A MULTIPLE AGE CLASS POPULATION MODEL

WITH DELAYED RECRUITMENT

by

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ABSTRACT

An exploited single-species population model with a density dependent reproductive function is constructed, in which recruitment to the adult breeding population may occur in one of several possible age classes. The parent is assumed capable of giving birth only once. It is also assumed that all density dependence is concentrated in the first year of life. A linearized stability analysis of the multiplydelayed difference equation model is carried out and a sufficient condition for stability is derived for the general case, while necessary and sufficient conditions are found in specific examples. Some indication of the complicated bifurcation structure of the model is given by a series of computer simulation plots. Finally, the method of Lagrange multipliers is used to find the optimal equilibrium escapement level for the original exploited population model.

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DEDICATION

This thesis is dedicated to Dr. Pauline van den Driessche, who provided me with inspiration, encouragement, and the skills to pursue mathematical research.

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CHAPTER I

INTRODUCTION

For many species of organisms, population growth is discontinuous. The life history of such organisms may be subject to strong seasonal or periodic influences. Also, for many species, recruitment to the breeding stock may only occur several months or years after birth. There are species whose members reproduce only once in their lifetimes and die before their descendents' lives begin, for example, salmon or cicadas. To represent the population growth of such species, the only suitable model is a difference, or difference-delay equation (Maynard Smith 1968, May 1973, Clark 1976a, Pielou 1977).

Consider a biological population (P_k in generation k) which has discrete and nonoverlapping generations. The population dynamics may be described by the first order difference equation

$$P_{k+1} = F(P_k), \qquad (1)$$

which relates the population level P at time $t = t_{k+1}$ to the population level at a previous time $t = t_k$ by means of some given stock-recruitment function, F(P). In most cases of interest, the function F(P) is nonlinear and is usually constructed to allow the population to grow rapidly at low densities and level off or possibly decline at high densities.

Many explicit forms for the density dependent function F(P) have been proposed in the literature, and tables of specific forms used, with references, can be found in May, 1979 or May and Oster, 1976. One important example is the Ricker model (Ricker 1954) in which $F(P) = P \exp \{r(1 - P/K)\}$. This Ricker model is used extensively in the management of the Pacific salmon (Oncorhynchus species) populations (Clark 1976a). The dynamic behaviour of solutions of equation (1) for this case is surprisingly complicated, but now seems to be well understood, see Levin and Goodyear, 1980.

Clearly, equation (1), with F(P) as given above, always possesses a non-trivial equilibrium at $P^* = K$. It has been shown that this equilibrium is locally stable provided that $0 < r \leq 2$; but if r is increased beyond the value 2, the equilibrium becomes unstable and a new stable limit-cycle of period 2 bifurcates from the equilibrium. In fact, there is an increasing sequence $2 = r_1 < 2.526 = r_2 < \cdots$ such that when r increases past r_n a new and stable cycle of period 2^n bifurcates from the equilibrium. However, the sequence of bifurcation values for r are bounded above by a critical value $r^* = 2.692$, beyond which cycles of arbitrary period appear along with solutions that never settle into any finite cycle. The region beyond r^* has been called dynamic chaos since solutions are effectively indistinguishable from random fluctuations.

The term "chaos" was introduced in the mathematical paper by Li and Yorke, 1975. They show that if equation (1) has a solution of period 3, then for those same parameter values, solutions of any integer period can be found, as well as solutions that never settle into a periodic cycle. For a review of the mathematical details of the bifurcation structure of equations like equation (1) see May, 1976 or May and Oster, 1976.

Many real populations have several distinct but overlapping age classes, or the density dependent mechanisms operate with an explicit time delay, say n generations. In this case, a difference-delay equation of the form

$$P_{k+1} = P_k F(P_{k-n})$$
(2)

may be appropriate. Examples of such models, where the population at k+1 depends linearly on the previous population and nonlinearly on a single population at some time in the past, can be found in Maynard Smith, 1968; May, Conway, Hassell, and Southwood, 1974; Clark, 1976b; and Beddington, 1978.

Clark, 1976b, studied the delay equation $P_{k+1} = aP_k + F(P_{k-n})$, which has applications as a model of baleen whale population dynamics. Equilibrium stability and optimal exploitation policies were discussed. Here, a is the survival coefficient and $F(P_{k-n})$ is the recruitment to the breeding population at time k which was produced by the breeding population at time k-n. The local stability of an equilibrium, P*, for this difference-delay equation was shown to depend seperately on the survival coefficient, the slope of the recruitment function at the equilibrium, and the time delay in the recruitment. Clark has shown that increased delay implies reduced stability, in the sense that increasing the delay reduces the region in the parameter plane which possesses a stable equilibrium point. Goh and Agnew, 1978, considered Clark's, 1976b, difference-delay model equation for a population in which recruitment to the breeding class takes place several generations after birth. They employ a specific form for the recruitment function, F(P), namely, F(P) =AP exp $(-BP^2)$, where A and B are positive constants. It is shown that increasing the delay causes reduced stability, while increasing the survival coefficient, when the delay between birth and recruitment is small, tends to stabilize the population. However, when this delay is longer and the survival coefficient is not near one, then the stabilizing effects of the survival coefficient are overshadowed by the destabilizing effects of the time delay. Harvesting of the modeled population is studied and they conclude that, for populations that exhibit a sharp peak in their recruitment function, intermediate levels of constant effort harvesting can lead to destabilization.

