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OPTIMAL HARVESTING OF ANIMAL POPULATIONS

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Harvesting rates in pre-reproductive, reproductive and post-reproductive groups of animal populations are determined to ensure that the populations of the three groups do not die out. When the populations are more or less steady, it is shown that the permissible harvesting rate when only one group is harvested is in general more than the harvesting rate when all groups are harvested at the same uniform rate. A number of models for optimising the present value of profits over all time or for optimising the total biomass are discussed. A more general model when the population is divided into an arbitrary number n of age-groups is also given. The models and their results are compared with the earlier harvesting models of Doubleday (1975), Lefkovich (1969) and Williamson (1967).

1. THE BASIC MODEL

Let $x_1(t)$, $x_2(t)$, $x_3(t)$ be the populations of pre-reproductive, reproductive and post-reproductive fish at time t. Let the respective birth, death and harvesting rates in the three groups be $(0, b_2, 0)$, (d_1, d_2, d_3) and (h_1, h_2, h_3) and let m_1, m_2 denote the rates at which the animals of the first and second groups migrate into the second and third groups respectively on maturity and survival. Under these conditions we get the following system of differential equations for our model

$$\left.\begin{aligned} \frac{dx_1}{dt} &= b_2x_2 - (d_1 + m_1 + h_1)\,x_1 \\ \frac{dx_2}{dt} &= m_1x_1 - (d_2 + m_2 + h_2)\,x_2 \\ \frac{dx_3}{dt} &= m_2x_2 - (d_3 + h_3)\,x_3 \end{aligned}\right\} \qquad \ldots(1)$$

which can also be written in the matrix form

$$\frac{dX}{dt} = KX \qquad \ldots(2)$$

where

$$X(t) = \begin{bmatrix} x_1(t) \\ x_2(t) \\ x_3(t) \end{bmatrix},\; K = \begin{bmatrix} -(d_1 + m_1 + h_1) & b_2 & 0 \\ m_1 & -(d_2 + m_2 + h_2) & 0 \\ 0 & m_2 & -(d_3 + h_3) \end{bmatrix}. \qquad \ldots(3)$$

The three eigenvalues of K are the roots of

$$[\lambda^2 - \lambda(d_1 + m_1 + h_1 + d_2 + m_2 + h_2) + (d_1 + m_1 + h_1) \times (d_2 + m_2 + h_2) - 4b_2m_1] [\lambda + d_3 + h_3] = 0 \quad ...(4)$$

so that

$$\lambda_1, \lambda_2 = -\tfrac{1}{2} [d_1 + m_1 + h_1 + d_2 + m_2 + h_2] \pm \tfrac{1}{2} [(d_1 + m_1 + h_1 + d_2 + m_2 + h_2)^2 - 4(d_1 + m_1 + h_1)(d_2 + m_2 + h_2) + 4b_2m_1]^{1/2} \quad ...(5)$$

$$= -\tfrac{1}{2} [d_1 + m_1 + h_1 + d_2 + m_2 + h_2] \pm \tfrac{1}{2} [(d_1 + m_1 + h_1 - d_2 - m_2 - h_2)^2 + 4b_2m_1]^{1/2} \quad ...(6)$$

$$\lambda_3 = -(d_3 + h_3) \quad ...(7)$$

so that all the three eigenvalues are real and in general distinct. λ_2 and λ_3 are negative and λ_1 will be negative or positive according as

$$b_2m_1 \lesseqgtr (d_1 + m_1 + h_1)(d_2 + m_2 + h_2). \quad ...(8)$$

In general (2) can be written as

$$\frac{dX}{dt} = Y\Lambda Y^{-1}X(t) \quad ...(9)$$

where Λ is the diagonal matrix of the eigenvalues of K, Y is the matrix whose columns are the right eigenvectors of K and Y^{-1} is the inverse of Y. The solution of (9) is

$$X(t) = Y \exp(\Lambda t)\, Y^{-1}X(0) \quad ...(10)$$

which gives

$$x_1(t) = \frac{1}{m_1(\lambda_1 - \lambda_2)} \{e^{\lambda_1 t}(d_2 + m_2 + h_2 + \lambda) [m_1x_1(0) - (d_2 + m_2 + h_2 + \lambda_2) x_2(0)] + e^{\lambda_2 t}(d_2 + m_2 + h_2 + \lambda_2) \times [-m_1x_1(0) + (d_2 + m_2 + h_2 + \lambda_1) x_2(0)\} \quad ...(11)$$

$$x_2(t) = \frac{1}{m_1(\lambda_1 - \lambda_2)} \{e^{\lambda_1 t}m_1 [m_1x_1(0) - (d_2 + m_2 + h_2 + \lambda_2) x_2(0)] + e^{\lambda_2 t}m_1 [-m_1x_1(0) + (d_2 + m_2 + h_2 + \lambda_1) x_1(0)]\} \quad ...(12)$$

$$x_3(t) = \frac{1}{m_1(\lambda_1 - \lambda_2)} \{e^{\lambda_1 t} m_1 m_2 [m_1 x_1(0) - (d_2 + m_2 + h_2 + \lambda_2) x_2(0)]$$
$$\times [d_3 + h_3 + \lambda_1]^{-1} + e^{\lambda_2 t} m_1 m_2 [- m_1 x_1(0)$$
$$+ (d_2 + m_2 + h_2 + \lambda_1) x_2(0)] [d_3 + h_3 + \lambda_2]^{-1}$$
$$+ e^{\lambda_3 t}(\lambda_1 - \lambda_2) [m_1^2 m_2 x_1(0)$$
$$- m_1 m_2 (d_3 + h_3 - d_1 - m_1 - h_1) x_2(0)$$
$$+ m_1 (d_3 + h_3 + \lambda_1)(d_3 + h_3 + \lambda_2) x_2(0)]$$
$$\times [(d_3 + h_3 + \lambda_1)(d_3 + h_3 + \lambda_2)]^{-1}\}. \qquad ...(13)$$

Now λ_1, λ_2 are the roots of

$$f(\lambda) \equiv (\lambda + d_1 + m_1 + h_1)(\lambda + d_2 + m_2 + h_2) - b_2 m_1 = 0 \qquad ...(14)$$

so that

$$f(-\infty) > 0,\ f(-d_1 - m_1 - h_1) < 0,\ f(-d_2 - m_2 - h_2) < 0,\ f(\infty) > 0. \qquad ...(15)$$

As such λ_1 and λ_2 are respectively greater than and less than both $-(d_1 + m_1 + h_1)$ and $-(d_2 + m_2 + h_2)$ so that

$$d_1 + m_1 + h_1 + \lambda_2 < 0,\ d_2 + m_2 + h_2 + \lambda_2 < 0,$$
$$d_1 + m_1 + h_1 + \lambda_1 > 0,\ d_2 + m_2 + h_2 + \lambda_1 > 0. \qquad ...(16)$$

Also $\lambda_1 > \lambda_2$ and we assume $\lambda_2 > \lambda_3$. In this case terms containing $e^{\lambda_1 t}$ dominate in (11), (12) and (13) and since using (16)

$$m_1 x_1(0) - (d_2 + m_2 + h_2 + \lambda_2) \neq 0 \qquad ...(17)$$

we get

$$\operatorname*{Lt}_{t\to\infty} x_1(t) : x_2(t) : x_3(t) = (d_2 + m_2 + h_2 + \lambda_1)$$
$$\times (d_3 + h_3 + \lambda_1) : m_1(d_3 + h_3 + \lambda_1) : m_1 m_2. \qquad ...(18)$$

The ratios $x_1(t) : x_2(t) : x_3(t)$ determine the 'reproductive structure' of the population at time t and (18) gives the ultimate reproductive structure when harvesting rates are h_1, h_2, h_3.

