs when $\theta_{12}, \theta_{21} \rightarrow \infty$) is unstable, $\lambda_0 > 1$. The equilibria $\mathbf{x}_0^* \in X^s$ (when $\theta_{12}\theta_{21} = 1$) are all marginally stable, $\lambda_0 = 1$.

Also (see (37) and (38)) $\theta_{12}\theta_{21} < 1$ whenever \mathbf{x}_0^* lies above X^s (Fig. 1), and $\theta_{12}\theta_{21} > 1$ whenever \mathbf{x}_0^* lies below X^s . Since $\lambda_0 = 1$ can only occur when $\mathbf{x}_0^* \in X^s$, $\lambda_0 < 1$ when $\mathbf{x}_0^* = (x_{01}^s, x_{02}^s)$, and $\lambda_0 > 1$ when $\mathbf{x}_0^* = (0, 0)$ it

follows, assuming λ_0 is a continuous function of $\theta_{12} > 0$ and $\theta_{21} > 0$ and (22) holds for all coexistence equilibria, that $\lambda_0 < 1$ ($\lambda_0 > 1$), and \mathbf{x}_0^* is stable (unstable) whenever \mathbf{x}_0^* lies in Triangle I (Triangle II) of the rectangle shown in Fig. 1.

In the complex plane, roots of polynomials are continuous functions of polynomial coefficients, so that λ_0 is a continuous function of θ_{12} and θ_{21} . Also, since for any coexistence equilibrium, $0 < x_{01}^* < x_{01}^s$ and $0 < x_{02}^* < x_{02}^s$, and since ϕ'_1 and ϕ'_2 are both decreasing functions of their arguments,

$$\sum_{a=1}^n l_{aj} b_{aj} [\phi_j(x_{0j}^s) + x_{0j}^* \phi'_j(x_{0j}^s)] < 1 \quad (45)$$

is satisfied for all x_{01}^* and x_{02}^* in the rectangle provided that

$$\sum_{a=1}^n l_{aj} b_{aj} [\phi_j(x_{0j}^s) + x_{0j}^s \phi'_j(x_{0j}^s)] < 1. \quad (46)$$

The necessary and sufficient local stability results stated above thus hold.

Two Competing Species with no Special Conditions

From **M** (see Appendix 1) and the general eigenvector \mathbf{x} in (40), two non-trivial equations result from the spectral equation $\mathbf{M}\mathbf{x} = \lambda\mathbf{x}$ at the boundary equilibrium state $\mathbf{x}_0^* = (x_{01}^s, 0)$. These equations are

$$\sum_{a=1}^n \frac{1}{\lambda^a} (l_{a1} b_{a1} [\phi_1(x_{01}^s) + x_{01}^s \phi'_1(x_{01}^s)] - c l_{a2} b_{a2} \theta_{12} x_{01}^s \phi'_1(x_{01}^s)) = 1 \quad (47)$$

and

$$\sum_{a=1}^n \frac{1}{\lambda^a} l_{a2} b_{a2} \phi_2(\theta_{21} x_{01}^s) = 1. \quad (48)$$

There are two unknowns: the value of λ is determined by (48) and then c follows from (47). Equation (48) is the familiar Perron equation for the eigenvalues of a non-negative density independent Leslie matrix: so the dominant eigenvalue at the boundary equilibrium is real and positive. From the Perron Frobenius Theorem we get that

$$\lambda_0 > 1 \quad \text{if} \quad \sum_{a=1}^n l_{a2} b_{a2} \phi_2(\theta_{21} x_{01}^s) > 1$$

and

$$\lambda_0 < 1 \quad \text{if} \quad \sum_{a=1}^n l_{a2} b_{a2} \phi_2(\theta_{21} x_{01}^s) < 1. \quad (49)$$

By definition (Eqs. (6) and (7)) $\sum_{a=1}^n l_{a2} b_{a2} \phi_2(x_{02}^s) = 1$. Therefore, since ϕ_2 is a strictly decreasing function of its argument,

$$\sum_{a=1}^n l_{a2} b_{a2} \phi_2(\theta_{21} x_{01}^s) < 1 \quad \text{if } x_{01}^s > \frac{x_{02}^s}{\theta_{21}}$$

and

$$\sum_{a=1}^n l_{a2} b_{a2} \phi_2(\theta_{21} x_{01}^s) > 1 \quad \text{if } x_{01}^s < \frac{x_{02}^s}{\theta_{21}}. \tag{50}$$

From (49) and (50),

$$\lambda_0 < 1 \quad \text{if } x_{01}^s > \frac{x_{02}^s}{\theta_{21}}$$

and

$$\lambda_0 > 1 \quad \text{if } x_{01}^s < \frac{x_{02}^s}{\theta_{21}}. \tag{51}$$

At the other boundary equilibrium $\mathbf{x}_0^* = (0, x_{02}^s)$ we must have

$$\lambda_0 < 1 \quad \text{if } x_{02}^s > \frac{x_{01}^s}{\theta_{12}}$$

and

$$\lambda_0 > 1 \quad \text{if } x_{02}^s < \frac{x_{01}^s}{\theta_{12}}. \tag{52}$$

From the geometry of the isoclines (see Fig. 1), the reader can readily verify that results (51) and (52) imply that when the coexistence equilibrium is in Triangle I, both axis equilibria are unstable, and when the coexistence equilibrium is in Triangle II, the axis (i.e., boundary) equilibria will be locally stable.

If there are no coexistence equilibria, the boundary equilibria for the dominant species (the isocline for the dominant species is then the one which lies furthest from the origin of the phase plane) will be locally stable and the other will be unstable.

These local stability results suggest a simple rule governing the persistence of species in a two species competition model of this sort. However, as pointed out by Hutson and Moran (1982) and Hofbauer, Hutson, and Jansen (1987), persistence may have nothing to do with the local stability of boundary equilibria, since individual species may be

unstable and hence the solution can oscillate on the axis—even though an analysis of the mixed species model indicates that the coexistence equilibrium is locally stable. This is a limitation of the global applicability of local analyses.

GENETIC MODELS

Consider a genetically variable population consisting of m phenotypically distinct subpopulations (life history phenotypes). The m population model would apply if the subpopulations did not interbreed. In the m population model let all individuals make the same contributions to density dependence regardless of their subpopulation affiliations; i.e., $\theta_{jk} = 1$ for all $j, k = 1, \dots, m$. For this case, the factors $\phi_j^{-1} [1/\sum_{a=1}^n b_{aj} l_{aj}]$ will in general all be different, and the only equilibria in Eq. (17) will be the set of boundary equilibria for all $j = 1, 2, \dots, m$,

$$x_{0j}^* = x_{0j}^s, \quad x_{0i}^* = 0, \quad j \neq i, \quad i = 1, \dots, m, \quad (53)$$

and the solution $x_{0j}^* = 0, j = 1, 2, \dots, m$. However, if $x_{01}^s = x_{02}^s = \dots = \kappa$, then the m equations in (18) become identical, and the solution is indeterminate. In this case there are an unbounded number of equilibria satisfying

$$x_{01}^* + x_{02}^* + x_{03}^* + \dots + x_{0m}^* = \kappa. \quad (54)$$

If there are three genotypes, then in the x_{01}, x_{02}, x_{03} phase space the coexistence equilibria defined a plane.

Sufficient stability results for this model follow as a special case of result (21). However, it is noted that the equilibrium set is no longer a number of discrete isolated points but an infinite set of connected points. For any one equilibrium state, another can be found which is arbitrarily close to the first. Hence the equilibria defined in (54) are marginally stable, $\lambda_0 = 1$ (see, e.g., Luenberger, 1979).

Consider now a genetic model in which life history strategy is determined by two alleles, a_1 and a_2 , at a single locus, under panmixis (as defined in Charlesworth, 1980, p. 126). Let $x_{0,11}$, $x_{0,22}$, and $x_{0,12}$ be the zygote variables for the homozygous types $a_1 a_1$ and $a_2 a_2$ and the heterozygous type $a_1 a_2$, respectively. The numbers of diploid zygotes of each type immediately following fertilization at the beginning of year t are given by $x_{0,11}(t)$, $x_{0,12}(t)$, and $x_{0,22}(t)$. Let the numbers of haploid gametes a_1 and a_2 immediately prior to fertilization be $A_1(t)$ and $A_2(t)$. Therefore

$$A_1(t) = 2 \sum_{a=1}^n b_{a,11} x_{a,11}(t) + \sum_{a=1}^n b_{a,12} x_{a,12}(t) \quad (55)$$

and

$$A_2(t) = 2 \sum_{a=1}^n b_{a,22} x_{a,22}(t) + \sum_{a=1}^n b_{a,12} x_{a,12}(t). \quad (56)$$

In delay-difference form, Eqs. (55) and (56) become

$$A_1(t) = 2 \sum_{a=1}^n b_{a,11} l_{a,11} x_{0,11}(t-a) \phi_{11}(x_{0,11}(t-a) + x_{0,12}(t-a) + x_{0,22}(t-a)) \\ + \sum_{a=1}^n b_{a,12} l_{a,12} x_{0,12}(t-a) \phi_{12}(x_{0,11}(t-a) + x_{0,12}(t-a) + x_{0,22}(t-a)) \quad (57)$$

$$A_2(t) = 2 \sum_{a=1}^n b_{a,22} l_{a,22} x_{0,22}(t-a) \phi_{22}(x_{0,11}(t-a) + x_{0,12}(t-a) + x_{0,22}(t-a)) \\ + \sum_{a=1}^n b_{a,12} l_{a,12} x_{0,12}(t-a) \phi_{12}(x_{0,11}(t-a) + x_{0,12}(t-a) + x_{0,22}(t-a)). \quad (58)$$

The relationship between diploids and haploids after random mating has occurred is

$$x_{0,11}(t) = \frac{(A_1(t))^2}{2(A_1(t) + A_2(t))} \quad (59)$$

$$x_{0,12}(t) = \frac{2A_1(t) A_2(t)}{2(A_1(t) + A_2(t))} \quad (60)$$

$$x_{0,22}(t) = \frac{(A_2(t))^2}{2(A_1(t) + A_2(t))} \quad (61)$$

(Charlesworth, 1980). Let $H = (A_1(t) + A_2(t))/2$ be the total number of zygotes present at the beginning of year t , that is,

$$H = \sum_{a=1}^n b_{a,11} l_{a,11} x_{0,11}(t-a) \phi_{11}(c(t-a)) \\ + \sum_{a=1}^n b_{a,12} l_{a,12} x_{0,12}(t-a) \phi_{12}(c(t-a)) \\ + \sum_{a=1}^n b_{a,22} l_{a,22} x_{0,22}(t-a) \phi_{22}(c(t-a)), \quad (62)$$

where

$$c(t-a) = x_{0,11}(t-a) + x_{0,12}(t-a) + x_{0,22}(t-a). \quad (63)$$

For brevity we define

$$h_{a,q} = b_{a,q} t_{a,q} \quad q = 11, 12, 22. \quad (64)$$

Substituting Eqs. (57) and (58) into (59), (60), and (61), diploid zygote levels are

$$x_{0,11}(t) = \frac{\left((2 \sum_{a=1}^n h_{a,11} x_{0,11}(t-a) \phi_{11}(c(t-a)) + \sum_{a=1}^n h_{a,12} x_{0,12}(t-a) \phi_{12}(c(t-a)))^2 \right)}{4H} \quad (65)$$

$$x_{0,12}(t) = 2 \left(2 \sum_{a=1}^n h_{a,11} x_{0,11}(t-a) \phi_{11}(c(t-a)) + \sum_{a=1}^n h_{a,12} x_{0,12}(t-a) \phi_{12}(c(t-a)) \right) \times \frac{\left((\sum_{a=1}^n h_{a,12} x_{0,12}(t-a) \phi_{12}(c(t-a)) + 2 \sum_{a=1}^n h_{a,22} x_{0,22}(t-a) \phi_{22}(c(t-a))) \right)}{4H} \quad (66)$$

$$x_{0,22} = \frac{\left((2 \sum_{a=1}^n h_{a,22} x_{0,22}(t-a) \phi_{22}(c(t-a)) + \sum_{a=1}^n h_{a,12} x_{0,12}(t-a) \phi_{12}(c(t-a)))^2 \right)}{4H}. \quad (67)$$