In the paper by May et al., 1974, conditions that give rise to stability and oscillations in a single species population interacting with a maintained resource were studied. Considered first were discrete generation difference equation models with density dependent mortality and fecundity. If the rate at which a population takes to return towards an equilibrium level is called the characteristic return time, this paper contends "that it is the relationship of this time to the time delays in the system (e.g. the length of a generation) that determines whether the population approaches the equilibrium monotonically or 'overshoots' and oscillates about the equilibrium"

(May et al. 1974: 747). They found that instability follows from this return time being too small compared with the time delays.

Consideration is then given to multiple age class models, and a model with two overlapping age classes is studied in detail. Of course, the stability properties of these multiple age class populations is more complicated, but they are shown to be similar to those of multispecies systems. The local stability of an equilibrium is shown to be determined by the dominant eigenvalue of a matrix of parameters characterizing the slopes of the density dependent relationships between age classes.

Diamond, 1976, presented techniques for estimating the size and shape of regions of local stability for difference equations. These techniques are based on a class of discrete Liapunov functions, and a "restricted recipe" for finding these Liapunov functions along with an algorithm for calculating Liapunov contours is given. The estimation methods are applied to a single species model with two age classes.

Levin and May, 1976, gave stability criteria for the differencedelay equation (2). They presented general analytic formulas describing the boundary between monotonic damping and oscillatory damping toward a stable equilibrium point, P*, and for the boundary seperating the regions of stability and instability of P*. As was found also by Clark, 1976b, May et al., 1974, and Goh and Agnew, 1978, an increase in the explicit time delay, n in equation (2), leads the system to be more prone to oscillations and instability. An adaptation of the

linearized stability analysis presented by Levin and May, 1976, is used in this thesis.

Extensions of the difference-delay model equation (2) to allow for multiple age spawning populations where density dependence is expressed in terms of the population levels of both present and several preceding generations, i.e.,

$$P_{k+1} = P_k F(P_k, P_{k-1}, \dots, P_{k-n}),$$
(3)

have been considered by Allen and Basasibwaki, 1974, Ross, 1978, and Levin and Goodyear, 1980.

Allen and Basasibwaki, 1974, studied a class of models incorporating multiple age structure where recruitment to the population is the product of fecundity and a survival rate. This first year survival rate was assumed to vary with the size and structure of the population. The population after recruitment is described by a life table with constant survival rates. Necessary conditions for the stability of an equilibrium and properties of oscillations about an unstable equilibrium were considered using a combination of analytical and simulation techniques.

Ross, 1978, considered a special case of equation (3) of the form $P_{k+1} = aP_k^{1-b}P_{k-1}^{-c}$. In this case, the model can be written as a linear second order recurrence relation in the logarithm of the population and explicit solutions to this recurrence relation were derived and classified according to various parameter values.

In the paper by Levin and Goodyear, 1980, a multiple age spawning

population model with Ricker type stock-recruitment relationship was examined. Their model assumed that all density dependent effects occur within the first year of life. A density dependent Leslie matrix was developed and linearization techniques applied to various simplified models. Very complicated stability properties were shown to be dependent on two opposing delays in the system, the reproductive delay associated with deferring reproduction and the truncation delay associated with an eventual leveling off of fecundity in later age classes. The balance between these delays was shown to be at the root of the overall dynamics of the system. Computer simulations found in the paper of Levin and Goodyear, 1980, are very similar to figures which may be found in this thesis, and indicate some of the spectacular dynamics which can occur when an equilibrium is in a region of instability.

This thesis examines an exploited single-species population model with a density dependent reproductive function, in which recruitment to the breeding population occurs in one of m+1 (m = 0, 1, 2, ...) possible ages. In this model however, the adult breeder can give birth only once, and then dies. Harvesting is assumed to occur only among the breeder population.

An example of a species whose characteristics closely approximate these is chum salmon (Oncorhynchus keta), whose spawning grounds are from Alaska to California. The young chums quickly go to sea in their first year of life, ranging far into the Pacific Ocean. They mature

mainly after three, four, or five growing seasons in the ocean, although a very small percentage will reproduce in their second or sixth year of life. Also, their pelagic annual natural mortality rate seems to 'remain fairly constant, that is, after the first year of life. Chum salmon return to coastal regions only as they are approaching maturity, so that there is no harvesting of chums in local waters one or more years before maturity (Ricker 1980).

A model equation for the adult breeding population of the form

$$P_{k} = F(P_{k-n}, P_{k-n-1}, \dots, P_{k-n-m})$$
 (4)

is constructed first, where there are m+l possible ages for breeding, n being the first possible age. Following this is an analysis of the local stability of an equilibrium solution, P*. A sufficient condition for local stability of P* is derived for general n and m, while necessary and sufficient conditions are examined in detail for the special case of m = 1. Note that the case m = 0 reduces to Clark's, 1976b, model with survival coefficient equal to zero. Considered next are a few specific examples for the density dependent reproductive function. Finally, the problem of economically optimal exploitation of a population modeled by an equation similar to (4) is considered and a formula determining the optimal equilibrium escapement level, S*, is derived.

CHAPTER II

THE MODEL

A single-species population model with a density dependent reproductive function will be constructed. Characteristics of the species to be modeled include recruitment to the mature adult (female) breeding population in one, and only one, year of life. Assume there are m+l possible breeding ages, with n being the first possible age of reproduction. A member of this species dies immediately after giving birth. Assume also that the period of years from birth to maturity is spent well away from the spawning area and only mature members are subject to harvesting as they return.

Fix n and n+m as the first and last possible ages for reproduction. Let P_k represent the parental, or adult breeding, population in year k, while $Q_{j,k}$ represents the population of j-year-olds in year k. If H_k is the number of mature stock harvested in year k, then the escapement will be $S_k = P_k - H_k$. The model can be represented schematically as in Figure 1.