(i) If $b_2 m_1 < (d_1 + m_1)(d_2 + m_2)$ ...(19)

then $\lambda_1, \lambda_2, \lambda_3$ are negative even when there is no harvesting and animal populations of all three groups will eventually die out.

(ii) If $b_2 m_1 > (d_1 + m_1)(d_2 + m_2)$ ...(20)

then in the absence of harvesting $\lambda_1 > 0$ and as such all group populations will increase in the absence of harvesting.

(iii) If $b_2 m_1 \geqslant (d_1 + m_1 + h_1)(d_2 + m_2 + h_2)$ ...(21)

then we can undertake harvesting at rates h_1, h_2 without dooming the animal populations to extinction.

(iv) If (21) is a strict inequality, the three group populations will grow in spite of harvesting, but if

$$b_2 m_1 = (d_1 + m_1 + h_1)(d_2 + m_2 + h_2) \qquad ...(22)$$

$\lambda_1 = 0$ and the populations will tend to constant values as $t \to \infty$. Equation (22) gives in some sense the permissible limits for harvesting in the first two groups. There is no such limit in the harvesting of the third group except that

$$h_3 \geqslant 0. \qquad ...(23)$$

2. Permissible Harvesting

Harvesting can be done at any rate subject to the populations not dying out, i.e., subject to $\lambda_1 \geqslant 0$ or subject to (21) being satisfied. The minimum birth rate which will permit harvesting at rates h_1, h_2 without extinction of populations of animals is given by (22).

Now h_3 occurs only in (13) so that the populations of the first and second groups are not affected by the harvesting rate of the third population. This is otherwise obvious. However, the ultimate ratios of the three populations as given by (18) are influenced by h_3 and as h_3 increases the populations of the pre-reproductive and reproductive groups increase relative to that of the post-reproductive group, though the ratio of the populations of the first two groups does not change. We can therefore give h_3 any value greater than zero. We shall however permit h_1, h_2 only such values as satisfy (21).

If $h_1 = h_2 = h$ i.e. if we harvest the same proportion of the first two groups, then (22) gives

$$b_2 m_1 = (d_1 + m_1 + h)(d_2 + m_2 + h) \qquad ...(24)$$

or

$$h = -\tfrac{1}{2}(d_1 + m_1 + d_2 + m_2) + \tfrac{1}{2}[(d_1 + m_1 - d_2 - m_2)^2 + 4b_2 m_1]^{1/2}. \qquad ...(25)$$

If we harvest only the first group, we get

$$b_2 m_1 = (d_1 + m_1 + h_1)(d_2 + m_2) \qquad ...(26)$$

or

$$h_1 = \frac{b_2 m_1}{d_2 + m_2} - (d_1 + m_1). \qquad ...(27)$$

Now $h_1 > h$ if

$$\left[\frac{b_2 m_1}{d_2 + m_2} - \frac{d_1 + m_1}{2} + \frac{d_2 + m_2}{2}\right]^2$$

$$> \tfrac{1}{4}[(d_1 + m_1 - d_2 - m_2)^2 + 4b_2 m_1]$$

or $$b_2 m_1 > (d_1 + m_1)(d_2 + m_2) \qquad ...(28)$$

which is same as (20) and is supposed to be satisfied.

Thus if harvesting is done in such a way that the animal populations neither grow nor die out and h denotes the common proportions of the first two groups if both groups are harvested at same rate and if h_1 denotes the proportion when only the first group is harvested, $h_1 > h$. Similarly if h_2 is the corresponding proportion of the second group when this alone is harvested, then the above argument gives

$$h_2 > h \qquad ...(29)$$

This result is the same as deduced by Williamson (1967) from the Lewis-Leslie model (Lewis 1942; Leslie 1945, 1948) for a particular example (Usher 1972).

3. Optimal Harvesting : First Model

If p_1, p_2, p_3 are the profits per unit of the three types of animals and if δ is the instantaneous discount rate, then the present value of the profits is given by

$$P = \int_0^\infty e^{-\delta t}[p_1 h_1 x_1(t) + p_2 h_2 x_2(t) + p_3 h_3 x_3(t)]\, dt. \qquad ...(30)$$

Substituting from (11), (12) and (13) and integrating we get

$$\begin{aligned} P = \frac{1}{m_1(\lambda_1 - \lambda_2)} & \{[m_1 x_1(0) - (d_2 + m_2 + h_2 + \lambda_2)\, x_2(0)]\, [\delta - \lambda_1]^{-1} \\ & \times [p_1 h_1 (d_2 + m_2 + h_2 + \lambda_1) + p_2 h_2 m_1 \\ & + p_3 h_3 m_1 m_2 (d_3 + h_3 + \lambda_1)^{-1}] \\ & + [- m_1 x_1(0) + (d_2 + m_2 + h_2 + \lambda_1)\, x_2(0)]\, [\delta - \lambda_2]^{-1} \\ & \times [p_1 h_1 (d_2 + m_2 + h_2 + \lambda_2) \\ & + p_2 h_2 m_1 + p_3 h_3 m_1 m_2 (d_3 + h_3 + \lambda_2)^{-1}] \\ & + p_3 h_3 (\lambda_1 - \lambda_2)(\delta - \lambda_3)^{-1}\, [m_1^2 m_2 x_1(0) \\ & - m_1 m_2 (d_3 + h_3 - d_1 - m_1 - h_1)\, x_2(0) \\ & + m_1 (d_3 + h_3 + \lambda_1)(d_3 + h_3 + \lambda_2)\, x_3(0)] \\ & \times [(d_3 + h_3 + \lambda_1)(d_3 + h_3 + \lambda_2)]^{-1}. \end{aligned} \qquad ...(31)$$

Now P has to be maximized as a function of h_1, h_2, h_3 subject to (6), (7), (21) and

$$h_1, h_2, h_3 \geqslant 0. \qquad \text{...(32)}$$

We can consider the simpler problem of maximixing P subject to (22) so that

$$\lambda_1 = 0,\ \lambda_2 = -\ [d_1 + m_1 + h_1 + d_2 + m_2 + h_2],$$

$$b_2 m_1 = (d_1 + m_1 + h_1)(d_2 + m_2 + h_2) \qquad \text{...(33)}$$

and P reduces to a function of two variables h_1, h_3 to be maximized subject to (32).

If P_1, P_2, P_3 are the selling prices of animals per unit of the three types and $c_1(x_1, x_2, x_3)$, $c_2(x_1, x_2, x_3)$, $c_3(x_1, x_2, x_3)$ are the respective costs of catching these types, then P becomes

$$P = \int_0^\infty e^{-\delta t}\{[P_1 - c_1(x_1, x_2, x_3)]\, h_1 x_1(t) + [P_2 - c_2(x_1, x_2, x_3)]\, h_2 x_2(t)$$
$$+ [P_3 - c_3(x_1, x_2, x_3)]\, h_3 x_3(t)\}\, dt. \qquad \text{...(34)}$$

Since $x_1(t), x_2(t), x_3(t)$ are known functions of t, we can always integrate and express P as a function of h_1, h_2, h_3 which has to be maximized subject to appropriate constraints. The integrations are particularly simple if c_1, c_2, c_3 are constants or are linear functions of x_1, x_2, x_3.