At equilibrium let

$$\kappa = x_{0,11}^* + x_{0,12}^* + x_{0,22}^*; \quad (68)$$

that is,

$$H^* = x_{0,11}^* \sum_{a=1}^n h_{a,11} \phi_{11}(\kappa) + x_{0,22}^* \sum_{a=1}^n h_{a,22} \phi_{22}(\kappa) + x_{0,12}^* \sum_{a=1}^n h_{a,12} \phi_{12}(\kappa). \quad (69)$$

Genetic material must be conserved, so that the number of zygotes produced after genetic sorting is equal to half the number of gametes present immediately before fertilization; i.e., $H^* = \kappa$. From (68) and (69), conservation of genetic material requires that

$$x_{0,11}^* + x_{0,12}^* + x_{0,22}^* = x_{0,11}^* \sum_{a=1}^n h_{a,11} \phi_{11}(\kappa) + x_{0,12}^* \sum_{a=1}^n h_{a,12} \phi_{12}(\kappa) + x_{0,22}^* \sum_{a=1}^n h_{a,22} \phi_{22}(\kappa). \quad (70)$$

At equilibrium, (65), (66), and (67) give

$$x_{0,11}^* = \frac{(2x_{0,11}^* \sum_{a=1}^n h_{a,11} \phi_{11}(\kappa) + x_{0,12}^* \sum_{a=1}^n h_{a,12} \phi_{12}(\kappa))^2}{4\kappa} \quad (71)$$

$$x_{0,12}^* = 2 \left(2x_{0,11}^* \sum_{a=1}^n h_{a,11} \phi_{11}(\kappa) + x_{0,12}^* \sum_{a=1}^n h_{a,12} \phi_{12}(\kappa) \right) \times \frac{(x_{0,12}^* \sum_{a=1}^n h_{a,12} \phi_{12}(\kappa) + 2x_{0,22}^* \sum_{a=1}^n h_{a,22} \phi_{22}(\kappa))}{4\kappa} \quad (72)$$

$$x_{0,22}^* = \frac{(2x_{0,22}^* \sum_{a=1}^n h_{a,22} \phi_{22}(\kappa) + x_{0,12}^* \sum_{a=1}^n h_{a,12} \phi_{12}(\kappa))^2}{4\kappa}. \quad (73)$$

The equilibrium state is found by solving the five equations, (69), (70), (71), (72), and (73), in the four unknowns, κ , $x_{0,11}^*$, $x_{0,12}^*$ and $x_{0,22}^*$. Equation (69) is equal to the sum of Eqs. (71), (72), and (73), so there are actually four equations in four unknowns. If each genotype in isolation has the same equilibrium value κ , then equations like (18) apply and we obtain

$$\sum_{a=1}^n h_{a,11} \phi_{11}(\kappa) = \sum_{a=1}^n h_{a,12} \phi_{12}(\kappa) = \sum_{a=1}^n h_{a,22} \phi_{22}(\kappa) = 1, \quad (74)$$

so that Eq. (70) becomes an identity. If (74) holds, then $x_{0,11}^*$, $x_{0,12}^*$, and $x_{0,22}^*$ are subject to the three equations (71), (72), and (73) which reduce to the two relationships

$$x_{0,11}^* = (\sqrt{\kappa} - \sqrt{x_{0,22}^*})^2, \quad (75)$$

$$x_{0,12}^* = 2 \sqrt{x_{0,11}^* x_{0,22}^*} = \kappa - x_{0,11}^* - x_{0,22}^*. \quad (76)$$

Equations (75) and (76) define a curve lying on the plane $x_{0,11}^* + x_{0,12}^* + x_{0,22}^* = \kappa$. That is, genetic conditions reduce the indeterminacy associated with (54) from a plane (for $m = 3$) to a curve on that plane. However, in contrast to the m species model with $\theta_{jk} = 1$ for all j, k , and $x_{0,11}^s \neq x_{0,12}^s \neq x_{0,22}^s$, it is still possible to have a single equilibrium state under panmixis at which all the genotypes coexist.

In Appendix 2 it is shown that the existence condition for a coexistence equilibrium state is

$$\beta_{12} = 1 \pm \sqrt{(\beta_{11} - 1)(\beta_{22} - 1)}, \quad (77)$$

where

$$\beta_q = \sum_{a=1}^n h_{a,q} \phi_q(\kappa). \quad (78)$$

Equation (77) can only have real roots if $(\beta_{11} - 1)$ and $(\beta_{22} - 1)$ have the same sign. Because of (70) we also need to satisfy

$$\beta_{12} = 1 + \sqrt{(\beta_{11} - 1)(\beta_{22} - 1)} \quad 0 < \beta_{11}, \beta_{22} < 1 \quad (79)$$

and

$$\beta_{12} = 1 - \sqrt{(\beta_{11} - 1)(\beta_{22} - 1)} \quad \beta_{11}, \beta_{22} > 1. \quad (80)$$

Note from (20) (using (64) and (78)) that $\beta_{11}(x_{0,11}^s) = 1$, $\beta_{12}(x_{0,12}^s) = 1$, and $\beta_{22}(x_{0,22}^s) = 1$. Since a population can never consist solely of heterozygous genotypes, $x_{0,12}^s$ is a purely mathematical artefact which satisfies $\beta_{12}(x_{0,12}^s) = 1$. From (79) and (80),

$$\kappa > x_{0,11}^s, x_{0,22}^s \quad \text{whenever} \quad x_{0,12}^s > x_{0,11}^s, x_{0,22}^s \quad (81)$$

$$\kappa < x_{0,11}^s, x_{0,22}^s \quad \text{whenever} \quad x_{0,12}^s < x_{0,11}^s, x_{0,22}^s, \quad (82)$$

which is a result already reported by Charlesworth (1980) for a general age structured model. Therefore, in terms of boundary equilibria, the heterozygous genotype must be either underdominant or overdominant for a coexistence equilibrium to occur.

Genetic Coexistence

The linearized population matrix for the genetic model is derived in Appendix 3 to produce sufficient conditions for the local stability of the polymorphic equilibrium state (see Appendix 3 for these conditions). Here we use the linearized population matrix to examine the stability of homozygous genotype equilibria in the presence of small amounts of the other gene.

From Appendix 3, also applying the approach in Appendix 1, the general form of all eigenvectors of the transformed, linearized population matrix \mathbf{M} can be written as

$$\mathbf{x} = \left(1, \frac{1}{\lambda}, \frac{1}{\lambda^2}, \dots, \frac{1}{\lambda^{n-1}}; b, \frac{b}{\lambda}, \frac{b}{\lambda^2}, \dots, \frac{b}{\lambda^{n-1}}; c, \frac{c}{\lambda}, \frac{c}{\lambda^2}, \dots, \frac{c}{\lambda^{n-1}} \right). \quad (83)$$

The spectral equation $\mathbf{M}\mathbf{x} = \lambda\mathbf{x}$ produces three nontrivial equations (cf. Eq. (140) of Appendix 1). Recalling Identity (68), these are

$$\begin{aligned} & \sum_{a=1}^n \lambda^{-a} h_{a,11} \left[\left(1 - \frac{x_{0,22}^*}{\kappa} \right) \phi_{11}(\kappa) + x_{0,11}^* \phi'_{11}(\kappa) \right] \\ & + \sum_{a=1}^n b \lambda^{-a} h_{a,12} \left[\frac{1}{2} \frac{x_{0,12}^*}{\kappa} \phi_{11}(\kappa) + x_{0,11}^* \phi'_{11}(\kappa) \right] \\ & + \sum_{a=1}^n c \lambda^{-a} h_{a,22} \left[- \frac{x_{0,11}^*}{\kappa} \phi_{11}(\kappa) + x_{0,11}^* \phi'_{11}(\kappa) \right] = 1, \quad (84) \end{aligned}$$

$$\begin{aligned} & \sum_{a=1}^n \lambda^{-a} h_{a,11} \left[2 \frac{x_{0,22}^*}{\kappa} \phi_{12}(\kappa) + x_{0,12}^* \phi'_{12}(\kappa) \right] \\ & + \sum_{a=1}^n b \lambda^{-a} h_{a,12} \left[\left(1 - \frac{x_{0,12}^*}{\kappa} \right) \phi_{12}(\kappa) + x_{0,12}^* \phi'_{12}(\kappa) \right] \\ & + \sum_{a=1}^n c \lambda^{-a} h_{a,22} \left[2 \frac{x_{0,11}^*}{\kappa} \phi_{12}(\kappa) + x_{0,12}^* \phi'_{12}(\kappa) \right] = b, \end{aligned} \quad (85)$$

and

$$\begin{aligned} & \sum_{a=1}^n \lambda^{-a} h_{a,11} \left[- \frac{x_{0,22}^*}{\kappa} \phi_{22}(\kappa) + x_{0,22}^* \phi'_{22}(\kappa) \right] \\ & + \sum_{a=1}^n b \lambda^{-a} h_{a,12} \left[\frac{1}{2} \frac{x_{0,12}^*}{\kappa} \phi_{22}(\kappa) + x_{0,22}^* \phi'_{22}(\kappa) \right] \\ & + \sum_{a=1}^n c \lambda^{-a} h_{a,22} \left[\left(1 - \frac{x_{0,11}^*}{\kappa} \right) \phi_{22}(\kappa) + x_{0,22}^* \phi'_{22}(\kappa) \right] = c. \end{aligned} \quad (86)$$

In principle one can proceed to derive the characteristic equation using Eqs. (84)–(86) and then apply the Schur–Cohn criteria (see Appendix 1) to derive necessary and sufficient stability conditions. The derivation, however, is even more cumbersome than for the competing species model (see Appendix 1). Thus we only present stability conditions for the more manageable boundary equilibrium cases.