Let α_j (0 < $\alpha_j \leq 1$) be the proportion of (n+j-l)-year-olds that reproduce, j = 1, 2, ..., m+l. Since n+m is the last possible breeding age, it follows that $\alpha_{m+1} = 1$. Thus, it is possible to write:



Figure 1. A schematic representation of the model for the special case m = 1.

$$P_{k} = \alpha_{1}Q_{n,k} + \alpha_{2}Q_{n+1,k} + \cdots + \alpha_{m}Q_{n+m-1,k} + Q_{n+m,k}.$$
 (5)

Now, if σ_j is the density independent natural survival rate from age j-1 to age j (0 < σ_j < 1, j = 1, 2, ..., n+m), then the following equations describe the age classes of the population:

$$Q_{1,k+1} = \sigma_1 f(S_k)$$
(6)

$$Q_{i,k+1} = \sigma_i Q_{i-1,k}, i = 2, 3, ..., n$$
 (7)

$$Q_{n+j,k+1} = \sigma_{n+j}(1 - \alpha_j)Q_{n+j-1,k}, j = 1, 2, ..., m$$
 (8)

where the term $f(S_k)$ is the density dependent reproductive function. It follows now from equations (5) and (8) that

$$P_{k} = \alpha_{1}Q_{n,k} + \alpha_{2}\sigma_{n+1}(1-\alpha_{1})Q_{n,k-1} + \alpha_{3}\sigma_{n+2}(1-\alpha_{2})\sigma_{n+1}(1-\alpha_{1})Q_{n,k-2} + \cdots + \alpha_{m}\sigma_{n+m-1}(1-\alpha_{m-1})\sigma_{n+m-2}(1-\alpha_{m-2})\cdots\sigma_{n+1}(1-\alpha_{1})Q_{n,k-m+1} + \sigma_{n+m}(1-\alpha_{m})\sigma_{n+m-1}(1-\alpha_{m-1})\cdots\sigma_{n+1}(1-\alpha_{1})Q_{n,k-m'}$$

or in more compact notation

$$P_{k} = \alpha_{1}Q_{n,k} + \sum_{j=1}^{m} \{\alpha_{j+1}Q_{n,k-j} (\prod_{i=1}^{j} \sigma_{n+i}(1 - \alpha_{i}))\}.$$
(9)

It can also be easily seen that the population of n-year-olds satisfies the following:

$$Q_{n,k} = (\sigma_n \sigma_{n-1} \cdots \sigma_1) f(S_{k-n}).$$
⁽¹⁰⁾

For some simplicity of notation, define

$$\mathbf{F}(\mathbf{x}) = (\sigma_1 \sigma_2 \cdots \sigma_n) \mathbf{f}(\mathbf{x}), \qquad (11)$$

so that

$$Q_{n,k+n} = F(S_k).$$
(12)

Thus is obtained the difference-delay equation providing the population dynamics for the adult breeding population:

$$P_{k+n} = \sum_{j=0}^{m} a_{j+1} F(S_{k-j}), \qquad (13)$$

where

$$a_1 = \alpha_1$$

and

$$a_{j} = \alpha_{j} \prod_{i=1}^{j-1} \sigma_{n+i}(1 - \alpha_{i}), j = 2, 3, ..., m+1.$$
(14)

What follows next is a consideration of stability criteria for an equilibrium solution of equation (13) with no harvesting, i.e., $S_k = P_k$.

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CHAPTER III

STABILITY

Stability properties of an equilibrium solution, P*, of the model equation with no harvesting

$$P_{k+n} = \sum_{j=0}^{m} a_{j+1} F(P_{k-j})$$
(15)

are analyzed in this section. Considered first will be a sufficient condition for the local stability of P^* and a numerical scheme for defining the boundaries of the local stability regions will be sketched. A detailed examination of local stability will be presented for the trivial case m = 0 and the not so trivial case of m = 1.

Let P* be a non-trivial equilibrium for the delay equation (15). Then

$$P^* = F(P^*) \sum_{j=0}^{m} a_{j+1}$$
 (16)

Now linearize about P* by writing $P_k = P* + x_k$, so that

$$P_{k+n} - P^{*} = \sum_{j=0}^{m} a_{j+1} (F(P_{k-j}) - F(P^{*}))$$
(17)

and so

$$x_{k+n} = \sum_{j=0}^{m} (a_{j+1}F'(P^*)x_{k-j} + O(x_{k-j}^2)), \qquad (18)$$

where F'(P*) is the derivative of F evaluated at P*. Define

$$A = a_{1}F'(P^{*})$$
(19)

and

$$\lambda_{j} = a_{j+1}/a_{1}.$$
 (20)

Thus, the linearization is obtained:

$$x_{k+n} = Ax_{k} + \sum_{j=1}^{m} \lambda_{j}Ax_{k-j}.$$
 (21)

Express x_k as $z^k x_0$ to obtain the characteristic equation

$$z^{n+m} - A(z^m + \sum_{j=1}^m \lambda_j z^{m-j}) = 0.$$
(22)

It is easily seen that P* is locally stable if and only if all roots of the characteristic equation (22) have modulus |z| < 1.

First it shall be proven that the condition

$$|\mathbf{A}| < 1/(1 + \lambda_1 + \lambda_2 + \cdots + \lambda_m)$$
(23)

is sufficient for local stability of P*.