4. A Second Optimization Model

In this model, the amounts of animals of each group harvested per unit time are not proportional to the animal populations of the three groups, but are given by $h_1(t), h_2(t), h_3(t)$ so that we have

$$\left.\begin{aligned} \frac{dx_1}{dt} &= b_2 x_2 - (d_1 + m_1)\, x_1 - h_1(t) \\ \frac{dx_2}{dt} &= m_1 x_1 - (d_2 + m_2)\, x_2 - h_2(t) \\ \frac{dx_3}{dt} &= m_2 x_2 - d_3 x_3 - h_3(t) \end{aligned}\right\} \qquad \text{...(35)}$$

and we have to choose $h_1(t), h_2(t), h_3(t)$ so as to maximize

$$P = \int_0^\infty e^{-\delta t}\{[P_1 - c_1(x_1, x_2, x_3)]\, h_1(t) + [P_2 - c_2(x_1, x_2, x_3)]\, h_2(t)$$
$$+ [P_3 - c_3(x_1, x_2, x_3)]\, h_3(t)\}\, dt \qquad \text{...(36)}$$

or we have to choose $x_1(t), x_2(t), x_3(t)$ so as to maximize

$$P = \int_0^\infty e^{-\delta t} \{[P_1 - c_1(x_1, x_2, x_3)] [b_2 x_2 - (d_1 + m_1) x_1 - x_1']$$
$$+ [P_2 - c_2(x_1, x_2, x_3)] [m_1 x_2 - (d_2 + m_2) x_2 - x_2']$$
$$+ [P_3 - c_3(x_1, x_2, x_3)] [m_2 x_2 - d_3 x_3 - x_3']\} \, dt. \quad \ldots(37)$$

Using Euler-Lagrange equations of calculus of variations and simplifying we get the following three equations for determining $x_1(t)$, $x_2(t)$, $x_3(t)$

$$\left(\frac{\partial c_2}{\partial x_1} - \frac{\partial c_1}{\partial x_2}\right) x_2' + \left(\frac{\partial c_3}{\partial x_1} - \frac{\partial c_1}{\partial x_3}\right) x_3'$$
$$= [P_1 - c_1(x_1, x_2, x_3)][d_1 + m_1 + \delta]$$
$$+ [P_2 - c_2(x_1, x_2, x_3)][- m_1] + \frac{\partial c_1}{\partial x_1} [b_2 x_2 - (d_1 + m_1) x_1]$$
$$+ \frac{\partial c_2}{\partial x_1} [m_1 x_1 - (d_2 + m_2) x_2] + \frac{\partial c_3}{\partial x_1} [m_2 x_2 - d_3 x_3] \quad \ldots(38)$$

$$\left(\frac{\partial c_3}{\partial x_2} - \frac{\partial c_2}{\partial x_3}\right) x_3' + \left(\frac{\partial c_1}{\partial x_2} - \frac{\partial c_2}{\partial x_1}\right) x_1'$$
$$= [P_1 - c_1(x_1, x_2, x_3)] [- b_2] + [P_2 - c_2(x_1, x_2, x_3)] [d_2 + m_2 + \delta]$$
$$+ [P_3 - c_3((x_1, x_2, x_3)] [-m_2] + \frac{\partial c_1}{\partial x_2} (b_2 x_2 - (d_1 + m_1) x_1]$$
$$+ \frac{\partial c_2}{\partial x_2} [m_1 x_1 - (d_2 + m_2) x_2] + \frac{\partial c_3}{\partial x_2} [m_2 x_2 - d_3 x_3] \quad \ldots(39)$$

$$\left(\frac{\partial c_1}{\partial x_3} - \frac{\partial c_3}{\partial x_1}\right) x_1' + \left(\frac{\partial c_2}{\partial x_3} - \frac{\partial c_3}{\partial x_2}\right) x_2'$$
$$= [P_3 - c_3(x_1, x_2, x_3)] [d_3 + \delta]$$
$$+ \frac{\partial c_1}{\partial x_3} (b_2 x_2 - (d_1 + m_1) x_1] + \frac{\partial c_2}{\partial x_3} [m_1 x_1 - (d_2 + m_2) x_2]$$
$$+ \frac{\partial c_3}{\partial x_3} [m_2 x_2 - d_3 x_3]. \quad \ldots(40)$$

Knowing $x_1(0)$, $x_2(0)$, $x_3(0)$, we can solve (38) - (40) to find $x_1(t)$, $x_2(t)$, $x_3(t)$ and then we can determine $h_1(t)$, $h_2(t)$, $h_3(t)$ from (35).

The equations simplify when

$$\frac{\partial c_1}{\partial x_2} = \frac{\partial c_2}{\partial x_1}, \frac{\partial c_1}{\partial x_3} = \frac{\partial c_3}{\partial x_1}, \frac{\partial c_2}{\partial x_3} = \frac{\partial c_3}{\partial x_2} \quad \text{...(41)}$$

in which case we get the solution

$$x_1(t) = \mathbf{x}_1,\ x_2(t) = \mathbf{x}_2,\ x_3(t) = \mathbf{x}_3 \quad \text{...(42)}$$

and

$$\left.\begin{aligned} h_1(t) &= b_2\mathbf{x}_2 - (d_1 + m_1)\,\mathbf{x}_1, \\ h_2(t) &= m_1\mathbf{x}_1 - (d_2 + m_2)\,\mathbf{x}_2, \\ h_3(t) &= m_2\mathbf{x}_2 - d_3\mathbf{x}_3. \end{aligned}\right\} \quad \text{...(43)}$$

At the start we adopt the policy of maximum harvesting in that group or groups where the initial population is more than the equilibrium population and of no harvesting where the initial population is less than or equal to the equilibrium population. We continue using this policy till we reach population sizes $\mathbf{x}_1$, $\mathbf{x}_2$, $\mathbf{x}_3$ and then always use harvesting rates given by (43) so as to get harvests

$$[b_2\mathbf{x}_2 - (d_1 + m_1)\,\mathbf{x}_1],\ [m_1\mathbf{x}_1 - (d_2 + m_2)\,\mathbf{x}_2],\ [m_2\mathbf{x}_2 - d_3\mathbf{x}_3] \quad \text{...(44)}$$

per unit time and the present value of the future profits at this instant of time is given by

$$\begin{aligned} \frac{1}{\delta} \{&[P_1 - c_1(\mathbf{x}_1, \mathbf{x}_2, \mathbf{x}_3)]\,[b_2\mathbf{x}_2 - (d_1 + m_1)\,\mathbf{x}_1] \\ &+ [P_2 - c_2(\mathbf{x}_1, \mathbf{x}_2, \mathbf{x}_3)]\,[m_1\mathbf{x}_1 - (d_2 + m_2)\,\mathbf{x}_2] \\ &+ [P_3 - c_3(\mathbf{x}_1, \mathbf{x}_2, \mathbf{x}_3)]\,[m_2\mathbf{x}_2 - d_3\mathbf{x}_3]\}. \end{aligned} \quad \text{...(45)}$$