Consider the stability state of the boundary equilibrium solution $x_{0,11}^* = x_{0,11}^s$, $x_{0,12}^* = 0$, $x_{0,22}^* = 0$. Note from Identity (68) that now $\kappa = x_{0,11}^s$. Equations (84)–(86) reduce to

$$\begin{aligned} & \sum_{a=1}^n \lambda^{-a} h_{a,11} [\phi_{11}(x_{0,11}^s) + x_{0,11}^s \phi'_{11}(x_{0,11}^s)] + \sum_{a=1}^n b \lambda^{-a} h_{a,12} x_{0,11}^s \phi'_{11}(x_{0,11}^s) \\ & + \sum_{a=1}^n c \lambda^{-a} h_{a,22} [-\phi_{11}(x_{0,11}^s) + x_{0,11}^s \phi'_{11}(x_{0,11}^s)] = 1, \end{aligned} \quad (87)$$

$$\sum_{a=1}^n b \lambda^{-a} h_{a,12} \phi_{12}(x_{0,11}^s) + \sum_{a=1}^n c \lambda^{-a} h_{a,22} 2\phi_{12}(x_{0,11}^s) = b, \quad (88)$$

and

$$c = 0. \quad (89)$$

Since, from (89), $c = 0$, Eq. (88) reduces to

$$\sum_{a=1}^n \lambda^{-a} h_{a,12} \phi_{12}(x_{0,11}^s) = 1. \quad (90)$$

Equation (90) has the basic Perron form and so the dominant eigenvalue, λ_0 , is, by the Perron Frobenius Theorem, real and positive, and

$$\lambda_0 > 1 \quad \text{if} \quad \sum_{a=1}^n b_{a,12} l_{a,12} \phi_{12}(x_{0,11}^s) > 1$$

or

$$\lambda_0 < 1 \quad \text{if} \quad \sum_{a=1}^n b_{a,12} l_{a,12} \phi_{12}(x_{0,11}^s) < 1. \quad (91)$$

Together with the fact that ϕ_{12} is a decreasing function of its argument, and by definition $\sum_{a=1}^n h_{a,12} \phi_{12}(x_{0,12}^s) = 1$, it can be verified by the same reasoning that was applied to the two species competition model that

$$\lambda_0 > 1 \quad \text{if} \quad x_{0,12}^s > x_{0,11}^s$$

and

$$\lambda_0 < 1 \quad \text{if} \quad x_{0,12}^s < x_{0,11}^s. \quad (92)$$

Similarly at the other boundary equilibrium state,

$$\lambda_0 > 1 \quad \text{if} \quad x_{0,12}^s > x_{0,22}^s$$

and

$$\lambda_0 < 1 \quad \text{if} \quad x_{0,12}^s < x_{0,22}^s. \quad (93)$$

Both boundary equilibria are therefore unstable when the heterozygous genotype is overdominant. However, using a simple example, W. M. Getz and V. Kaitala (unpublished manuscript) have demonstrated that the population may nevertheless be reduced to one genotype that oscillates around an unstable equilibrium. That is, even though the heterozygous genotype is overdominant, oscillations can occur on the axis. *To rule out this possibility, the additional condition that isolated genotypes reach a stable equilibrium state must be satisfied* (Charlesworth, 1980, p. 172).

We can use a phase representation to clarify the local stability results. Substitution of the expressions for $x_{0,11}(t-a)$, $x_{0,12}(t-a)$, and $x_{0,22}(t-a)$ from Eqs. (59)–(61) into Eqs. (57) and (58) produces the two equilibrium relationships ($A_1(t-a) = A_1$ and $A_2(t-a) = A_2$)

$$A_1 \left(1 - \sum_{a=1}^n h_{a,11} \phi_{11} \left(\frac{A_1 + A_2}{2} \right) \right) = A_2 \left(1 - \sum_{a=1}^n h_{a,12} \phi_{12} \left(\frac{A_1 + A_2}{2} \right) \right) \quad (94)$$

$$A_2 \left(1 - \sum_{a=1}^n h_{a,22} \phi_{22} \left(\frac{A_1 + A_2}{2} \right) \right) = A_1 \left(1 - \sum_{a=1}^n h_{a,12} \phi_{12} \left(\frac{A_1 + A_2}{2} \right) \right). \quad (95)$$

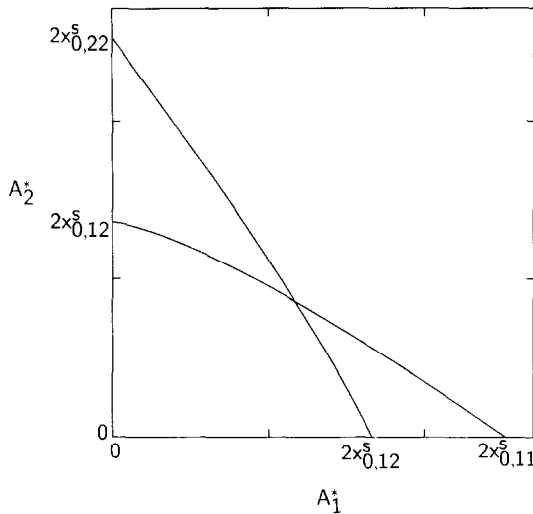


FIG. 3. Plot of the isocline lines given by (94) and (95) for the case when the heterozygous genotype is underdominant.

Equations (94) and (95) define two curved isoclines in the $A_1(t)-A_2(t)$ coordinate plane (see Fig. 3). Equation (95) has abscissa and ordinate axis intercepts of $2x_{0,11}^s$ and $2x_{0,12}^s$, respectively, and Eq. (94) has abscissa and ordinate axis intercepts of $2x_{0,12}^s$ and $2x_{0,22}^s$. If the isoclines intersect in the positive quadrant of the coordinate plane then there is a biologically meaningful polymorphic equilibrium state. The configuration of the phase plane diagram is very similar to that for two competing species. The condition for persistent genetic polymorphisms obtained here is geometrically analogous to the conditions obtained earlier for coexistence in the model of competing species in terms of the location of isocline intercepts (subject to stability of the axis equilibria), except that now the isoclines are curved rather than straight.

SIMPLE EXAMPLES AND SIMULATIONS

To illustrate the results obtained so far, we consider Deriso's (1980) simplification of the age-structured model used here.

In what follows, s is adult survivorship, τ is age at maturity, l_τ is survivorship from birth to first maturity, and ρ is the Brody coefficient in

$$b_{a+1} = b_a + \rho(b_a - b_{a-1}). \tag{96}$$

When, as in Deriso's model, $b_{\tau-1} = 0$, then from (96) the terms $b_a l_a$ are given by

$$\begin{aligned} b_a l_a &= 0 & a < \tau \\ b_a l_a &= r s^{a-\tau} \left(\sum_{k=0}^{a-\tau} \rho^k \right) & a \geq \tau, \end{aligned} \quad (97)$$

where $r = b_\tau l_\tau$. The dynamics of $x_0(t)$ are given by the delay-difference equation

$$x_0(t+1) = (1 + \rho) s x_0(t) - \rho s^2 x_0(t-1) + r x_0(t-\tau+1) \phi(x_0(t-\tau+1)). \quad (98)$$

If adult fecundity-at-age is proportional to adult body mass-at-age, $b_a = \eta w_a$, then, since $x_0(t) = \sum_{a=\tau}^{\infty} b_a x_a(t) = \eta \sum_{a=\tau}^{\infty} w_a x_a(t) = \eta B(t)$, the dynamics of population biomass $B(t)$ are given by

$$B(t+1) = (1 + \rho) s B(t) - \rho s^2 B(t-1) + r B(t-\tau+1) \phi(\eta B(t-\tau+1)). \quad (99)$$

From (97) note that

$$\sum_{a=1}^{\infty} b_a l_a = \frac{r}{(1-s)(1-\rho s)}. \quad (100)$$

We introduce the following form for ϕ (from Deriso, 1978; Schnute, 1985):

$$\phi(x) = (1 - \gamma x)^{1/\gamma}. \quad (101)$$

Figures 4-6 illustrate the local stability results which were obtained for the two species competition model using the Deriso model as an example. The value of γ used is sufficiently close to -1 to guarantee the stability of axis equilibria (see Bergh and Getz, 1988), so that the coexistence conditions based on the local stability analyses in this paper are valid. Figure 4 is an example of the system dynamics when the coexistence equilibrium is an attractor. In Figure 5 the coexistence equilibrium is unstable and both of the boundary equilibria are stable, attracting solutions depending on initial conditions. Finally, Figure 6 shows an example where there is no biologically meaningful coexistence equilibrium point and the system evolves towards the boundary equilibrium of the dominant species.

We consider now the case for which the θ_{jk} are all equal to 1, and in which panmictic breeding conditions prevail in a one locus two allele model. Let

$$a_{11} = \frac{r_{11}}{(1-s_{11})(1-\rho_{11}s_{11})} \quad (102)$$

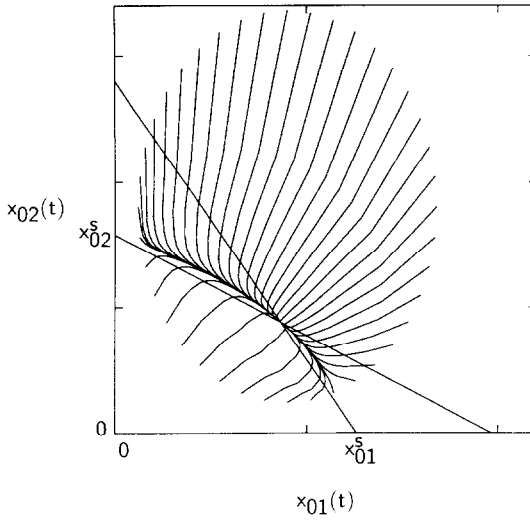


FIG. 4. Dynamics of the two species interaction model described in Table I, plotted in the $x_{0,1}(t)-x_{0,2}(t)$ plane and for various initial states lying on a circle. The straight lines are the isoclines defined by Eqs. (32) and (33). The coexistence equilibrium lies in Triangle I and is therefore an attractor.

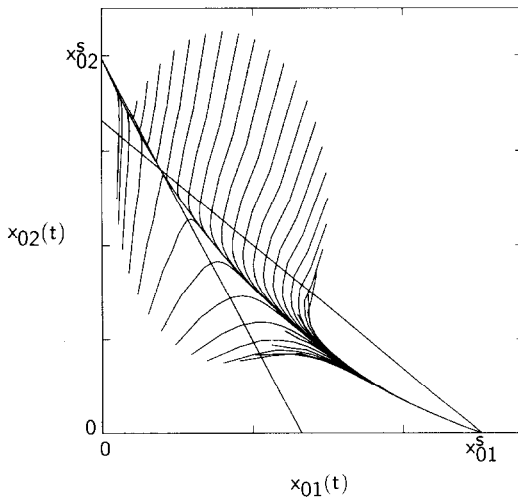


FIG. 5. The same model used for Fig. 4, but the coexistence equilibrium now lies in Triangle II and is therefore locally unstable. Depending on initial conditions, the system may evolve towards either of the isolation equilibria.