Let $g(z) = z^{n+m}$ and let $h(z) = -A(z^m + \sum_{j=1}^m \lambda_j z^{m-j})$. Suppose that $|A| < 1/(1 + \lambda_1 + \lambda_2 + \cdots + \lambda_m)$; then the following is true: $|h(z)| = |A| |z^m + \lambda_1 z^{m-1} + \cdots + \lambda_m|$. So that $|h(z)| \le |A| (|z|^m + \lambda_1 |z|^{m-1} + \cdots + \lambda_m)$, and so for |z| = 1: $|h(z)| \le |A| (1 + \lambda_1 + \cdots + \lambda_m) < 1 = |g(z)|$. By Rouche's theorem, g(z) and g(z) + h(z) have the same number of zeros (namely n+m) in the interior of the unit circle. Thus, the condition (23) is sufficient to ensure the local stability of P*.



Figure 2. The intersection of z^{n+m} and $A(z^m+\lambda_1 z^{m-1}+\cdots+\lambda_m)$ gives a real root $z_0 > 1$, when $A > 1/(1+\lambda_1+\cdots+\lambda_m)$.

Now suppose that $A > 1/(1 + \lambda_1 + \cdots + \lambda_m)$, and consider the graphs of z^{n+m} and $A(z^m + \sum_{j=1}^m \lambda_j z^{m-j})$, where $z \in \mathbb{R}$ (see Figure 2). Clearly, the intersection of these graphs always gives a real root (> 1) of the characteristic equation (22).

It would seem appropriate here to introduce the notion of 'region of stability', but first more notation is needed to facilitate ease of presentation. Let $\Lambda_{\rm m} = \sum_{j=1}^{\rm m} \lambda_j$, then it is possible to speak of the parameter plane ($\Lambda_{\rm m}$,A). A ($\Lambda_{\rm m}$,A) region of local stability will be the set of parameter values for which P* is locally stable.

From the preceeding discussion it is possible to conclude that, for any n, the upper bound of the (Λ_m, A) region of local stability is always $A = 1/(1 + \Lambda_m)$. By equation (23), the lower bound, $A = A_n(\Lambda_m)$, must always satisfy

$$A_{n}(\Lambda_{m}) \leq -1/(1 + \Lambda_{m}).$$
⁽²⁴⁾

A modified Schur-Cohn criterion (see Freeman, 1965) is now presented, by which the local stability of P*, for specific values of the parameters (A, λ_1 , λ_2 , ..., λ_m), may be numerically determined from the characteristic equation (22).

Let

$$G(z) = c_{q} z^{q} + c_{q-1} z^{q-1} + \dots + c_{1} z + c_{0}$$
(25)

where $c_q > 0$. Define the inverse polynomial $G^{-1}(z) = z^q G(z^{-1})$, then

$$G^{-1}(z) = c_0 z^q + c_1 z^{q-1} + \cdots + c_{q-1} z + c_q.$$
 (26)

The roots of $G^{-1}(z)$ are the inverses of the roots of G(z) with respect to the circle |z| = 1. In addition, $(G^{-1}(z))^{-1} = G(z)$. Let

$$G^{-1}(z)/G(z) = \beta_0 + G_1^{-1}(z)/G(z).$$
 (27)

The remainder, $G_1^{-1}(z)$, will be a polynomial of degree q-1 and the quotient term $\beta_0 = c_0/c_q$. Continue in this way:

$$G_{i}^{-1}(z)/G_{i}(z) = \beta_{i} + G_{i+1}^{-1}(z)/G_{i}(z),$$

$$i = 0, 1, 2, ..., q-2$$
(28)

where $G_0(z) = G(z)$.

The necessary and sufficient condition that all roots of the equation G(z) = 0 lie in the interior of the unit circle in the z-plane

is that all of the following are satisfied:

(a)
$$G(1) > 0$$

(b₁) $G(-1) < 0$ for q odd
(b₂) > 0 for q even
(c) $|\beta_i| < 1, i = 0, 1, 2, ..., q-2.$

Application of this method with G(z) replaced by the characteristic equation (22) is straightforward when parameter values are known, however it does not seem feasable to obtain closed form expressions for the stability region with general n and m. One interesting result can nevertheless be gleaned from condition (a). If G(z) = $z^{n+m} - A(z^m + \lambda_1 z^{m-1} + \cdots + \lambda_m)$, then condition (a) requires that $A < 1/(1 + \lambda_1 + \cdots + \lambda_m) = 1/(1 + \Lambda_m)$, which is merely the upper bound of the (Λ_m, A) region of stability derived previously. This modified Schur-Cohn criterion will also be made use of in the detailed analysis of some special cases for m and n to follow.

Special case: m = 0.

In this case the population being modeled is one that has n age classes, but only the n^{th} age class reproduces. The adult breeding population is described by

$$P_{k} = Q_{n,k} = F(P_{k-n})$$
 (29)

so that an equilibrium is simply given by $P^* = F(P^*)$. The characteristic

equation (22) becomes $z^n - F'(P^*) = 0$. Thus, it is clear that P* is locally stable if and only if

$$-1 < F'(P^*) < 1.$$
 (30)

Note that this special case with m = 0 is Clark's, 1976b, model with the simplification of the survival coefficient being zero. The next special case is more interesting, requiring more rigorous analysis.

Special case: m = 1.

In this case the population being modeled is one that has n+1 age classes, and only members of the final two can reproduce. The adult breeding population is described by

$$P_{k+1} = a_1 F(P_{k-n+1}) + a_2 F(P_{k-n})$$
(31)

so that an equilibrium is given by

$$P^* = (a_1 + a_2)F(P^*).$$
(32)

The characteristic equation (22) in this case becomes

$$z^{n+\perp} - Az - \lambda_1 A = 0.$$
 (33)

From general results already derived it is known that the upper bound of the (λ_1, A) region of local stability for P* is $A = 1/(1 + \lambda_1)$, for all n; while the lower bound depends on n and satisfies

$$A_{n}(\lambda_{1}) \leq -1/(1 + \lambda_{1}).$$
(34)

Now, closed form expressions for two of these lower bounds, $A_1(\lambda_1)$ and $A_2(\lambda_1)$, will be derived using the modified Schur-Cohn criterion (Freeman 1965) as presented earlier.