5. A THIRD OPTIMIZATION MODEL

In this case we want to keep the population sizes steady so that we harvest per unit time as much as is biologically produced in that time and we want to maximize the total biomass per unit time. If $\omega_1, \omega_2, \omega_3$ are the biomasses of the three types of animals, we want to maximize

$$\omega_1 h_1 x_1 + \omega_2 h_2\, x_2 + \omega_3 h_3 x_3 \quad \text{...(46)}$$

where x_1, x_2, x_3 are given by

$$\left.\begin{aligned} b_2x_2 - (d_1 + m_1)\,x_1 &= h_1x_1 \\ m_1x_1 - (d_2 + m_2)\,x_2 &= h_2x_2 \\ m_2x_2 - d_3x_3 &= h_3x_3. \end{aligned}\right\} \quad \text{...(47)}$$

Since (47) give only the steady-state ratios of x_1, x_2, x_3, we impose the normalizing condition

$$x_1 + x_2 + x_3 = 1. \quad \text{...(48)}$$

We, therefore, have the problem of maximizing

$$\omega_1 [b_2 x_2 - (d_1 + m_1) x_1] + \omega_2 [m_1 x_1 - (d_2 + m_2) x_2] + \omega_3 [m_2 x_2 - d_3 x_3] \quad \text{...(49)}$$

subject to (49) and

$$\left.\begin{array}{l} b_2 x_2 - (d_1 + m_1) x_1 \geqslant 0; \; m_1 x_1 - (d_2 + m_2) x_2 \geqslant 0; \; m_2 x_2 - d_3 x_3 \geqslant 0 \\ \qquad x_1 \geqslant 0; \qquad x_2 \geqslant 0; \qquad x_3 \geqslant 0. \end{array}\right\} \quad \text{...(50)}$$

This is a standard linear programming problem and maxima and minima can be at the vertices of the polyhedron region determined by (48) and (50). There are four vertices of interest satisfying these conditions viz.

$$\left.\begin{array}{ll}
\text{(i)} & \dfrac{b_2}{b_2 + d_1 + m_1}, \; \dfrac{d_1 + m_1}{b_2 + d_1 + m_1}, \; 0 \\[2ex]
\text{(ii)} & \dfrac{d_2 + m_2}{d_2 + m_2 + m_1}, \; \dfrac{m_1}{d_2 + m_2 + m_1}, \; 0 \\[2ex]
\text{(iii)} & \dfrac{d_3(d_2 + m_2)}{d_3(d_2 + m_2) + m_1 d_3 + m_1 m_2}, \; \dfrac{m_1 d_3}{d_3(d_2 + m_2) + m_1 d_3 + m_1 m_2}, \\[2ex]
& \dfrac{m_1 m_2}{d_3(d_2 + m_2) + m_1 d_3 + m_1 m_2} \\[2ex]
\text{(iv)} & \dfrac{d_3 b_2}{d_3 b_2 + (d_1 + m_1)(d_3 + m_2)}, \; \dfrac{d_3(d_1 + m_1)}{d_3 b_2 + (d_1 + m_1)(d_3 + m_2)}, \\[2ex]
& \dfrac{m_2(d_1 + m_1)}{d_3 b_2 + (d_1 + m_1)(d_3 + m_2)}.
\end{array}\right\} \quad \text{...(51)}$$

The values of the function (49) at these four vertices are :

$$\left.\begin{array}{ll}
\text{(i)} & \omega_2 \dfrac{m_1 b_2 - (d_1 + m_1)(d_2 + m_2)}{b_2 + d_1 + m_1} + \omega_3 \dfrac{m_2(d_1 + m_1)}{b_2 + d_1 + m_1} \\[2ex]
\text{(ii)} & \omega_1 \dfrac{b_2 m_1 - (d_1 + m_1)(d_2 + m_2)}{d_2 + m_2 + m_1} + \omega_3 \dfrac{m_1 m_2}{d_2 + m_2 + m_1} \\[2ex]
\text{(iii)} & \omega_1 d_3 \dfrac{b_2 m_1 - (d_1 + m_1)(d_2 + m_2)}{d_3(d_2 + m_3) + m_1 d_3 + m_1 m_2} \\[2ex]
\text{(iv)} & \omega_2 d_3 \dfrac{b_2 m_1 - (d_1 + m_1)(d_2 + m_2)}{d_3 b_2 + (d_3 + m_2)(d_1 + m_1)}.
\end{array}\right\} \quad \text{...(52)}$$

We are of course assuming $b_3 m_1 > (d_1 + m_2)(d_2 + m_2)$. In (i) we harvest second and third groups of animals; in (ii) we harvest first and third groups of animals; in (iii) we harvest animals of the first group only; in (iv) we harvest animals of the second group only. Out of these four policies we adopt the one which gives the maximum profit.

In case total food available is restricted to F and the first, second and third type of animals require f_1, f_2, f_3 units of food per individual per unit time, we can replace (48) by

$$f_1 x_1 + f_2 x_2 + f_3 x_3 = F. \qquad \text{...(53)}$$

6. A General Model

In this model, the population is divided into n age-groups of which the $(p+1)$th to $(p+q)$th belong to the reproductive group. Let $x_j(t)$ be the population of the jth group and let b_j, d_j, m_j be the birth, death and migration parameters for it [$j = 1, 2, ..., n$; $b_j = 0$ for $j = 1, 2, ..., p$; $p+q+1, ..., p+q+r = n$; $m_n = 0$]. The differential equations for this model are

$$\left.\begin{aligned} \frac{dx_1}{dt} &= b_{p+1}x_{p+1} + \ldots + b_{p+q}x_{p+q} - (d_1 + m_1 + h_1)\, x_1 \\ \frac{dx_j}{dt} &= m_{j-1}x_{j-1} - (d_j + m_j + h_j)\, x_j;\; j = 2, 3, \ldots, n. \end{aligned}\right\} \qquad \text{...(54)}$$

These can be written in matrix form as

$$\frac{dX}{dt} = KX \qquad \text{...(55)}$$

where

$$X(t) = [x_1(t), x_2(t), \ldots, x_n(t)]' \qquad \text{...(56)}$$

and K is an $n \times n$ matrix whose diagonal elements are $-(d_j + m_j + h_j)$ whose main subdiagonal elements are m_j, whose $(p+1)$th to $(p+q)$th elements of the first row are $b_{p+1}, b_{p+2}, \ldots, b_{p+q}$ and the rest of whose elements are zero. Out of its n eigenvalues r are given by

$$-(d_j + m_j + h_j) \text{ for } j = p+q+1, p+q+2, \ldots, p+q+r = n. \qquad \text{...(57)}$$

The remaining $p + q$ eigenvalues are roots of the equation

$$\begin{aligned} \phi(\lambda) \equiv \prod_{j=1}^{p+q} (d_j + m_j + h_j + \lambda) \\ &- m_1 m_2 \ldots m_p [b_{p+1}(d_{p+2} + m_{p+2} + h_{p+2} + \lambda) \ldots (d_{p+q} + m_{p+q} + h_{p+q} + \lambda) \\ &+ b_{p+2}m_{p+1}(d_{p+3} + m_{p+3} + h_{p+3} + \lambda) \ldots (d_{p+q} + m_{p+q} + h_{p+q} + \lambda) \\ &+ \ldots \quad \ldots \quad \ldots \quad \ldots + \ldots \quad \ldots \quad \ldots \quad \ldots \\ &+ b_{p+q}m_{p+1}m_{p+2} \ldots m_{p+q-1}] = 0. \end{aligned} \qquad \text{...(58)}$$