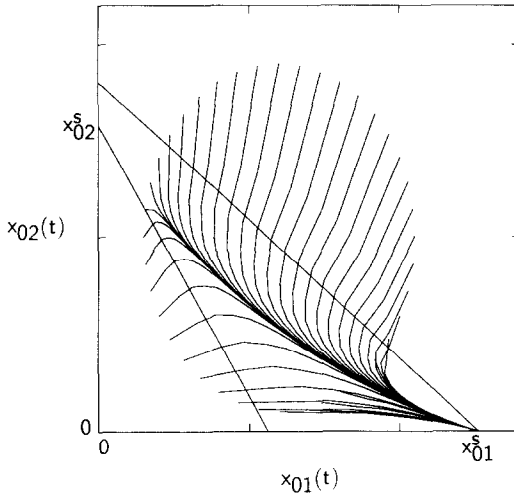


FIG. 6. The same model used for Fig. 4, but for which there is no coexistence equilibrium state and the isolation equilibrium state of the dominant species is an attractor (see text for a definition of the dominant species).

and similarly for 12 and 22 (that is $a_q = \sum_{a=1}^n b_{aq} l_{aq}$ for $q = 11, 12, 22$ as defined in Appendix 3).

The dynamics of Eq. (98) under panmixis follow analogously from the general model, (62)–(67), but the details are omitted here.

The conditions under which three genotypes can coexist at equilibrium for the case $\phi_{11} = \phi_{12} = \phi_{22} = \phi$ are therefore, from Eqs. (79) and (80),

$$[a_{12}\phi(\kappa) - 1]^2 = [a_{11}\phi(\kappa) - 1][a_{22}\phi(\kappa) - 1] \tag{103}$$

TABLE I

Parameters Used for Figs. 4, 5, and 6 in the Two Species Interaction Model Described by Eq. (14) with the Special Assumptions of the Deriso Model ((96), (97), and (99)) with ϕ Given by (101) and $\tau = 2$ in All Cases

Figure	Species j	θ_{jk}	ρ	s	γ	r
4	1	1.4	0.11	0.6	-1.11	5
	2	0.4	0.12	0.4	-1.01	5
5	1	1.9	0.11	0.6	-1.01	5
	2	1.2	0.14	0.4	-1.01	5
6	1	1.4	0.11	0.6	-1.01	5
	2	1.4	0.12	0.4	-1.01	5

which yields two solutions for κ , either $\kappa = 0$ or

$$\kappa = \phi^{-1} \left[\frac{2a_{12} - a_{11} - a_{22}}{a_{12}^2 - a_{11}a_{22}} \right]. \tag{104}$$

Figure 7 shows attraction towards the coexistence equilibrium state when the heterozygous genotype is overdominant. When the heterozygote is underdominant, then both of the homozygous boundary equilibria can be attractors, depending on initial conditions, as illustrated in Fig. 8. If there is no equilibrium, then (see Fig. 9) the system evolves towards A_1 if $x_{0,11}^s > x_{0,22}^s$, and towards A_2 if $x_{0,22}^s > x_{0,11}^s$. If Condition (74) holds, Fig. 10 illustrates that all the points on the coincident isoclines given by (75) and (76) are attractors. If the recruitment functions for constituent genotypes are overcompensatory, then there may be sustained oscillations if the coexistence equilibrium loses stability via a complex root (Fig. 11).

Harvesting

An important application of the ideas in this paper is reported by Desharnais *et al.* (1985), using the continuous time analog of our discrete time age-structured model. Desharnais *et al.* (1985) obtained conditions for the maintenance of genetic polymorphisms in a population subjected to

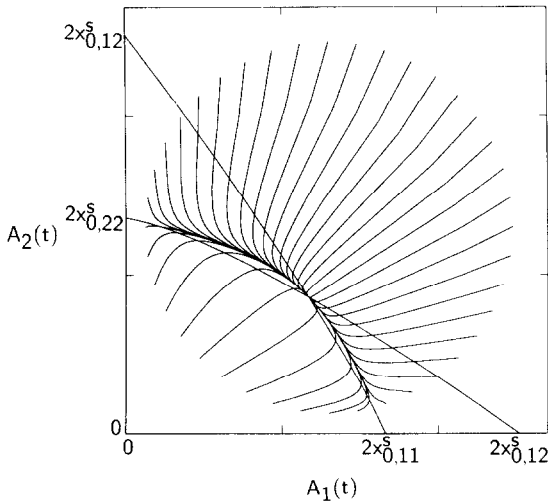


FIG. 7. Dynamics plotted in the $A_1(t)$ - $A_2(t)$ plane of a panmictic breeding model in which life history strategy is determined by two alleles at one locus, for genotype specific parameters given in Table II. Initial conditions lie on a circular set as indicated. The two curved lines are isoclines (see Eqs. (94) and (95)). The heterozygous genotype is overdominant and therefore, as predicted by existing results for scalar models, the coexistence equilibrium state is stable (i.e., attracting).

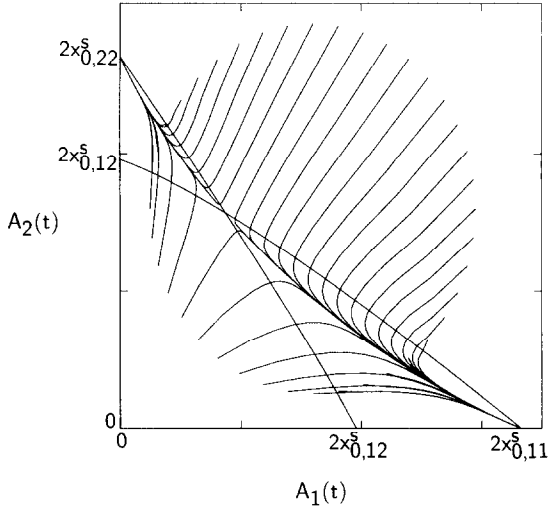


FIG. 8. The same model as used in Fig. 7, but now the heterozygous genotype is underdominant, so the coexistence state is unstable. Depending on initial conditions the system evolves towards either of the homozygous isolation equilibrium states.

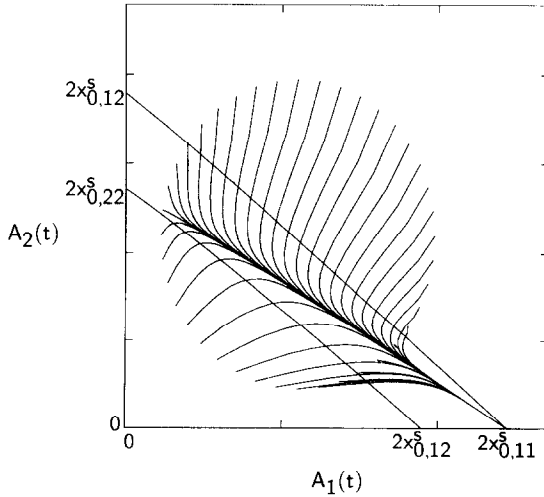


FIG. 9. Same model as used in Fig. 7, but now the heterozygous genotype is neither over- nor underdominant so there is no coexistence equilibrium state. The system evolves towards the homozygous a_1 isolation equilibrium state if $x_{0,11}^s > x_{0,22}^s$ and towards the homozygous a_2 isolation equilibrium state if $x_{0,22}^s > x_{0,11}^s$.

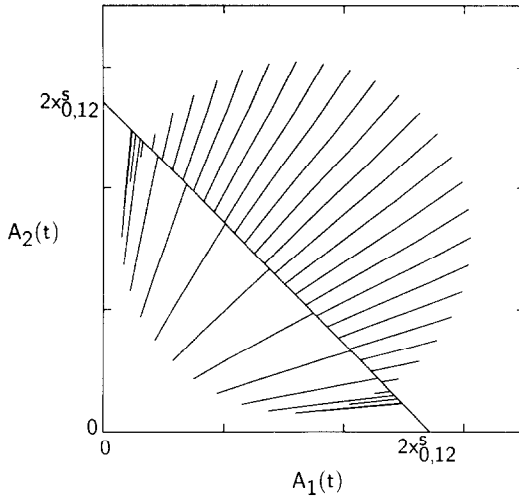


FIG. 10. Same model as used in Fig. 7, but now the conditions described by (74), (75), and (76) hold. The system is attracted onto one of an infinite number of equilibria lying on the line given by the coincidence of the isoclines shown in Fig. 3.

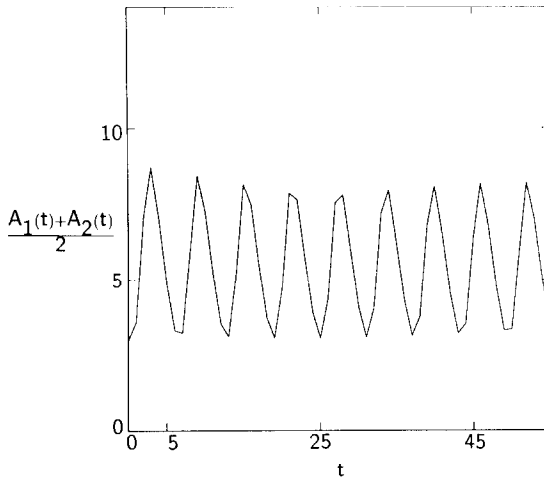


FIG. 11. Sustained oscillations about the mixed genotype equilibrium point in the panmictic breeding model when the heterozygous genotype is overdominant. The plot shows the progress of the total number of zygotes $(A_1(t) + A_2(t))/2$ versus time t .

TABLE II
Parameters Used for Figs. 7-11 in the Three Genotype Model ((65), (66), and (67))
with the Special Assumptions of the Deriso Model ((96), (97), and (99)) with
 ϕ Given by (101) and $\tau = 2$ in All Cases

Figure	Genotype	ρ	s	γ	r
7	11	0.1122	0.6	-1.05	5
	12	0.1222	0.5	-1.05	5
	22	1.2046	0.4	-1.05	5
8	11	0.1122	0.6	-1.05	5
	12	0.0103	0.5	-1.05	5
	22	1.2046	0.4	-1.05	5
9	11	0.1122	0.6	-1.05	5
	12	0.7564	0.5	-1.05	5
	22	1.5856	0.4	-1.05	5
10	11	0.1122	0.6	-1.05	5
	12	0.5077	0.5	-1.05	5
	22	0.9455	0.4	-1.05	5
11	11	0.1122	0.6	-0.0015	29
	12	1.1222	0.5	-0.0015	29
	22	1.2046	0.4	-0.0015	29

exploitation, and expressed these conditions in terms of a minimum legal fish size and an instantaneous fishing mortality.

We now pursue similar lines to those reported by Desharnais *et al.* to understand the effects of harvesting.

Fishing causes a reduction in the survivorship of those age classes which are fished. The work reported here has identified boundary equilibria as being important for understanding coexistence in genetically interacting population systems. If different genotypes are caught at different rates, then the various boundary equilibria may be reduced to varying extents. Let f_{aj} be the proportion of individuals aged a that survive fishing. The boundary equilibria under fishing, $x_{0,j}^f$, are (cf. Eq. (20))

$$x_{0j}^f = \phi_j^{-1} \left(\frac{1}{\sum_{a=1}^n b_{aj} l_{aj}^f} \right), \quad (105)$$

where $l_{aj}^f = s_{0j} f_{0j} \times s_{1j} f_{1j} \times \dots \times s_{(a-1)j} f_{(a-1)j}$.