In the case under consideration, $G(z) = z^{n+1} - Az - \lambda_1 A$. As already stated, condition (a) requires that $A < 1/(1 + \lambda_1)$, which is merely the upper bound derived previously. For n even, condition (b₁) requires that $A(1 - \lambda_1) < 1$; and for n odd, condition (b₂) requires that $A(\lambda_1 - 1) < 1$.

For n = 1, all that condition (c) requires is that $|\beta_0| < 1$. Since $G^{-1}(z)/G(z) = -\lambda_1 A + (-Az^n - \lambda_1 A^2 z + (1 - \lambda_1^2 A^2))/G(z)$, it follows that $\beta_0 = -\lambda_1 A$, and since they will be needed shortly it is found that $G_1^{-1}(z) = -Az^n - \lambda_1 A^2 z + (1 - \lambda_1^2 A^2)$ so that $G_1(z) = (1 - \lambda_1^2 A^2)z^n - \lambda_1 A^2 z^{n-1} - A$. Therefore, condition (c) requires that $|\lambda_1 A| < 1$. Combining this with conditions (a) and (b₂) gives the (λ_1, A) region of



Figure 3. The (λ_1, A) region of local stability (shaded area) for n = 1 and m = 1.

local stability for n = 1 (see Figure 3).

For n = 2, condition (c) requires that $|\beta_0| < 1$ and $|\beta_1| < 1$. Since $G_1^{-1}(z)/G_1(z) = -A/(1 - \lambda_1^2 A^2) + G_2^{-1}(z)/G_1(z)$, where $G_2^{-1}(z) = (-\lambda_1 A^3/(1 - \lambda_1^2 A^2))z^{n-1} - \lambda_1 A^2 z + (1 - \lambda_1^2 A^2 - A^2/(1 - \lambda_1^2 A^2))$, it follows that $\beta_1 = -A/(1 - \lambda_1^2 A^2)$. Combining this with $|\lambda_1 A| < 1$ and conditions (a) and (b₁) gives the (λ_1, A) region of local stability for n = 2:

$$(1 - \sqrt{1 + 4\lambda_1^{2'}})/2\lambda_1^2 < A < 1/(1 + \lambda_1)$$
 (35)

(see Figure 4).

In attempting to use this criterion for n = 3 it is necessary to solve a cubic equation, for n = 4 a quartic, etc.; hence it is not feasable to make use of this Schur-Cohn criterion for finding closed form expressions for $A_n(\lambda_1)$ for $n \ge 3$. However, it is useful to note here that the stability region for any n must contain the region for



Figure 4. The (λ_1, A) region of local stability (shaded area) for n = 2 and m = 1.

n+1. If this fact is combined with the sufficiency condition (23), the progression of lower bounds, $A_n(\lambda_1)$, follows:

$$A_{1}(\lambda_{1}) \leq \cdots \leq A_{n}(\lambda_{1}) \leq A_{n+1}(\lambda_{1}) \leq \cdots \leq -1/(1+\lambda_{1}).$$
(36)

Further results for $n\geq 2$, employing another approach, are now derived.

Following Levin and May, 1976, and Clark, 1976b, consider again the characteristic equation (33), $z^{n+1} - Az - \lambda_1 A = 0$, with $n \ge 2$, and express z as $\text{Re}^{i\theta}$, R > 0. Note that for $A = A_n(\lambda_1)$, equation (33) must have a root $z = e^{i\theta}$, i.e., with R = 1. Rewrite equation (33) in the form

$$1 = Az^{-n} + A\lambda_{1}z^{-(n+1)}.$$
 (37)

Substitute $z = e^{i\theta}$ and equate real and imaginary parts to obtain

$$\sin(n\theta) + \lambda_1 \sin\{(n+1)\theta\} = 0$$
(38)

and

$$A\cos(n\theta) + A\lambda_1\cos\{(n+1)\theta\} = 1.$$
(39)

Equation (38) has a unique root $\theta = \theta_n(\lambda_1)$ such that $\pi/(n+1) < \theta_n(\lambda_1)$ < π/n , although of course, there are infinitely many other roots > $\theta_n(\lambda_1)$.

Given some $\lambda_1 > 0$, equation (38) can be solved for $\theta_n(\lambda_1)$ and thus $A = A_n(\lambda_1)$ can be found from equation (39). It is shown here that this process determines the lower boundary of the stability region. Recall that for $n \ge 2$ it has been demonstrated that this lower boundary is in the region $0 > A_n(\lambda_1) > -1$. So, by examining the derivative of R with respect to λ_1 it is shown that at R = 1, $dR/d\lambda_1 > 0$; provided that 0 > A > -1. Thus, as λ_1 increases, R can only cross the boundary R = 1 from below, so that once a root leaves the stability region it cannot reenter.