If $d + m + h$ is the smallest value of $d_j + m_j + h_j$ for $j = 1, 2, \ldots, p + q$, we get

$$\phi(-d - m - h) < 0, \ \phi(\infty) > 0 \qquad \ldots(59)$$

so that there is a real eigenvalue greater than $-(d + m + h)$. The eigenvalue will be positive if $\phi(0) < 0$ and will be zero if $\phi(0) = 0$, i.e., if

$$\phi(0) = \prod_{j=1}^{p+q} (d_j + m_j + h_j) - m_1 m_2 \ldots m_p [b_{p+1}(d_{p+2} + m_{p+2} + h_{p+2}) \ldots$$
$$\ldots (b_{p+q} + m_{p+q} + h_{p+q})$$
$$+ b_{p+2} m_{p+1}(d_{p+3} + m_{p+3} + h_{p+3}) \ldots (d_{p+q} + m_{p+q} + h_{p+q})$$
$$+ \quad \ldots \quad \ldots \quad \ldots \quad \ldots$$
$$+ b_{p+q} m_{p+1} m_{p+2} \ldots m_{p+q-1}] = 0. \qquad \ldots(60)$$

Equation (60) determines a relation between harvesting rates $h_1, h_2, \ldots, h_{p+q}$ for the populations to be asymptotically constant. If (58) is satisfied for a positive value of λ, then the populations of the various groups grow asymptotically as $e^{\lambda t}$.

If possible we choose $h_1, h_2, \ldots, h_{p+q}$ so that (58) is satisfied for some value of $\lambda \geqslant 0$. We now consider three alternative policies of harvesting.

(i) $h_1 = h_2 = \ldots = h_{p+1} = h_{p+2} = \ldots = h_{p+q} = h$ so that all the $p + q$ groups are harvested at a uniform rate h. In this case (58) gives

$$\prod_{j=1}^{p+1} (d_j + m_j + h + \lambda) \prod_{j=p+2}^{p+q} (d_j + m_j + \lambda)$$
$$= m_1 m_2 \ldots m_p [b_{p+1}(d_{p+2} + m_{p+2} + \lambda) \ldots (d_{p+q} + m_{p+q} + \lambda)$$
$$+ b_{p+2} m_{p+1} \frac{d_{p+2} + m_{p+2} + \lambda}{d_{p+2} + m_{1+2} + h + \lambda} (d_{p+3} + m_{p+3} + \lambda) \ldots (d_{p+q} + m_{p+q} + \lambda)$$
$$+ \quad \ldots \quad \ldots \quad \ldots \quad \ldots$$
$$+ b_{p+q} m_{p+1} \ldots m_{p+q-1} \frac{(d_{p+2} + m_{p+2} + \lambda) \ldots (d_{p+q} + m_{p+q} + \lambda)}{(d_{p+2} + m_{p+2} + h + \lambda) \ldots (d_{p+q} + m_{p+q} + h + \lambda)}]$$
$$< m_1 m_2 \ldots m_p [b_{p+1}(d_{p+2} + m_{p+2} + \lambda) \ldots (d_{p+q} + m_{p+q} + \lambda)$$
$$+ b_{p+q} m_{p+1}(d_{p+3} + m_{p+3} + \lambda) \ldots (d_{p+q} + m_{p+q} + \lambda)$$
$$+ b_{p+q} m_{p+1} m_{p+2} \ldots m_{p+q-1}]. \qquad \ldots(61)$$

(ii) $h_1 = h_2 = \ldots = h_{p+1} = h'$; $h_{p+2} = \ldots = h_{p+q} = 0$, so that we harvest at a uniform rate h' in the first $p + 1$ groups and we do no harvesting in the remaining $q - 1$ groups. In this case (58) gives

$$\prod_{j=1}^{p+1} (d_j + m_j + h' + \lambda) \prod_{j=p+2}^{p+q} (d_j + m_j + \lambda)$$

$$= m_1 m_2 \ldots m_p [b_{p+1}(d_{p+2} + m_{p+2} + \lambda) \ldots (d_{p+q} + m_{p+q} + \lambda)$$
$$+ b_{p+2} m_{p+1}(d_{p+3} + m_{p+3} + \lambda) \ldots (d_{p+q} + m_{p+q} + \lambda)$$
$$+ \quad \ldots \quad \ldots \quad \ldots \quad \ldots$$
$$+ b_{p+q} m_{p+1} m_{p+2} \ldots m_{p+q-1}]. \qquad \ldots(62)$$

(iii) $h_{i_1} = h_{i_2} = \ldots = h_{i_s} = h''$, $h_{i_{s+1}} = \ldots = h_{i_{p+1}} = 0$,

$$h_{p+1} = \ldots = h_{p+q} = 0$$

where $i_1, i_2, \ldots, i_{p+1}$ is a permutation of the first $p + 1$ integers and $s < p + 1$ so that we do harvesting at a uniform rate h'' in s of the first $p + q$ groups and no harvesting in the remaining $p + q - s$ groups. In this case (58) gives

$$\prod_{j=i_1}^{i_s} (d_j + m_j + h'' + \lambda) \prod_{j=i_{s+1}}^{i_{p+1}} (d_j + m_j + \lambda) \prod_{j=p+1}^{p+q} (d_j + m_j + \lambda)$$

$$= m_1 m_2 \ldots m_p [b_{p+1}(d_{p+2} + m_{p+2} + \lambda) \ldots (d_{p+q} + m_{p+q} + \lambda)$$
$$+ b_{p+2} m_{p+1}(d_{p+3} + m_{p+3} + \lambda) \ldots (d_{p+q} + m_{p+q} + \lambda)$$
$$+ \quad \ldots \quad \ldots \quad \ldots \quad \ldots$$
$$+ b_{p+q} m_{p+1} \ldots m_{p+q-1}]. \qquad \ldots(63)$$

From (61) and (62), we deduce

$$\prod_{i=1}^{p+1} (d_j + m_j + h + \lambda) < \prod_{j=1}^{p+1} (d_j + m_j + h' + \lambda) \qquad \ldots(64)$$

so that $$h' > h. \qquad \ldots(65)$$

From (62) and (63) we deduce

$$\prod_{i=i_1}^{i_s} (d_j + m_j + h'' + \lambda) \prod_{j=i_{s+1}}^{i_{p+1}} (d_j + m_j + \lambda)$$

$$= \prod_{j=i_1}^{i_s} (d_j + m_j + h' + \lambda) \prod_{j=i_{s+1}}^{i_{p+1}} (d_j + m_j + h' + \lambda) \qquad \ldots(66)$$

so that $h'' > h'$. $\qquad \ldots(67)$

From (65) and (67) we deduce the following result.

Suppose populations grow in the absence of harvesting and suppose that harvesting rates are so adjusted that populations still grow asymptotically as $e^{\lambda t}$

where $\lambda \geqslant 0$ and suppose that the uniform rate of harvesting in all the $p+q$ groups (p pre-reproductive and q reproductive) to ensure this is h, then the uniform rate of harvesting h' in the first $p+1$ groups when there is no harvesting in the remaining $q-1$ groups which will ensure the same asymptotic growth rate is greater than h. If further we want to do uniform-rate harvesting in some of the $p+1$ groups only and no harvesting in others, then the rate of harvesting h'' which will ensure the same asymptotic rate of growth is greater than both h' and h.