Consider the two species competition model first. The isocline slopes of the phase portrait (see Figs. 1 and 2) are intrinsic properties of the system which do not change when fishing occurs. However, the abscissa and ordinate axis intercepts, $x_{0,1}^f$ and $x_{0,2}^f$, do change. Clearly, if

$$\frac{x_{0,1}^f}{x_{0,2}^f} = \frac{x_{0,1}^s}{x_{0,2}^s}, \quad (106)$$

then the relative proportions of species 1 versus species 2 remain unchanged by fishing; otherwise there will be a change in relative abundance (but *total* abundance decreases with fishing). If under fishing

$$\frac{x_{0,1}^f}{x_{0,2}^f} \neq \frac{x_{0,1}^s}{x_{0,2}^s}, \quad (107)$$

then coexistence requires that

$$\frac{x_{0,2}^f}{\theta_{21}} < x_{0,1}^f \quad (108)$$

$$\frac{x_{0,1}^f}{\theta_{12}} > x_{0,2}^f. \quad (109)$$

If these conditions are not met then species 1 or 2 could very well disappear from the population. The stronger statement of certain extinction cannot be made because of our previously stated reservations concerning the limited local nature of the stability analysis.

Consider the genetic model with an overdominant heterozygous genotype (i.e., genetic coexistence occurs). Fishing may cause the heterozygous genotype to become intermediate,

$$x_{0,11}^f < x_{0,12}^f < x_{0,22}^f, \quad (110)$$

or underdominant. In both cases the inception of fishing starts a progression towards homozygosity. For example, in Fig. 12, the unexploited coexistence equilibrium is stable, since the heterozygous genotype is overdominant (see trajectory i). Under fishing the heterozygous genotype becomes intermediate, hence there is no exploited coexistence equilibrium, and a movement towards homozygosity occurs (see trajectory ii).

Consider the alternative situation in which the unexploited population is homozygous. We illustrate how a previously rare gene can become prevalent under fishing. Figure 13 shows a situation in which the unexploited heterozygous genotype is underdominant. For a given initial state, the system thus becomes homozygous in one of the genotypes (see trajectory i). However, if a mutation of a_2 to a_1 (in Fig. 13 the a_2 allele is dominant) maintains a_1 at a low density, and the heterozygous genotype is overdominant under fishing, then fishing will cause trajectory ii to move towards the exploited coexistence state (our simulation shows that this is stable).

The last possibility treated here is that the unexploited boundary equilibria are approximately equal, either in a competition model such as (15) or in a genetic model such as (65)–(67), and that the conditions for stable

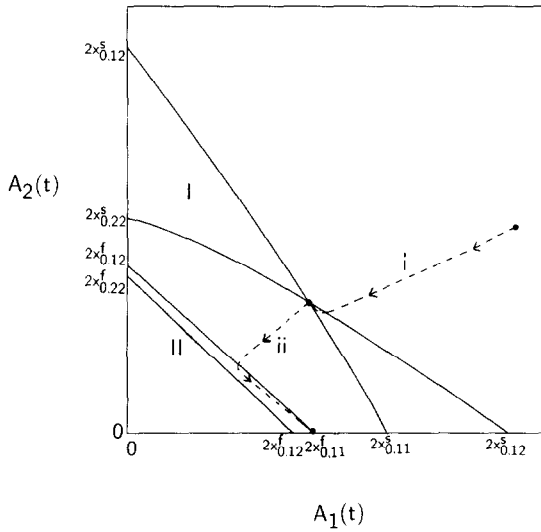


FIG. 12. Dynamics of the genetic model for parameter values given in Table III. In the $A_1(t)-A_2(t)$ plane, trajectory i shows the unexploited system moving to a stable coexistence equilibrium (overdominant heterozygous genotype). The unexploited isocline pair is denoted by I. The resultant trajectory under fishing is ii, and the new isoclines, II, indicate that there is no coexistence equilibrium. Hence the system evolves towards the dominant homozygous equilibrium state.

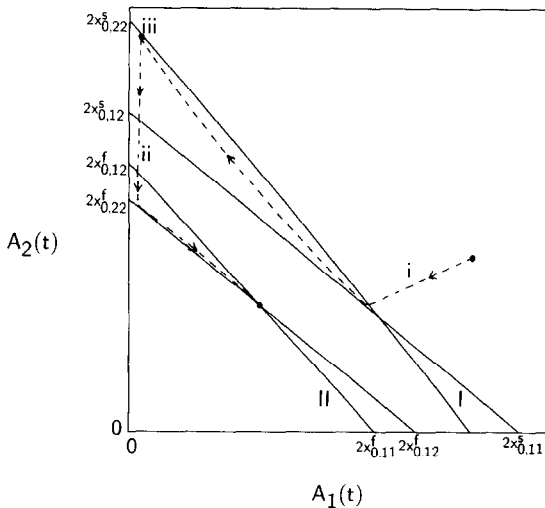


FIG. 13. Dynamics for the genetic model (see Table III). For the unexploited system, the heterozygous genotype is underdominant and the system evolves to a homozygous state (trajectory i). If the other gene existed in a rare state via mutations, this would keep the system in state iii. Under fishing the heterozygous genotype might then become overdominant, with isoclines given by II. The coexistence equilibrium is now stable, and the system moves along trajectory ii to the new coexistence equilibrium.

TABLE III

Parameters Used in Figs. 12 and 13 in the Genetic Model ((65), (66), and (67)) with the Special Assumptions of the Deriso Model ((96), (97), and (99)) with ϕ Given by (101) and $\tau = 2$ in All Cases (Column sf is the Annual Adult Survivorship under Exploitation)

Figure	Genotype (q)	ρ	s	γ	r	sf	x_{0q}^s	x_{0q}^f
12	11	1.2046	0.4	-1.05	5	0.32	16.65	11.95
	12	0.1222	0.5	-1.05	5	0.3	24.42	10.6
	22	0.1122	0.6	-1.05	5	0.48	13.58	9.92
13	11	0.1122	0.6	-1.05	5	0.36	13.58	7.66
	12	0.1346	0.5	-1.05	5	0.425	10.54	8.86
	22	0.7728	0.4	-1.05	5	0.24	12.05	7.59

coexistence are met in the unexploited state. Further, a very common situation is that net mesh size or hook size induces a strong dependence of catchability on body size parameters and that body mass is proportional to fecundity. Due to the resultant catchability differentials, fishing will cause differences in the x_{0j}^f . This enhances the chances of losing the coexistence equilibrium in either the competing species or panmictic model. For example, for two competing species, as fishing effort increases, the coexistence equilibrium progresses towards a greater proportion of the small body size species. This eventually leads to the loss of the coexistence equilibrium and complete dominance by the small body size type. For the genetic model, preferential harvesting of larger individuals can cause a loss of the coexistence equilibrium state or loss of the stability of that equilibrium, with subsequent dominance by the small body size phenotype.

In Appendix 4, we consider Model (98) with $\rho = 0$. If there is a set of genotypes which coexist at equilibrium with exactly equal boundary equilibria, then it follows that under this constraint the smaller body size phenotype always has a smaller MSY (Maximum Sustainable Yield). Furthermore, if catchability increases sufficiently with increasing adult body size, then it turns out that the boundary equilibrium size of the phenotype with the largest adult body size (largest MSY in isolation, smallest adult survivorship) is reduced the most for a given level of applied fishing effort.

CONCLUSIONS

We have developed a simple rule for the coexistence of a pair of competing species in a biologically important demographic model which is valid when each species reaches a stable equilibrium state in the absence of

the other species, i.e., the axis equilibria are stable. A similar rule applies for the genetic analogue of this model; i.e., genotypes will coexist if the heterozygous genotype is overdominant, as shown by Charlesworth (1971, 1980), subject to stability of the axis equilibria.

The genetic model presented here thus indicates that if heterozygosity occurs, then it implies the existence of a coexistence equilibrium that is larger (greater abundance) than either of the homozygous genotypes in isolation, when the homozygous genotypes reach a stable equilibrium state in the absence of other genes. Thus the loss of the coexistence equilibrium point leads not only to loss of genetic diversity (with all the related problems—see Ryman and Utter, 1986), but to declines in abundance as well.

We have demonstrated that the consequences of harvesting depend on the initial state of the system and on the impact that fishing makes on the various boundary equilibria. Some scenarios have been outlined here. For example, if genetic diversity is initially present, then it may be lost soon after fishing starts. Another possibility is that the unexploited stock is largely genetically homogeneous, but contains inferior genotypes maintained at low levels by mutation rates. Then fishing could reduce the fitness (i.e., boundary equilibrium state) of the dominant genotypes in the unexploited population so that the previously inferior genotypes rise either to complete dominance or to a state of coexistence with the previously dominant genes.

There may be many situations in which it is valid to argue that coexistence requires approximate equality between the boundary equilibria of competing species or genotypes. We investigated the implications of this constraint using a simple demographic system with a general specification of the recruitment function. If, in addition, catchabilities increase strongly with body size and fecundity is proportional to body size, then our study suggests that fishing causes a relative (to other species/genotypes) decrease in the boundary equilibrium size and hence actual abundance of the species/genotype which in isolation would produce the largest maximum sustainable yield.

APPENDIX 1: STABILITY OF THE EQUILIBRIUM STATE FOR m COMPETING SPECIES

From Eqs. (1) and (4) it follows that Eq. (14) can be rewritten as

$$x_{1j}(t+1) = l_{1j} \sum_{a=1}^n b_{aj} x_{aj}(t) \phi_j \left(\sum_{p=1}^m \theta_{jp} \sum_{a=1}^n b_{ap} x_{ap}(t) \right). \quad (111)$$