Again, let $z = Re^{i\theta}$, R > 0, and substitute into equation (37). Separate real and imaginary parts to obtain

$$R^{n+1} = AR\cos(n\theta) + A\lambda_{1}\cos\{(n+1)\theta\}$$
(40)

$$0 = \operatorname{ARsin}(n\theta) + A\lambda_1 \sin\{(n+1)\theta\}.$$
(41)

From these equations it follows that

$$R = -\lambda_1 \sin\{(n+1)\theta\} / \sin(n\theta)$$
(42)

and

$$\lambda_{1}^{n} = (-1)^{n} \operatorname{Asin}^{n}(n\theta) \sin(\theta) / \sin^{n+1} \{ (n+1)\theta \}.$$
(43)

Differentiate each side of equation (43) with respect to θ and equate to obtain

$$(n/\lambda_1) (d\lambda_1/d\theta) = n^2 \cot(n\theta) + \cot(\theta) - (n+1)^2 \cot\{(n+1)\theta\}.$$
(44)

Now differentiate equation (42) with respect to θ , so

$$(1/R) (dR/d\theta) = (1/\lambda_1) (d\lambda_1/d\theta) + (n+1) \cot\{(n+1)\theta\} - n \cdot \cot(n\theta), \quad (45)$$

but $d\lambda_1/d\theta$ can be found from equation (44), so that

$$(n/R) (dR/d\theta) = \cot(\theta) - (n+1)\cot\{(n+1)\theta\}.$$
(46)

Now for R = 1, put $z = e^{i\theta}$ into equation (33), separate real and imaginary parts, and obtain the following:

$$\cos\{(n+1)\theta\} = A\cos(\theta) + A\lambda_{1}$$
(47)

$$\sin\{(n+1)\theta\} = A\sin(\theta).$$
(48)

Considering equations (38) and (39), it is easily seen that

$$\cot\{(n+1)\theta\} = -\{1 - A\cos(n\theta)\}/A\sin(n\theta), \qquad (49)$$

while from equations (47) and (48) obtain

$$\cot(\theta) = -\{1 - A\cos(n\theta) - \lambda_1^2 A^2\} / A\sin(n\theta).$$
 (50)

Use the identities given by equations (49) and (50) to determine the following from equation (46):

$$(n/R) (dR/d\theta) \Big|_{R=1} = (n\{1 - A\cos(n\theta)\} + \lambda_1^2 A^2) / A\sin(n\theta), \qquad (51)$$

and from equation (44):

$$(n/\lambda_{1}) (d\lambda_{1}/d\theta) \big|_{R=1} = (n^{2} + 2n\{1 - A\cos(n\theta)\} + \lambda_{1}^{2}A^{2})/A\sin(n\theta).$$
(52)

so,

$$(\lambda_{1}/R) (dR/d\lambda_{1})|_{R=1} = \frac{n\{1 - A\cos(n\theta)\} + \lambda_{1}^{2}A^{2}}{n^{2} + 2n\{1 - A\cos(n\theta)\} + \lambda_{1}^{2}A^{2}},$$
(53)

but -1 < A < 0, so $1 - A\cos(n\theta) > 0$. Thus, it follows from equation (53) that $(\lambda_1/R) (dR/d\lambda_1)|_{R=1} > 0$, but $\lambda_1 > 0$, so it is proven that $(dR/d\lambda_1)|_{R=1} > 0$ when 0 > A > -1.

As a consequence of this result, the lower bound of the stability region in the (λ_1, A) plane can be found using equations (38) and (39). Although closed form expressions for $A_n(\lambda_1)$ do not seem feasable for $n \ge 3$, graphs of the lower bound can easily be plotted for any $n \ge 2$ (see Figure 5). Note that $\pi/(n+1) < \theta_n(\lambda_1) < \pi/n$, so $n\theta_n(\lambda_1) \to \pi$ as $n \to +\infty$. Thus as expected, for any $\lambda_1 > 0$, $A_n(\lambda_1) + -1/(1 + \lambda_1)$ as $n \to +\infty$. Some specific examples of the density dependent reproductive function F(P) will now be discussed, applying some of the results that have been derived.

Example 1.

As a first example, consider a quadratic, or logistic type, reproductive function. Suppose that

$$f(P) = rP(1 - P/K),$$
 (54)

where r is the average fecundity per adult and K is the carrying capacity of the adult population.

The equilibrium population, P*, of equation (16) is given by

$$P^* = K(1 - B_{m,n}/r),$$
 (55)

where



Figure 5. A plot of $A_n(\lambda_1)$ for m = 1 and n = 2, 3, 4, and 5. Note that $A_n(\lambda_1) + -1/(1 + \lambda_1)$ as $n \to +\infty$.

$$1/B_{m,n} = \alpha_1 \sigma_1 \cdots \sigma_n (1 + \Lambda_m).$$
(56)

Note that for $P^* > 0$, it is required that $r > B_{m,n}$. Recall that $A = \alpha_1 F'(P^*)$, so it is easily seen that

$$A = (2 - r/B_{m,n})/(1 + \Lambda_m).$$
 (57)

The sufficient condition for local stability of P*, equation (23), in this example becomes

$$B_{m,n} < r < 3B_{m,n'}$$
(58)

and for the special case of m = 1, it follows from equation (36) that there exists a positive number $\varepsilon_n(B_{1,n})$ such that P* is stable if and only if

$$B_{1,n} < r < 3B_{1,n} + \varepsilon_{n'}$$
 (59)

a result very similar to one derived by Clark, 1976b.

Example 2.

Consider in this example a reproductive function that is of exponential, or Ricker, type, i.e.,

$$f(P) = rP \exp(-P/K)$$
. (60)

Now, the equilibrium population, P*, of equation (16) is given by

$$P^* = K \log (r/B_{m,n}),$$
 (61)

where $B_{m,n}$ is as in Example 1. Again, for a feasible equilibrium it is required that $r > B_{m,n}$. In this example

$$A = \{1 + \log(B_{m,n}/r)\}/(1 + \Lambda_{m}), \qquad (62)$$

so that the sufficient condition for local stability of P* becomes

$$\log(B_{m,n}) < \log(r) < 2 + \log(B_{m,n}).$$
 (63)

As in the first example, equation (36) implies that there is a positive number $\varepsilon_n(B_{1,n})$ such that P* is locally stable if and only if

$$\log(B_{1,n}) < \log(r) < 2 + \log(B_{1,n}) + \varepsilon_n.$$
(64)

This concludes the analysis of local stability for the model equation (15). Following are several computer simulations of the model, where the density dependent reproduction function f(P) was chosen from example 1. Parameter values were chosen as likely estimates to give some indication of the very complicated dynamics arising from the bifurcation structure. Very similar figures may be found in the paper by Levin and Goodyear, 1980.