7. Variations of Rates of Harvesting With λ

Now h, h', h'' can be obtained by solving polynomial equation of degree $p+q$, $p+1$, s respectively. These will depend on λ and as such may be denoted by $h(\lambda)$, $h'(\lambda)$, $h''(\lambda)$ respectively. These are defined only when $\lambda \leqslant \lambda_1$. When $\lambda = \lambda_1$, we have of course.

$$h(\lambda_1) = 0,\ h'(\lambda_1) = 0,\ h''(\lambda_1) = 0 \qquad ...(68)$$

$h(0)$, $h'(0)$, $h''(0)$ will denote the harvesting rates for the case when the populations remain asymptotically stable provided of course that $\phi(0) < 0$ or $\lambda_1 > 0$.

(i) From (58), we find that in case (1) when all the populations are harvested at a uniform rate

$$h(\lambda) + \lambda = \text{constant} = h(0) + 0 = h(\lambda_1) + \lambda_1 = \lambda_1 \qquad ...(69)$$

so that

$$h(\lambda) = \lambda_1 - \lambda;\ h(0) = \lambda_1 \ \text{ if } \lambda_1 > 0. \qquad ...(70)$$

Thus if $\lambda_1 > 0$ and if we do harvesting at a uniform rate λ_1 in all the groups, the populations, of all groups would be asymptotically constant. Even when $\lambda_1 < 0$ we can still do uniform harvesting at rate h in all the groups, but then the populations will decay as $e^{(\lambda_1 - h)t}$.

(ii) From (62) we get

$$\frac{\prod_{j=1}^{p+1} (d_j + m_j + h'(\lambda) + \lambda)}{\prod_{j=1}^{p+1} (d_j + m_j + h'(\mu) + \mu)} = \frac{b_{p+1} + b_{p+2}m_{p+1}(d_{p+2} + m_{p+2} + \lambda)^{-1} + \ldots + b_{p+q}(d_{p+2} + m_{p+2} + \lambda)^{-1} \ldots (d_{p+q} + m_{p+q} + \lambda)^{-1}}{b_{p+1} + b_{p+2}m_{p+1}(d_{p+2} + m_{p+2} + \mu)^{-1} + \ldots + b_{p+q}(d_{p+2} + m_{p+2} + \mu)^{-1} \ldots (d_{p+q} + m_{p+q} + \mu)^{-1}} \qquad ...(71)$$

so that

$$h'(\lambda) + \lambda_1 < h'(\mu) + \mu \ \text{ if } \lambda > \mu. \qquad ...(72)$$

In particular

$$h'(\lambda_1) + \lambda_1 < h'(\lambda) + \lambda \text{ if } \lambda_1 > \lambda$$

or

$$h'(\lambda) \geqslant \lambda_1 - \lambda \text{ if } \lambda \leqslant \lambda_1. \qquad ...(73)$$

Also

and
$$\left.\begin{aligned} h'(\lambda) + \lambda < h'(0) \text{ if } \lambda > 0 \text{ and } \lambda_1 > 0 \\ h'(\lambda) + \lambda > h'(0) \text{ if } \lambda < 0 \text{ and } \lambda_1 > 0. \end{aligned}\right\} \qquad ...(74)$$

(iii) From (57) we get

$$\frac{\prod_{j=i_1}^{i_s} (d_j + m_j + h''(\lambda) + \lambda)}{\prod_{j=i_1}^{i_s} (d_j + m_j + h''(\mu) + \mu)}$$

$$= \frac{b_{p+1} + b_{p+2}m_{p+1}(d_{p+2} + m_{p+2} + \lambda)^{-1} + \dots + b_{p+q}(d_{p+2} + m_{p+2} + \lambda)^{-1} \dots (d_{p+q} + m_{p+q} + \lambda)^{-1}}{b_{p+1} + b_{p+2}m_{p+1}(d_{p+2} + m_{p+2} + \mu)^{-1} + \dots + b_{p+q}(d_{p+2} + m_{p+2} + \mu)^{-1} \dots (d_{p+q} + m_{p+q} + \mu)^{-1}}$$

$$\times \prod_{j=i_{s+1}}^{i_{p+1}} \frac{(d_j + m_j + \mu)}{(d_j + m_j + \lambda)} \qquad ...(75)$$

so that we conclude

$$h''(\lambda) + \lambda \leqslant h''(\mu) + \mu \text{ if } \lambda > \mu \qquad ...(76)$$

and

$$\left.\begin{aligned} & h''(\lambda) \geqslant \lambda_1 - \lambda \quad \text{if } \lambda \leqslant \lambda_1 \\ & h''(\lambda) + \lambda < h''(0) \text{ if } \lambda > 0, \lambda_1 > 0 \\ & h''(\lambda) + \lambda > h''(0) \text{ if } \lambda < 0, \lambda_1 > 0. \end{aligned}\right\} \qquad ...(77)$$

The graph of $h(\lambda)$ against λ is a straight line and everywhere lies below the graphs of $h'(\lambda)$ and $h''(\lambda)$.

8. Optimization for the General Model

For the first optimization model; eqns. (30) and (34) become

$$P = \int_0^\infty e^{-\delta t} \left[\sum_{i=1}^{n} p_i h_i x_i(t) \right] dt \qquad ...(78)$$

and

$$P = \int_0^\infty e^{-\delta t} \left[\sum_{i=1}^{n} P_i - c_i(x_1, x_2, \ldots, x_n) \right] h_i x_i(t)] \, dt. \qquad \ldots(79)$$

Equation (10) still holds but now Λ is an $n \times n$ diagonal matrix of the n eigenvalues and Y is the matrix whose columns are the right eigenvectors of the matrix K. Since $x_1(t), x_2(t), \ldots, x_n(t)$ are known functions of t, P can be expressed explicitly as function of $h_1, h_2, \ldots, h_n$ and can then be maximized under appropriate restrictions.

For the seond optimization model, eqn. (37) becomes

$$\begin{aligned} P = \int_0^\infty e^{-\delta t} \{ & [(P_1 - c_1(x_1, x_2, \ldots, x_n)] [b_{p+1} x_{p+1} + \ldots + b_{p+q} x_{p+q} \\ & - (d_1 + m_1) x_1 - \dot{x}_1] \\ & + \sum_{j=2}^{n} [P_j - c_j(x_1, x_2, \ldots, x_n)] [m_{j-1} x_{j-1} - (d_j + m_j) x_j - \dot{x}_j] \} \, dt. \end{aligned} \qquad \ldots(80)$$

By using Euler-Lagrange equations, we get n ordinary simultaneous differential equations to solve for $x_1(t), x_2(t), \ldots, x_n(t)$. The equations simplify if

$$\frac{\partial c_i}{\partial x_j} = \frac{\partial c_j}{\partial x_i} \, (i, j = 1, 2, \ldots, n; \; i \neq j). \qquad \ldots(81)$$

In this case we get solutions $\mathbf{x}_1, \mathbf{x}_2, \ldots, \mathbf{x}_n$ and we get yields

$$\begin{aligned} & b_{p+1} \mathbf{x}_{p+1} + \ldots + b_{p+q} \mathbf{x}_{p+q} - (d_1 + m_1) \mathbf{x}_1, \; m_1 \mathbf{x}_1 - (d_2 + m_2) \mathbf{x}_2, \; m_2 \mathbf{x}_2 \\ & - (d_3 + m_3) \mathbf{x}_3, \ldots, m_{n-1} \mathbf{x}_{n-1} - d_n \mathbf{x}_n \end{aligned} \qquad \ldots(82)$$

per unit time.