From (18) and (20) it follows that

$$\sum_{p=1}^m \theta_{jp} \sum_{a=1}^n b_{ap} x_{ap}^* = x_{0j}^s. \tag{112}$$

Define $\mathbf{z}(t) = (\mathbf{x}_1(t) - \mathbf{x}_1^*, \mathbf{x}_2(t) - \mathbf{x}_2^*, \dots, \mathbf{x}_m(t) - \mathbf{x}_m^*)'$, where $\mathbf{x}_j(t) - \mathbf{x}_j^* = x_{0j}(t) - x_{0j}^*, x_{1j}(t) - x_{1j}^*, \dots, x_{mj}(t) - x_{mj}^*$ and let

$$\mathbf{z}(t+1) = \mathbf{A}\mathbf{z}(t) \tag{113}$$

be the linearization of Eq. (15) around $(\mathbf{x}_1^*, \mathbf{x}_2^*, \dots, \mathbf{x}_m^*)'$, that is, \mathbf{A} is the Jacobian matrix. The matrix \mathbf{A} can be expressed in terms of sub-matrices which each deal only with interactions arising from any two species. The expanded matrix notation for this linearized system is

$$\begin{pmatrix} \mathbf{z}_1(t+1) \\ \mathbf{z}_2(t+1) \\ \vdots \\ \mathbf{z}_m(t+1) \end{pmatrix} = \begin{pmatrix} \mathbf{A}_{11} & \mathbf{A}_{12} & \cdots & \mathbf{A}_{1m} \\ \mathbf{A}_{21} & \mathbf{A}_{22} & \cdots & \mathbf{A}_{2m} \\ \vdots & \vdots & \ddots & \vdots \\ \mathbf{A}_{m1} & \mathbf{A}_{m2} & \cdots & \mathbf{A}_{mm} \end{pmatrix} \begin{pmatrix} \mathbf{z}_1(t) \\ \mathbf{z}_2(t) \\ \vdots \\ \mathbf{z}_m(t) \end{pmatrix}, \tag{114}$$

where $\mathbf{z}_i = (z_{1i}, \dots, z_{ni})'$. It is easily shown (taking appropriate derivatives) that

$$\mathbf{A}_{jj} = \begin{pmatrix} l_{1j} f_{jj}(1) & l_{1j} f_{jj}(2) & \cdots & l_{1j} f_{jj}(n) \\ s_{1j} & 0 & \cdots & 0 \\ 0 & s_{2j} & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & \cdots & s_{n-1,j} & 0 \end{pmatrix}, \tag{115}$$

where

$$f_{jj}(a) = b_{aj} \phi_j(x_{0j}^s) + b_{aj} x_{0j}^* \phi_j'(x_{0j}^s), \tag{116}$$

and for $j \neq k$,

$$\mathbf{A}_{jk} = \begin{pmatrix} l_{1j} f_{jk}(1) & l_{1j} f_{jk}(2) & \cdots & l_{1j} f_{jk}(n) \\ 0 & 0 & \cdots & 0 \\ 0 & 0 & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \cdots & 0 \end{pmatrix}, \tag{117}$$

where

$$f_{jk}(a) = b_{ak} \theta_{jk} x_{0j}^* \phi_j'(x_{0j}^s). \quad (118)$$

Let \mathbf{C} be a diagonal matrix made up of the diagonal sub-matrices $\mathbf{C}_1, \mathbf{C}_2, \dots, \mathbf{C}_m$;

$$\mathbf{C} = \begin{pmatrix} \mathbf{C}_1 & 0 & \dots & 0 & 0 \\ 0 & \mathbf{C}_2 & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & \dots & \mathbf{C}_{m-1} & 0 \\ 0 & 0 & \dots & 0 & \mathbf{C}_m \end{pmatrix}. \quad (119)$$

The transformation $\mathbf{M} = \mathbf{C}^{-1} \mathbf{A} \mathbf{C}$ gives

$$\mathbf{M} = \begin{pmatrix} \mathbf{C}_1^{-1} \mathbf{A}_{11} \mathbf{C}_1 & \mathbf{C}_1^{-1} \mathbf{A}_{12} \mathbf{C}_2 & \dots & \mathbf{C}_1^{-1} \mathbf{A}_{1m} \mathbf{C}_m \\ \mathbf{C}_2^{-1} \mathbf{A}_{21} \mathbf{C}_1 & \mathbf{C}_2^{-1} \mathbf{A}_{22} \mathbf{C}_2 & \dots & \mathbf{C}_2^{-1} \mathbf{A}_{2m} \mathbf{C}_m \\ \vdots & \vdots & \vdots & \vdots \\ \mathbf{C}_m^{-1} \mathbf{A}_{m1} \mathbf{C}_1 & \mathbf{C}_m^{-1} \mathbf{A}_{m2} \mathbf{C}_2 & \dots & \mathbf{C}_m^{-1} \mathbf{A}_{mm} \mathbf{C}_m \end{pmatrix}. \quad (120)$$

It can then be verified that if \mathbf{C}_j is the diagonal matrix (recall that $l_{aj} = \prod_{r=0}^{a-1} s_{rj}$)

$$\mathbf{C}_j = \text{diag}[l_{1j}, l_{2j}, \dots, l_{nj}] \quad (121)$$

(i.e., $\mathbf{C}_j^{-1} = \text{diag}[1/l_{1j}, 1/l_{2j}, \dots, 1/l_{nj}]$), then the matrix \mathbf{M} can be expressed as

$$\mathbf{M} = \begin{pmatrix} \mathbf{M}_{11} & \mathbf{M}_{12} & \dots & \mathbf{M}_{1m} \\ \mathbf{M}_{21} & \mathbf{M}_{22} & \dots & \mathbf{M}_{2m} \\ \vdots & \vdots & \vdots & \vdots \\ \mathbf{M}_{m1} & \mathbf{M}_{m2} & \dots & \mathbf{M}_{mm} \end{pmatrix}, \quad (122)$$

where

$$\mathbf{M}_{jj} = \begin{pmatrix} l_{1j} f_{jj}(1) & l_{2j} f_{jj}(2) & \dots & l_{nj} f_{jj}(n) \\ 1 & 0 & \dots & 0 \\ 0 & 1 & \dots & 0 \\ \vdots & \vdots & \vdots & \vdots \\ 0 & \dots & 1 & 0 \end{pmatrix}, \quad (123)$$

and for $j \neq k$,

$$\mathbf{M}_{jk} = \begin{pmatrix} l_{1k} f_{jk}(1) & l_{2k} f_{jk}(2) & \cdots & l_{nk} f_{jk}(n) \\ 0 & 0 & \cdots & 0 \\ 0 & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & \cdots & 0 \end{pmatrix}. \tag{124}$$

Necessary and Sufficient Stability Conditions

We consider now the necessary and sufficient conditions for stability for the case $m=2$ using the modified Routh–Hurwitz conditions for discrete systems (i.e., the Schur–Cohn conditions; Jury, 1974). Explicitly, matrix \mathbf{M} has the form

$$\mathbf{M} = \left(\begin{array}{cccc|cccc} a_1 & a_2 & \cdots & a_n & \alpha_1 & \alpha_2 & \cdots & \alpha_n \\ 1 & 0 & \cdots & 0 & 0 & 0 & \cdots & 0 \\ 0 & 1 & \cdots & 0 & 0 & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & \cdots & 1 & 0 & 0 & 0 & \cdots & 0 \\ \hline \gamma_1 & \gamma_2 & \cdots & \gamma_n & g_1 & g_2 & \cdots & g_n \\ 0 & 0 & \cdots & 0 & 1 & 0 & \cdots & 0 \\ 0 & 0 & \cdots & 0 & 0 & 1 & \cdots & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & \cdots & 0 & 0 & \cdots & 1 & 0 \end{array} \right), \tag{125}$$

where

$$\begin{aligned} a_a &= l_{a1} b_{a1} [\phi_1(x_{01}^s) + x_{01}^* \phi_1'(x_{01}^s)] \\ \alpha_a &= l_{a2} b_{a2} [\theta_{12} x_{01}^* \phi_1'(x_{01}^s)] \\ \gamma_a &= l_{a1} b_{a1} [\theta_{21} x_{02}^* \phi_2'(x_{02}^s)] \end{aligned}$$

and

$$g_a = l_{a2} b_{a2} [\phi_2(x_{02}^s) + x_{02}^* \phi_2'(x_{02}^s)]. \tag{126}$$

From the definition of \mathbf{M} in (125), $\mathbf{M}\mathbf{x} = \lambda \mathbf{x}$ implies that the eigenvectors of \mathbf{M} have the general form

$$\mathbf{x} = \left(1, \frac{1}{\lambda}, \dots, \frac{1}{\lambda^{n-1}}; c, \frac{c}{\lambda}, \dots, \frac{c}{\lambda^{n-1}} \right). \tag{127}$$

Using (125) and (127), the spectral equation $\mathbf{M}\mathbf{x} = \lambda\mathbf{x}$ reduces to the two equations

$$\sum_{a=1}^n \lambda^{-a} a_a + c \sum_{a=1}^n \lambda^{-a} \alpha_a = 1 \quad (128)$$

and

$$\sum_{a=1}^n \lambda^{-a} \gamma_a + c \sum_{a=1}^n \lambda^{-a} g_a = c. \quad (129)$$

The characteristic equation is obtained by eliminating c between (128) and (129). The resultant polynomial has the form

$$f(\lambda) = \sum_{a=0}^{2n} q_a \lambda^{2n-a} = 0, \quad (130)$$

where

$$\begin{aligned} q_0 &= 1 \\ q_1 &= -(a_1 + g_1) \\ q_a &= -(a_a + g_a) - \sum_{k=1}^{a-1} (a_{a-k} g_k - \alpha_{a-k} \gamma_k) \quad a = 2, 3, \dots, n \\ q_a &= \sum_{r=a-n}^n (\alpha_r \gamma_{a-r} - a_r g_{a-r}) \quad a = n+1, n+2, \dots, 2n. \end{aligned} \quad (131)$$

The Schur-Cohn criteria can be applied in tabular form using the procedure described in Schwarz and Friedland (1965, p. 421). This involves constructing a matrix with first two rows,

$$\begin{pmatrix} q_0 & q_1 & \cdots & q_k \\ q_k & q_{k-1} & \cdots & q_0 \end{pmatrix}. \quad (132)$$

The next two rows,

$$\begin{pmatrix} v_0 & v_1 & \cdots & v_{k-1} \\ v_{k-1} & v_{k-2} & \cdots & v_0 \end{pmatrix}, \quad (133)$$

are given in terms of the preceding two rows by the determinant relationship

$$v_r = \begin{vmatrix} q_0 & q_{k-r} \\ q_k & q_r \end{vmatrix} \quad r = 0, 1, \dots, k-1.$$

Subsequent pairs of rows are related to the preceding pairs of rows in the same way. The process is continued until the last row contains three entries, $s_0, s_1,$ and s_2 . For $q_0 > 0$, the necessary and sufficient conditions for the eigenvalues of $f(\lambda)$ to lie within the unit circle (Schwarz and Friedland, 1965) are

$$\begin{aligned}
 f(1) &> 0 \\
 (-1)^{2n} f(-1) &> 0 \\
 q_0 &> |q_k| \\
 |v_0| &> |v_{k-1}| \\
 &\vdots \\
 |s_0| &> |s_2|.
 \end{aligned}
 \tag{134}$$

The first two conditions in (134) are

$$\begin{aligned}
 1 - (a_1 + g_1) - \sum_{a=2}^n \left[a_a + g_a - \sum_{k=1}^{a-1} (a_{a-k} g_k - \alpha_{a-k} \gamma_k) \right] \\
 + \sum_{l=n+1}^{2n} \left[\sum_{r=l-n}^n (\alpha_r \gamma_{l-r} - a_r g_{l-r}) \right] > 0
 \end{aligned}$$

and

$$\begin{aligned}
 1 + (a_1 + g_1) - \sum_{a=2}^n (-1)^{2n-a} \left[a_a + g_a - \sum_{k=1}^{a-1} (a_{a-k} g_k - \alpha_{a-k} \gamma_k) \right] \\
 + \sum_{l=n+1}^{2n} (-1)^{2n-l} \left[\sum_{r=l-n}^n (\alpha_r \gamma_{l-r} - a_{a-k} g_k) \right] > 0.
 \end{aligned}
 \tag{135}$$

In terms of the original model parameters, the next condition, $|q_k| < 1$, is given by

$$\begin{aligned}
 l_{n2} b_{n2} l_{n1} b_{n1} |[\theta_{12} x_{01}^* \phi_1'(x_{01}^s)][\theta_{21} x_{02}^* \phi_2'(x_{02}^s)] \\
 - [\phi_1(x_{01}^s) + x_{01}^* \phi_1'(x_{01}^s)][\phi_2(x_{02}^s) + x_{02}^* \phi_2'(x_{02}^s)]| < 1.
 \end{aligned}
 \tag{136}$$

Subsequent conditions involve equations with ever increasing levels of complexity. Although these conditions can be applied to a particular problem with known parameter values, they are cumbersome to implement in practice, and do not lead to succinct analytical results.