Computer simulations.

The simulations presented here employ the reproduction function $f(x_j) = rx_j(1 - x_j)$ of Example 1, where the carrying capacity, K, has been scaled out, i.e., $P_j = Kx_j$. The figures all come in pairs, the



Figure 6a. Simulation of the modeled population for n = 1 and m = 1. Equilibrium is $x^* = 0.695$ and is stable.



Figure 6b. Simulation of the model for n = 1 and m = 1, showing a plot of yearlings versus age class two.

first of each pair shows the dynamics of the adult breeder population and the second shows one-year-olds plotted against two-year-olds.

In the first simulation, shown in Figures 6a and 6b, a simple case with m = 1 and n = 1 is considered. Parameters chosen were: $\alpha_1 = 0.7$, $\sigma_1 = 0.2$, $\sigma_2 = 0.4$, and r = 20.0. Thus the equilibrium is $x^* = 0.695$, A = -0.589, $A_1 = 1.171$, and $B_{1,1} = 6.098$. The r value is outside the sufficiency range of equation (58) but within the stability bounds as given in Figure 3. Clearly, the equilibrium is stable, but the approach to it is oscillatory.

Figures 7a and 7b show the dynamics for n = 1 and m = 4, where the parameters chosen were: $\alpha_1 = 0.05$, $\alpha_2 = 0.3$, $\alpha_3 = 0.6$, $\alpha_4 = 0.9$, $\sigma_1 = 0.2$, $\sigma_2 = \cdots = \sigma_5 = 0.5$, and r = 50.0. The equilibrium in this case is $x^* = 0.691$ while A = -0.192, $\Lambda_4 = 5.493$, and $B_{4,1} = 15.401$. Again, the r value is just outside the sufficiency range of equation (58), but the equilibrium is stable, though the approach to it is oscillatory.

Figures 8a and 8b show the dynamics of a population exactly the same as for Figures 7a,b except for the r value, which in this case is taken further outside the range of equation (58), namely, r = 70.0. Here $x^* = 0.779$, A = -0.392, while Λ_4 and $B_{4,1}$ are unchanged. There seems to be no period to the oscillations of Figure 8a, while in Figure 8b some age structure is evident in the precession of points around the curve.

Figures 9 through 13 indicate the dynamics for a population with n = 2 and m = 4. For each, the parameters $\alpha_1 = 0.02$, $\alpha_2 = 0.3$, $\alpha_3 = 0.5$,



re 7a. Simulation of the model for n = 1 and m = 4 showing parental population versus time. Equilibrium is $x^* = 0.691$ and is stable.



Figure 7b. Simulation of the model for n = 1 and m = 4 showing a plot of yearlings versus age class two.



Figure 8a. Simulation of the model for n = 1 and m = 4 showing parental population versus time. Equilibrium is $x^* = 0.779$ and is not stable.

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Figure 8b. Simulation of the model for n = 1 and m = 4 showing a plot of yearlings versus age class two.

 $\alpha_4 = 0.8$, $\sigma_1 = 0.2$, and $\sigma_2 = \cdots = \sigma_6 = 0.4$ remain unchanged. The r value is increasing though, through the values r = 100.0, 190.0, 200.0, 225.0, and 240.0 in succeeding figures. For Figures 9 and 10, r is within the stability region, while it appears that in Figure 11 there has been bifurcation to quasi-periodic oscillations of about seven years duration. In Figure 11b the cyclic nature of the age structure for oneand two-year-olds is evident. Figure 12a indicates a period of approximately fifty years, while Figure 12b shows an increasing complexity in age structure. Finally, Figures 13a and 13b reflect an r value deep into the region of instability. An analysis of the complicated bifurcation structure of the model is beyond the scope of this thesis, but it is hoped that these figures give some idea of this complex behaviour.



Figure 9a. Simulation of the model for n = 2 and m = 4 showing parental population versus time. Equilibrium is $x^* = 0.410$ and is stable.



Figure 9b. Simulation of the model for n = 2 and m = 4 showing a plot of yearlings versus age class two. (r = 100.0)





Figure 10b. Simulation of the model for n = 2 and m = 4 showing a plot of yearlings versus age class two. (r = 190.0)



Figure 11a. Simulation of the model for n = 2 and m = 4 showing parental population versus time. Equilibrium is $x^* = 0.705$ and is not stable.



Figure 11b. Simulation of the model with n = 2 and m = 4 showing a plot of yearlings versus age class two. (r = 200.0)



Figure 12a. Simulation of the model with n = 2 and m = 4 showing parental population versus time. Equilibrium is $x^* = 0.738$ and is not stable.







Figure 13a. Simulation of the model with n = 2 and m = 4 showing parental population versus time. Equilibrium is $x^* = 0.754$ and is not stable.



Figure 13b. Simulation of the model with n = 2 and m = 4 showing a plot of yearlings versus age class two. (r = 240.0)

CHAPTER IV

OPTIMALITY

In this section, the problem of economically optimal exploitation of a population modeled by the difference-delay equation (13) is discussed. The method of Lagrange multipliers is used to derive formally an optimal equilibrium condition.