For the third optimization model, we have to maximize

$$\begin{aligned} & \omega_1 (b_{p+1} x_{p+1} + \ldots + b_{p+q} x_{p+q} - (d_1 + m_1) x_1) \\ & + \sum_{j=2}^{n} \omega_j [m_{j-1} x_{j-1} - (d_j + m_j) x_j] \end{aligned} \qquad \ldots(83)$$

subject to the constraints

$$\left. \begin{aligned} & b_{p+1} x_{p+1} + \ldots + b_{p+p} x_{p+p} - (d_1 + m_1) x_1 \geqslant 0 \\ & m_{j-1} x_{j-1} - (d_j + m_j) x_j \geqslant 0 \quad j = 2, 3, \ldots, n \\ & x_1 \geqslant 0, \; x_2 \geqslant 0, \ldots, x_n \geqslant 0 \end{aligned} \right\} \qquad \ldots(84)$$

and

$$x_1 + x_2 + \dots + x_n = 1 \quad \text{or} \quad f_1x_1 + f_2x_2 + \dots + f_nx_n = F \qquad \dots(85)$$

which is again a linear programming problem.

For the fisheries problem where fishing is carried out with nets of fixed mesh and knife edge selection, a uniform proportion of all individuals over a certain size are selected and none under this size are selected. In this case

$$h_1 = h_2 = \dots = h_k = 0;\ h_{k+1} = h_{k+2} = \dots = h_n = h \qquad \dots(86)$$

and all the above problems are reduced to problems of maximization over h.

In the generalized third optimization model, we do less harvesting than is permissible for the steady case and let the populations grow exponentially. We then seek to maximize the present value of the total profits over a time span T. In this case eqns. (54) become

$$\left.\begin{aligned} \frac{dx_1}{dt} &= b_{p+1}x_{p+1} + \dots + b_{p+q}x_{p+q} - (d_1 + m_1 + h_1)\,x_1 = Kx_1 \\ \frac{dx_j}{dt} &= m_{j-1}x_{j-1} - (d_j + m_j + h_j)\,x_j = Kx_j; \quad (j = 2, 3, \dots, n) \end{aligned}\right\} \qquad \dots(87)$$

giving

$$x_i(t) = x_i(0)\,e^{Kt} \quad (i = 1, 2, 3, \dots, n). \qquad \dots(88)$$

We have to maximize

$$\int_0^T e^{-\delta t}\,[\sum_{i=1}^n p_ih_ix_i(t)]\,dt = \int_0^T e^{(K-\delta)t}\,[\sum_{i=1}^n p_ih_ix_i(0)]$$

$$= \frac{e^{(K-\delta)T} - 1}{(K - \delta)} \sum_{i=1}^n p_ih_ix_i(0). \qquad \dots(89)$$

We, therefore, first maximize

$$p_1\,[b_{p+1}x_{p+1}(0) + \dots + b_{p+q}x_{p+q}(0) - (d_1 + m_1 + K)\,x_1(0)]$$
$$+ \sum_{j=2}^n p_j\,[m_{j-1}x_{j-1}(0) - (d_j + m_j + K)\,x_j(0)] \qquad \dots(90)$$

subject to constraints

$$\left.\begin{aligned} & b_{p+1}x_{p+1}(0) + \dots + b_{p+q}x_{p+q}(0) - (d_1 + m_1 + K)\,x_1(0) \geqslant 0 \\ & m_{j-1}x_{j-1}(0) - (d_j + m_j + K)\,x_j(0) \geqslant 0; \quad (j = 2, 3, \dots, n) \\ & x_1(0) \geqslant 0, \dots, x_n(0) \geqslant 0 \\ & x_1(0) + x_2(0) + \dots + x_n(0) = 0. \end{aligned}\right\} \qquad \dots(91)$$

This is a linear programming problem and the maximum value is obtained in the same way as obtained for the third optimization problem, only ω_i there is replaced by p_i and d_i by $d_i + K$. Let the maximum value obtained be denoted by $\psi(K)$. Then we choose K so as to maximize $[e^{(K-\delta)T} - 1]\, \psi(K)/(K-\delta)$. We can always find a time span $T(K)$ so that for $T > T(K)$ this profit is greater than that for the steady case corresponding to $K = 0$.

9. Steady-State Harvesting when there is Density Dependence Fourth Optimization Problem

Let $\bar{x}_j$ be the steady-state values, then we get

$$\left.\begin{aligned} 0 = \frac{d\bar{x}_1}{dt} &= b_{p+1}\bar{x}_{p+1} + \ldots + b_{p+q}\bar{x}_{p+q} - (d_1 + m_1 + h_1)\,\bar{x}_1 \\ &\quad - K_1\bar{x}_1(\bar{x}_1 + \ldots + \bar{x}_n) \\ 0 = \frac{d\bar{x}_j}{dt} &= m_{j-1}\bar{x}_{j-1} - (d_j + m_j + h_j)\,\bar{x}_j \\ &\quad - K_j\bar{x}_j(\bar{x}_1 + \bar{x}_2 + \ldots + \bar{x}_n);\ j = 2, 3, \ldots, n. \end{aligned}\right\} \quad \ldots(92)$$

Let

$$\bar{x}_1 + \bar{x}_2 + \ldots + \bar{x}_n = \mu \quad \ldots(93)$$

$$d_j + m_j + h_j + K_j\mu = E_j \quad (j = 1, 2, \ldots, n) \quad \ldots(94)$$

then we get

$$\left.\begin{aligned} b_{p+1}\bar{x}_{p+1} + \ldots + b_{p+q}\bar{x}_{p+q} &= E_1\bar{x}_1 \\ m_{j-1}\bar{x}_{j-1} &= E_j\bar{x}_j \quad (j = 2, 3, \ldots, n). \end{aligned}\right\} \quad \ldots(95)$$

Eliminating $\bar{x}_1, \bar{x}_2, \ldots, \bar{x}_n$, we get

$$\begin{aligned} g(\mu) \equiv E_1E_2 \ldots E_{p+q} - m_1m_2 \ldots m_p\,[b_{p+1}E_{p+2} \ldots E_{p+q} + b_{p+2}m_{p+1}E_{p+3} \ldots \\ \ldots E_{p+q} + \ldots + b_{p+q}m_{p+1} \ldots m_{p+q-1}] = 0. \end{aligned} \quad \ldots(96)$$

In view of (92), μ has to be positive. Thus a necessary condition for the existence of a steady state is $g(0) < 0$. We assume that the condition is satisfied and a positive value μ_0 for μ exists. Equations (94) determine the ratios

$$\bar{x}_1 : \bar{x}_2 : \ldots : \bar{x}_n \quad \ldots(97)$$

and knowing μ_0, we can find all the steady-state population sizes when there is harvesting at the rates, $h_1, h_2, \ldots, h_n$.