Sufficient Conditions

Sufficient stability conditions are given in terms of a corollary to the Gerschgorin Circle theorem (Minc and Marcus, 1968). This states that the

modulus of the dominant eigenvalue of \mathbf{M} is smaller than or equal to the largest row sum of the absolute values of the elements of \mathbf{M} . That is, if we define m_{ij} to be an element from the i th column and j th row of \mathbf{M} , then the eigenvalues $\lambda_j, j = 1, 2, \dots, mn$ of \mathbf{M} satisfy

$$|\lambda_j| \leq \max_{p=1, \dots, nm} \sum_{i=1}^{nm} |m_{ip}|, \quad j = 1, 2, \dots, mn. \tag{137}$$

It follows from (122)–(124) that $\sum_{i=1}^{nm} |m_{ip}| \leq 1$ for all $p = 1, 2, \dots, nm$, if

$$\sum_{a=1}^n l_{aj} b_{aj} |\phi_j(x_{0j}^s) + x_{0j}^* \phi_j'(x_{0j}^s)| + \sum_{\substack{k=1 \\ k \neq j}}^m \sum_{a=1}^n l_{ak} b_{ak} |x_{0j}^* \theta_{jk} \phi_j'(x_{0j}^s)| \leq 1 \tag{138}$$

$j = 1, 2, \dots, m.$

Thus, if (138) is satisfied then all the eigenvalues of \mathbf{M} , and hence \mathbf{A} in Eq. (113), lie within or on the unit circle. The stability of the equilibrium point \mathbf{x}_0 can only be guaranteed, however, if $|\lambda_j| < 1, j = 1, 2, \dots, mn$. We now show that \mathbf{x}_0 is stable whenever Inequality (138) is strictly less than 1.

First note, from the definition of \mathbf{M} in (122)–(124), that $\mathbf{M}\mathbf{x} = \lambda \mathbf{x}$ implies (cf. (127))

$$\mathbf{x} = \left(d_1, \frac{d_1}{\lambda}, \dots, \frac{d_1}{\lambda^{n-1}}, \dots, d_m, \frac{d_m}{\lambda}, \dots, \frac{d_m}{\lambda^{n-1}} \right), \tag{139}$$

where

$$d_j = \sum_{a=1}^n \frac{d_j}{\lambda^a} l_{aj} b_{aj} [\phi_j(x_{0j}^s) + x_{0j}^* \phi_j'(x_{0j}^s)] + \sum_{\substack{k=1 \\ k \neq j}}^m \sum_{a=1}^n \frac{d_k}{\lambda^a} l_{ak} b_{ak} x_{0j}^* \theta_{jk} \phi_j'(x_{0j}^s) \tag{140}$$

$j = 1, 2, \dots, m.$

Now we suppose that Inequality (138) is strictly less than 1, but that $|\lambda_0| = 1$, where λ_0 is the dominant eigenvalue. In this case it follows from (140) that

$$|d_j| \leq |d_j| \sum_{a=1}^n l_{aj} b_{aj} |\phi_j(x_{0j}^s) + x_{0j}^* \phi_j'(x_{0j}^s)| + \sum_{\substack{k=1 \\ k \neq j}}^m \sum_{a=1}^n |d_k| l_{ak} b_{ak} x_{0j}^* \theta_{jk} \phi_j'(x_{0j}^s) \tag{141}$$

$j = 1, 2, \dots, m.$

Let j_1 be such that $|d_{j_1}| \geq |d_j|$ for all $j \neq j_1$. Then

$$1 \leq \sum_{a=1}^n l_{aj_1} b_{aj_1} |\phi_{j_1}(x_{0j_1}^s) + x_{0j_1}^* \phi_{j_1}'(x_{0j_1}^s)| + \sum_{\substack{k=1 \\ k \neq j_1}}^m \sum_{a=1}^n \frac{|d_k|}{|d_{j_1}|} l_{ak} b_{ak} x_{0j_1}^* \theta_{j_1 k} \phi_{j_1}'(x_{0j_1}^s); \tag{142}$$

that is, Inequality (138) does not hold strictly for $j = j_1$, since by assumption $|d_k|/|d_{j_1}| \leq 1$. Hence our assumption that $|\lambda_0| = 1$ leads to a contradiction when Inequality (138) holds strictly for all j . Thus if Inequality (138) is strictly satisfied, we have $|\lambda_0| < 1$ and \mathbf{x}_0^* is stable.

APPENDIX 2: CONDITIONS FOR A BIOLOGICALLY MEANINGFUL EQUILIBRIUM STATE UNDER PANMIXIS

If we set $z_{11} = x_{0,11}^*$, $z_{12} = x_{0,12}^*$, $z_{22} = x_{0,22}^*$, $\kappa = x_{0,11}^* + x_{0,12}^* + x_{0,22}^*$, $\beta_{11} = \sum_{a=1}^n h_{a,11} \phi_{11}(\kappa)$, $\beta_{12} = \sum_{a=1}^n h_{a,12} \phi_{12}(\kappa)$, and $\beta_{22} = \sum_{a=1}^n h_{a,22} \phi_{22}(\kappa)$, then the equilibrium relationships in the main text can be rewritten as

$$z_{11} + z_{12} + z_{22} = \beta_{11} z_{11} + \beta_{12} z_{12} + \beta_{22} z_{22} \tag{143}$$

$$\kappa = z_{11} + z_{12} + z_{22} \tag{144}$$

$$z_{11} = \frac{(2z_{11}\beta_{11} + z_{12}\beta_{12})^2}{4\kappa} \tag{145}$$

$$z_{12} = \frac{2(2z_{11}\beta_{11} + z_{12}\beta_{12})(2z_{22}\beta_{22} + z_{12}\beta_{12})}{4\kappa} \tag{146}$$

$$z_{22} = \frac{(2z_{22}\beta_{22} + z_{12}\beta_{12})^2}{4\kappa}. \tag{147}$$

From (145), (146), and (147), the solution must satisfy

$$z_{12} = +2\sqrt{z_{11}z_{22}}. \tag{148}$$

Combining this result with (144) gives

$$z_{11} = (\sqrt{\kappa} - \sqrt{z_{22}})^2 \tag{149}$$

$$z_{12} = 2\sqrt{z_{22}}(\sqrt{\kappa} - \sqrt{z_{22}}). \tag{150}$$

Substituting (149) and (150) into Eqs. (145) and (147), respectively, gives

$$4\kappa(\sqrt{\kappa} - \sqrt{z_{22}})^2 = (2\beta_{11}(\sqrt{\kappa} - \sqrt{z_{22}})^2 + 2\beta_{12}\sqrt{z_{22}}(\sqrt{\kappa} - \sqrt{z_{22}}))^2 \tag{151}$$

and

$$4\kappa z_{22} = (2\beta_{22}z_{22} + 2\beta_{12}\sqrt{z_{22}}(\sqrt{\kappa} - \sqrt{z_{22}}))^2. \tag{152}$$

These two equations simplify to give

$$\sqrt{\kappa}(1 - \beta_{11}) = \sqrt{z_{22}}(\beta_{12} - \beta_{11}) \tag{153}$$

and

$$\sqrt{\kappa}(1 - \beta_{12}) = \sqrt{z_{22}(\beta_{22} - \beta_{12})}. \quad (154)$$

Dividing (153) by (154) and cross-multiplying gives

$$\beta_{11} + \beta_{22} - 2\beta_{12} = \beta_{11}\beta_{22} - \beta_{12}^2, \quad (155)$$

which can be rearranged to obtain

$$(\beta_{12} - 1) = \pm\sqrt{(\beta_{11} - 1)(\beta_{22} - 1)}. \quad (156)$$

APPENDIX 3: LOCAL STABILITY ANALYSIS OF THE EQUILIBRIUM STATE UNDER PANMIXIS

In terms of the notation defined in the text,

$$x_{1,11}(t+1) = l_{1,11}x_{0,11}(t)\phi_{11}(x_{0,11}(t) + x_{0,12}(t) + x_{0,22}(t)) \quad (157)$$

$$x_{1,12}(t+1) = l_{1,12}x_{0,12}(t)\phi_{12}(x_{0,11}(t) + x_{0,12}(t) + x_{0,22}(t)) \quad (158)$$

$$x_{1,22}(t+1) = l_{1,22}x_{0,22}(t)\phi_{22}(x_{0,11}(t) + x_{0,12}(t) + x_{0,22}(t)), \quad (159)$$

and from Eqs. (65), (66), and (67), the following non-delay relationship also applies:

$$x_{0,11}(t) = \frac{(2\sum_{a=1}^n b_{a,11}x_{a,11}(t) + \sum_{a=1}^n b_{a,12}x_{a,12}(t))^2}{4(\sum_{a=1}^n b_{a,11}x_{a,11}(t) + \sum_{a=1}^n b_{a,12}x_{a,12}(t) + \sum_{a=1}^n b_{a,22}x_{a,22}(t))} \quad (160)$$

$$x_{0,12}(t) = \frac{2(2\sum_{a=1}^n b_{a,11}x_{a,11}(t) + \sum_{a=1}^n b_{a,12}x_{a,12}(t))}{4(\sum_{a=1}^n b_{a,11}x_{a,11}(t) + \sum_{a=1}^n b_{a,12}x_{a,12}(t) + \sum_{a=1}^n b_{a,22}x_{a,22}(t))} \\ \times \left(\sum_{a=1}^n b_{a,12}x_{a,12}(t) + 2\sum_{a=1}^n b_{a,22}x_{a,22}(t) \right) \quad (161)$$

$$x_{0,22}(t) = \frac{(2\sum_{a=1}^n b_{a,22}x_{0,22}(t) + \sum_{a=1}^n b_{a,12}x_{a,12}(t))^2}{4(\sum_{a=1}^n b_{a,11}x_{a,11}(t) + \sum_{a=1}^n b_{a,12}x_{a,12}(t) + \sum_{a=1}^n b_{a,22}x_{a,22}(t))}. \quad (162)$$

From Eqs. (157), (158), and (159), at equilibrium

$$\frac{\partial x_{1,p}(t+1)}{\partial x_{a,q}(t)} = \frac{\partial x_{0,p}(t)}{\partial x_{a,q}(t)} l_{1,p}\phi_p(\kappa) \\ + l_{1p}x_{0,p}^*\phi_p'(\kappa) \left(\frac{\partial x_{0,11}(t)}{\partial x_{a,q}(t)} + \frac{\partial x_{0,12}(t)}{\partial x_{a,q}(t)} + \frac{\partial x_{0,22}(t)}{\partial x_{a,q}(t)} \right), \quad (163)$$

where p and q are every possible combination of 11, 12, and 22, and as defined in the text, $\kappa = x_{0,11}^* + x_{0,12}^* + x_{0,22}^*$.