Suppose that the adult breeding population modeled by equation (13) is subject to exploitation, where H_k is the number of animals harvested in year k, so that

$$P_{k+1} = \sum_{j=0}^{m} a_{j+1} F(P_{k+1-n-j} - H_{k+1-n-j}), \qquad (65)$$

k = 0, 1, 2,

Clearly, H_k must satisfy the feasibility conditions

$$0 \leq H_k \leq P_k, k = 0, 1, 2, \dots$$
 (66)

Given a harvest policy $(H_0, H_1, H_2, ...)$, the future stock levels $(P_1, P_2, ...)$ are determined by equation (65) if the historical escapement levels

$$S_{-k} = P_{-k} - H_{-k}, \quad k = 1, 2, ..., n+m-1$$
 (67)

and the initial stock level, P_0 , are known. Let $\Pi = \Pi(P,H)$ be the net economic revenue resulting from a harvest H taken from an adult population

of size P. Following Clark, 1976a, assume that net economic revenue in year k is

$$\Pi(P_{k}, H_{k}) = \int_{P_{k}-H_{k}}^{P_{k}} \{p - C(P)\} dP, \qquad (68)$$

where p = price and C(P) = unit harvest cost when the population levelis P. In the usual fishery-production model (Clark 1976b), <math>C(P) = c/P, where c is a constant. It is assumed that the maximization of the discounted present value of net economic yield

$$\mathbf{J} = \sum_{k=0}^{\infty} \delta^{k} \Pi \left(\mathbf{P}_{k}^{H_{k}} \right)$$
(69)

is the objective of exploitation. Here, $\delta = 1/(1 + i)$ is the annual discount factor, where i = interest rate.

An optimal equilibrium condition is now derived using the method of Lagrange multipliers (Clark 1976a, 1976b). Consider the Lagrangean expression:

$$\mathbf{L} = \sum_{k=0}^{\infty} \left\{ \delta^{k} \Pi(\mathbf{P}_{k}, \mathbf{H}_{k}) - \xi_{k} \{ \mathbf{P}_{k+1} - \sum_{j=0}^{m} \mathbf{a}_{j+1} \mathbf{F}(\mathbf{P}_{k+1-n-j} - \mathbf{H}_{k+1-n-j}) \} \right\}.$$
(70)

Ignoring constraints, the necessary conditions are:

$$\partial L/\partial P_k = 0 \quad (k \ge 1)$$
 (71)

and

$$\partial L/\partial H_k = 0 \quad (k \ge 0).$$
 (72)

Assume there is an equilibrium solution to these conditions with

escapement level S, so that $P_k = P = \sum_{j=0}^{m} a_{j+1}F(S)$ and $H_k = P_k - S$.

It follows from equations (71) and (72) then that

$$\delta^{k} \Pi_{p} + F'(S) \sum_{j=0}^{m} a_{j+1} \xi_{k+n-1+j} = \xi_{k-1}$$
(73)

$$\delta^{k} \Pi_{H} - F'(S) \sum_{j=0}^{m} a_{j+1} \xi_{k+n-1+j} = 0,$$
 (74)

for k = 1, 2, Thus,

$$\xi_{\rm k} = \delta^{\rm k+1} (\Pi_{\rm P} + \Pi_{\rm H}).$$
 (75)

Hence, it follows from equations (75) and (73) that

$$1 = \{ (\Pi_{P} + \Pi_{H}) / \Pi_{H} \} F'(S) \sum_{j=0}^{m} \delta^{j+n} a_{j+1}.$$
(76)

The optimal equilibrium escapement level may now be found from equation (76) when the functions $\Pi(P,H)$ and F(S) are chosen.

CHAPTER V

DISCUSSION

In this section, the research will be examined in light of the results obtained herein and some conclussions will be drawn. Extrapolations will be considered whereby this work might be extended or generalized.

A model has been constructed which describes a species in which a member may reproduce in only one age class, the ages ranging from n to n+m. The natural survival rates from age j to j+l were assumed to be density independent, in fact, all density dependence was assumed to be concentrated in the first year of life. Thus, a difference-delay equation, with m delays, describing the adult breeding population was produced. A possible extension of this study would be a generalization to allow the survival rates to also be density dependent.

Stability of the unexploited model was studied next and, for general n and m, a simple condition sufficient for stability of an equilibrium was derived. This condition was shown to provide the upper bound for the region of local stability in the (Λ_m, A) parameter plane, where Λ_m reflects the effect of the life parameters of the species while A is a measure of the slope of the reproductive function at equilibrium. From this result, it can be concluded that for fixed A positive, increasing Λ_m reduces stability. The lower bound of this stability region, for arbitrary n and m, was seen to be more intractable. However, a numerical scheme was presented for determining stability, when specific parameters are given.

Two special cases for m were analyzed in detail and some closed form expressions were derived for the lower bound. It was clearly seen here that increasing the delay leads to reduced stability and, except for the case n = 1, for fixed A, increasing Λ_1 always takes a point out of the stable region. For the case n = 1 and m = 1 however, there is a range of values for A (-2 < A < -1) where increasing Λ_1 from zero takes a point from instability to stability and back to instability.

Two examples for the density dependent reproductive function employing commonly used functions were exhibited. A study of the global behaviour of the model and a detailed examination of the bifurcation structure is beyond the scope of this thesis, however, some interesting computer simulation plots were given, showing the complicated dynamics possible with the model and indicating that the bifurcation structure is indeed complex.

Finally, the exploited population model was considered again, and a condition derived, giving the optimal equilibrium escapement level for the general case. An examination of the optimal approach paths to this escapement level would be interesting, but, unfortunately, is also beyond the scope of this thesis.

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