The present value of the profits for all future time is

$$P = \frac{1}{\delta} \sum_{i=1}^{n} [P_i - c_i(\bar{x}_1, \bar{x}_2, \ldots, \bar{x}_n)]\, h_i\bar{x}_i. \quad \ldots(98)$$

Since $\bar{x}_1, \bar{x}_2, \ldots, \bar{x}_n$ are known functions of $h_1, h_2, \ldots, h_n$, our problem is to choose $h_1, h_2, \ldots, h_n$ which are non-negative, which make $g(0) < 0$ and which maximize P as a function of $\bar{x}_1, \bar{x}_2, \ldots, \bar{x}_n$. In the special case $p = q = r = 1$, we get

$$g(\mu) \equiv (d_1 + m_1 + h_1 + K_1\mu)(d_2 + m_2 + h_2 + K_2\mu) - b_2m_1 = 0 \qquad \ldots(99)$$

so that

$$\mu = \frac{1}{2K_1K_2}\{-K_1(d_2 + m_2 + h_2) - K_2(d_1 + m_1 + h_1) + [(K_2(d_1 + m_1 + h_1) - K_1(d_2 + m_2 + h_2))^2 + 4K_1K_2b_2m_1]^{1/2}\}. \qquad \ldots(100)$$

Also

$$\frac{\bar{x}_1}{(d_2 + m_2 + h_2 + K_2\mu)(d_3 + h_3 + K_2\mu)} = \frac{\bar{x}_2}{m(d_3 + h_3 + K_2\mu)} = \frac{\bar{x}_3}{m_1m_2}$$

$$= \frac{\mu}{(d_2 + m_2 + h_2 + K_3\mu)(d_3 + h_3 + K_3\mu) + m_1(d_3 + h_3 + K_3\mu) + m_1m_2}. \qquad \ldots(101)$$

We can substitute in (98) for $n = 3$ and then maximize the resulting expression for variations in h_1, h_2, h_3.

For maximizing the total biomass, we have to maximize

$$\omega_1[b_{p+1}x_{p+1} + \ldots + b_{p+q}x_{p+q} - (d_1 + m_1)x_1 - K_1x_1(x_1 + x_2 + \ldots + x_n)] + \sum_{j=2}^{n} \omega_j[m_{j-1}x_{j-1} - (d_j + m_j)x_j - K_jx_j(x_1 + x_2 + \ldots + x_n)] \qquad \ldots(102)$$

subject to

$$b_{p+1}x_{p+1} + \ldots + b_{p+q}x_{p+q} - (d_1 + m_1)x_1 - K_1x_1(x_1 + \ldots + x_n) \geqslant 0,$$

$$m_{j-1}x_{j-1} - (d_j + m_j)x_j - K_jx_j(x_1 + x_2 + \ldots + x_n) \geqslant 0, \; j = 2, 3, \ldots, n$$

$$x_1 \geqslant 0, x_2 \geqslant 0, \ldots, x_n \geqslant 0 \qquad \ldots(103)$$

which is a non-linear programming problem and in particular problem of maximizing a quadratic function subject to quadratic and non-negativity constraints.

One method of solving it is to substitute $x_1 + x_2 + \ldots + x_n = y$, then solve the linear programming problem for each fixed y treated as a parameter and finally to choose y so as to get the maximum biomass.

Thus from (52) we have to find

$$\max_{y>0}\left[\omega_2 y \frac{[m_1 b_2 - (d_1 + K_1 y + m_1)(d_2 + K_2 y + m_2)]}{b_2 + d_1 + k_1 y + m_1} + \omega_3 y \frac{m_2(d_1 + K_1 y + m_1)}{b_2 + d_1 + K_1 y + m_1}\right],$$

$$\max_{y>0}\left[\omega_1 y \frac{[b_2 m_1 - (d_1 + K_1 y + m_1)(d_2 + K_2 y + m_2)]}{d_2 + K_2 y + m_1 + m_2} + \omega_3 y \frac{m_1 m_2}{d_2 + k_2 y + m_1 + m_2}\right],$$

$$\max_{y>0}\left[\omega_1(d_3 + K_3 y)\, y \frac{b_2 m_1 - (d_1 + K_1 y + m_1)(d_2 + K_2 y + m_2)}{(d_3 + K_3 y)(d_2 + K_2 y + m_2) + m_1(d_2 + K_3 y) + m_1 m_2}\right],$$

$$\max_{y>0}\left[\omega_2(d_3 + K_3 y)\, y \frac{b_2 m_1 - (d_1 + K_1 y + m_1)(d_2 + K_2 y + m_2)}{(d_3 + K_3 y) b_2 + (d_2 + K_2 y + m_2)(d_1 + K_1 y + m_1)}\right]$$

and then find the greatest of these.

10. Comparison With Earlier Age-Dependent Harvesting Models

(i) Doubleday (1975), Lefkovich (1969) and Williamson (1967) have considered harvesting for Lewis-Leslie discrete-time discrete-age-scale algebraic population models (Lewis 1942; Leslie 1945, 1948). We have considered harvesting for our continuous-time discrete-age-scale matrix differential equation model (Kapur 1978 a–d).

(ii) They have considered only the third optimization problem leading to linear programming formulation. In this case our model also leads to a linear programming formulation. In our other models, we have used differential calculus or calculus of variations. We can also use non-linear programming, dynamic programming or Pontryagin's maximum principle. We can also formulate and solve similar optimization problems for Lewis-Leslie model.

(iii) They have considered effect of competition for limited food by incorporating this fact as a constraint in the linear programming formulation. We have given an additional alternative formulation by modifying the differential equations themselves.

(iv) The main result proved in section 6 was observed in laboratory experiments of Watt (1955, 1968) and Slobodkin and Richmond (1956). It was numerically demonstrated by Williamson (1967) and commented upon by Usher (1972). For the Leslie-Lewis matrix model, it was proved by Kapur (1978e). We have proved the result here for the continuous time model.

References

Doubleday, W. G. (1975). Harvesting in matrix population models. *Biometrics*, **31**, 189-200.

Kapur, J. N. (1978a). On the stability of reproductive structure of a population. *IIT/K Research Report.*

——— (1978b). An age- and-density-dependent population growth model. *IIT/K Research Report.*

——— (1978c). An age-dependent stochastic population growth model. *IIT/K Research Report.*

——— (1978d). A two-sex continuous-time population growth model. *IIT/K Research Report.*

——— (1978e). Harvesting in matrix animal populations. *IIT/K Research Report.*

Lefkovich, L. P. (1969). A theoretical evaluation of population growth after removal of individuals from some age groups. *Bull. Ent. Res.*, **57**, 437-43.

Leslie, P. H. (1945). On the use of matrices in certain population mathematics. *Biometrika*, **33**, 184-212.

——— (1948). Some further notes on the use of matrices in population mathematics. *Biometrika*, **35**, 213-45.

Lewis, E. G. (1942). On generation and growth of a population. *Sankhya*, **6**, 92-96.

Slobodkin, L. B., and Richmond (1956). The effect of removal of fixed percentages of the newborn on size and reliability in population of *Diaphnia pulicaria* (Forbes). *Limnol Oceanogi*, **1**, 209-37.

Usher, M. B. (1972). Developments in the Leslie matrix model. In Mathematical Models in Ecology. ed. J.N.R. Jeffers. Blachivel, Oxford.

Watt, K. E. F. (1955). Studies in population productivity I. Three approaches to the optimum yield problem for populations of Tribolium Confusion. *Ecolo. Monograph* **25**, 269-90.

——— (1968). Ecology and Resource Management. McGraw-Hill Book Co., Inc., New York.

Williamson, M. H. (1967). Introducing students to the concepts of population dynamics. The Teaching of Ecology, Editor J. M. Lambert. Blackwell & Co., Oxford.