From Eqs. (160), (161), and (162), the partial derivatives on the righthand side of Eq. (163) are given by

$$\frac{\partial x_{0,11}(t)}{\partial x_{a,11}(t)} = b_{a,11} \left(1 - \frac{x_{0,22}^*}{\kappa} \right) \tag{164}$$

$$\frac{\partial x_{0,11}(t)}{\partial x_{a,12}(t)} = b_{a,12} \frac{1}{2} \left(1 - \frac{x_{0,11}^*}{\kappa} - \frac{x_{0,22}^*}{\kappa} \right) \tag{165}$$

$$\frac{\partial x_{0,11}(t)}{\partial x_{a,22}(t)} = b_{a,22} \left(- \frac{x_{0,11}^*}{\kappa} \right) \tag{166}$$

$$\frac{\partial x_{0,22}(t)}{\partial x_{a,22}(t)} = b_{a,22} \left(1 - \frac{x_{0,11}^*}{\kappa} \right) \tag{167}$$

$$\frac{\partial x_{0,22}(t)}{\partial x_{a,12}(t)} = b_{a,12} \frac{1}{2} \left(1 - \frac{x_{0,11}^*}{\kappa} - \frac{x_{0,22}^*}{\kappa} \right) \tag{168}$$

$$\frac{\partial x_{0,22}(t)}{\partial x_{a,11}(t)} = b_{a,11} \left(- \frac{x_{0,22}^*}{\kappa} \right) \tag{169}$$

$$\frac{\partial x_{0,12}(t)}{\partial x_{a,11}(t)} = b_{a,11} \left(2 \frac{x_{0,22}^*}{\kappa} \right) \tag{170}$$

$$\frac{\partial x_{0,12}(t)}{\partial x_{a,22}(t)} = b_{a,22} \left(2 \frac{x_{0,11}^*}{\kappa} \right) \tag{171}$$

$$\frac{\partial x_{0,12}(t)}{\partial x_{a,12}(t)} = b_{a,12} \left(1 - \frac{x_{0,12}^*}{\kappa} \right). \tag{172}$$

It is now clear that in Eq. (163)

$$\frac{\partial x_{0,11}(t)}{\partial x_{a,q}(t)} + \frac{\partial x_{0,12}(t)}{\partial x_{a,q}(t)} + \frac{\partial x_{0,22}(t)}{\partial x_{a,q}(t)} = b_{a,q} \quad q = 11, 12, 22. \tag{173}$$

Therefore Eq. (163) can be rewritten as

$$\frac{\partial x_{1,p}(t+1)}{\partial x_{a,q}(t)} = \frac{\partial x_{0,p}(t)}{\partial x_{a,q}(t)} l_{1,p} \phi_p(\kappa) + b_{a,q} x_{0,p}^* l_{1,p} \phi'_p(\kappa). \tag{174}$$

As with the analysis set out in Appendix 1, define the matrices (see (115) and (117)) \mathbf{A}_{kk} and \mathbf{A}_{kj} with top row entries $f_{kk}(a)$ and $f_{jk}(a)$, respectively, where now

$$f_{kk} = \frac{\partial x_{1,k}(t+1)}{\partial x_{a,k}(t)} = \frac{\partial x_{0,k}(t)}{\partial x_{a,k}(t)} l_{1,k} \phi_k(\kappa) + x_{0,k}^* l_{1,k} \phi'_k(\kappa) \tag{175}$$

$$f_{jk} = \frac{\partial x_{1,j}(t+1)}{\partial x_{a,k}(t)} = \frac{\partial x_{0,j}(t)}{\partial x_{a,k}(t)} l_{1,j} \phi_j(\kappa) + x_{0,j}^* l_{1,j} \phi'_j(\kappa). \tag{176}$$

As in Appendix 1, let $\mathbf{M} = \mathbf{C}^{-1}\mathbf{A}\mathbf{C}$ where \mathbf{C} is the same as in Appendix 1. Again, stability occurs if the sums of the absolute values of the top row elements of the matrices $\mathbf{M}_{11,11}$, $\mathbf{M}_{11,12}$, $\mathbf{M}_{11,22}$ and $\mathbf{M}_{12,11}$, $\mathbf{M}_{12,12}$, $\mathbf{M}_{12,22}$ and $\mathbf{M}_{22,11}$, $\mathbf{M}_{22,12}$, $\mathbf{M}_{22,22}$ are each less than unity. Thus stability is guaranteed when all three of the following conditions are met:

$$\begin{aligned}
 & \left| \sum_{a=1}^n b_{a,11} l_{a,11} \left[\left(1 - \frac{x_{0,22}^*}{\kappa} \right) \phi_{11}(\kappa) + x_{0,11}^* \phi'_{11}(\kappa) \right] \right| \\
 & + \left| \sum_{a=1}^n b_{a,12} l_{a,12} \left[\frac{1}{2} \frac{x_{0,12}^*}{\kappa} \phi_{11}(\kappa) + x_{0,11}^* \phi'_{11}(\kappa) \right] \right| \\
 & + \left| \sum_{a=1}^n b_{a,22} l_{a,22} \left[-\frac{x_{0,11}^*}{\kappa} \phi_{11}(\kappa) + x_{0,11}^* \phi'_{11}(\kappa) \right] \right| < 1 \\
 & \left| \sum_{a=1}^n b_{a,11} l_{a,11} \left[2 \frac{x_{0,22}^*}{\kappa} \phi_{12}(\kappa) + x_{0,12}^* \phi'_{12}(\kappa) \right] \right| \\
 & + \left| \sum_{a=1}^n b_{a,12} l_{a,12} \left[\left(1 - \frac{x_{0,12}^*}{\kappa} \right) \phi_{12}(\kappa) + x_{0,12}^* \phi'_{12}(\kappa) \right] \right| \\
 & + \left| \sum_{a=1}^n b_{a,22} l_{a,22} \left[2 \frac{x_{0,11}^*}{\kappa} \phi_{12}(\kappa) + x_{0,12}^* \phi'_{12}(\kappa) \right] \right| < 1 \\
 & \left| \sum_{a=1}^n b_{a,11} l_{a,11} \left[-\frac{x_{0,22}^*}{\kappa} \phi_{22}(\kappa) + x_{0,22}^* \phi'_{22}(\kappa) \right] \right| \\
 & + \left| \sum_{a=1}^n b_{a,12} l_{a,12} \left[\frac{1}{2} \frac{x_{0,12}^*}{\kappa} \phi_{22}(\kappa) + x_{0,22}^* \phi'_{22}(\kappa) \right] \right| \\
 & + \left| \sum_{a=1}^n b_{a,22} l_{a,22} \left[\left(1 - \frac{x_{0,11}^*}{\kappa} \right) \phi_{22}(\kappa) + x_{0,22}^* \phi'_{22}(\kappa) \right] \right| < 1. \quad (177)
 \end{aligned}$$

APPENDIX 4: MAXIMUM SUSTAINABLE YIELD SUBJECT TO AN EQUAL BOUNDARY EQUILIBRIUM CONSTRAINT

The model

$$x_0(t+1) = sx_0(t) + rx_0(t-\tau+1) \phi(x_0(t-\tau+1)) \quad (178)$$

can be expressed in terms of adult biomass units if $w_j = \eta b_j$ (see, e.g., Bergh and Getz, 1988). Let $B(t) = \sum_{a=\tau}^{\infty} w_a x_a(t)$. Then the model is given by

$$B(t+1) = sB(t) + rB(t-\tau+1) \phi(\eta B(t-\tau+1)). \quad (179)$$

For convenience, absorb η into the function ϕ . If there is an annual harvest of $C(t)$ mass units of biomass which follows spawning each year, the model is

$$B(t + 1) = sB(t) + rB(t - \tau + 1) \phi(B(t - \tau + 1)) - C(t). \quad (180)$$

The unexploited boundary population biomass is given by

$$B^s = \phi^{-1} \left[\frac{1-s}{r} \right]. \quad (181)$$

Now let the phenotypes which coexist in the unexploited population have the same values of B^s , i.e.,

$$\phi^{-1} \left[\frac{1-s_1}{r_1} \right] = \phi^{-1} \left[\frac{1-s_2}{r_2} \right] = \dots = \phi^{-1} \left[\frac{1-s_m}{r_m} \right]. \quad (182)$$

Since ϕ^{-1} is a decreasing function of $(1-s)/r$, phenotypes which are subjected to heavier exploitation become less fit and decrease in abundance relative to other phenotypes. Note that since ϕ is always a decreasing function of its argument, ϕ' is strictly negative.

We show now that for phenotypes, j , which have the same ϕ functions and the same values of $(1-s_j)/r_j$, the phenotype with the largest MSY is that which has the largest value of r_j . From (180), equilibrium catch levels satisfy the equation

$$C = (1-s)B + rB\phi(B). \quad (183)$$

If we now regard C as a function of B then maximum sustainable yield is achieved at an adult biomass \hat{B} , where \hat{B} is the positive root of the first derivative of the sustainable yield function (183),

$$\frac{dC}{dB} = (1-s) + r\phi(B) + rB\phi'(B). \quad (184)$$

Thus it follows, setting $dC/dB = 0$, that

$$\hat{B} = \frac{-(1-s) - r\phi(\hat{B})}{r\phi'(\hat{B})}. \quad (185)$$

Because of the requirement $B^s = B_1^s = B_2^s = \dots = B_m^s$, r can be eliminated in (185) by replacing it with $(1-s)/\phi(B^s)$. Therefore (185) becomes

$$\hat{B} = -\phi(B^s) \frac{1 + \phi(\hat{B})/\phi(B^s)}{\phi'(\hat{B})}, \quad (186)$$

and, under the equal fitness constraint, the adult biomass level at which MSY is achieved is an implicit function of B^s and ϕ only. Substituting this value of \hat{B} into Eq. (183) produces the following result for the MSY catch \hat{C} :

$$\hat{C} = -(1-s) \frac{\phi(B^s)}{\phi'(\hat{B})} \left(1 - \frac{\phi(\hat{B})}{\phi(B^s)} \right)^2. \quad (187)$$

The only dependence of \hat{C} on s comes from the term $(1-s)$. Since $\phi'(\hat{B})$ is negative, \hat{C} increases with decreasing s , achieving a maximum in the limit $s=0$ or alternatively at the smallest possible value of s . From (182) this is achieved for the largest possible value of r . Recall, from Eq. (97), that $r = b_\tau l_\tau$. We assume that b_τ is proportional to αw_τ and further that $w_a = w_\tau$, $a > \tau$. For phenotypes which have larger values of r , (182) requires that their s values be smaller. It follows that if l_τ remains the same for all phenotypes, then by (182) a smaller s necessitates a larger r and hence a larger adult body size w_τ . Furthermore if smaller adult survivorships mean that the juvenile survivorship l_τ will also be smaller, then a smaller s requires, again by (182), that the associated adult body size must be larger.

Therefore, phenotypes with the smallest adult survivorship are also the easiest to catch if catchability increases with body size. It has already been shown that the largest MSY is achieved with a phenotype with the largest adult body size. Since these are also the easiest to catch, fishing must reduce the boundary equilibrium level (and hence fitness) of the phenotype given the largest sustainable yield relative to others.

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