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Source: *Ecology*, Vol. 53, No. 5 (Sep., 1972), pp. 797-807

Published by: [Ecological Society of America](#)

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DELAY-LINE MODELS OF POPULATION GROWTH¹

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Abstract. Replacing the usual principle of conservation of numbers with the equivalent principle of continuity of flow (or rates) leads to a very heuristic approach to modeling time lags in populations. The approach allows the direct use of unequal time lags (or age classes of unequal lengths) without the implicit assumption of a stable age distribution. Furthermore, for simple, linear natality processes, it allows direct estimation of the biotic potential and of the frequencies of inherent oscillations.

INTRODUCTION

Pure-birth processes have been described by a fairly large number of diverse mathematical models (see Keyfitz 1967 and Goodman 1967). In light of the complex and stochastic nature of various natality processes, one should not be particularly surprised at the ever-increasing diversity and complexity in the published models. In fact, one finds that the most sophisticated and complex models are those describing the natality process that is probably the simplest and most primitive, binary fission (see Bronk, Dienes, and Paskin 1968). When more-complex birth processes are treated with similar attention to detail, the models promise to be extremely complicated and difficult to manage analytically.

Most deterministic models of pure-birth processes are elaborations of one of three basic models (for an excellent review of stochastic models, see Bhattacharya-Reid 1960): the differential form of the Malthusian equation (see Pielou 1969):

$$\frac{dN}{dt} = \alpha N \quad (1)$$

where α is the intrinsic birth rate and N is the total population; a form of the renewal equation (Lotka's equation) (Feller 1941):

$$\frac{dN}{dt} = G(t) + \int_0^t \alpha(\gamma) \frac{dN}{dt} \Big|_{t-\gamma} d\gamma \quad (2)$$

where γ is age, $\alpha(\gamma)$ is the age-dependent natality, and $G(t)$ is the continuing contribution to the birth rate by the initial members of the population (those alive at time 0); and a discrete approximation to the renewal equation, the Leslie-Lewis vector difference equation (Parlett 1971):

$$N_{t+1} = AN_t \quad (3)$$

where A is an extremely sparse matrix that describes

the age dependence of natality and N is a vector comprising age cohorts. Since eq. (2) represents the aging process in implicit form, it occasionally is coupled with an explicit representation of aging, the basic von Foerster equation² (von Foerster 1959, Sinko and Streifer 1967, Fredrickson 1971):

$$\frac{\partial N(t, \gamma)}{\partial t} = - \frac{\partial N(t, \gamma)}{\partial \gamma} \quad (4)$$

$N(t, \gamma)$ is population density at age γ . Death processes, migration terms, and density dependence of course can be added to any of these models (sometimes at the expense of analytical manageability); and the effects of time delays, many of which are carried implicitly in eq. (2), (3), and (4), can be incorporated in eq. (1) by converting it to a simple differential-difference equation such as that proposed by Tognetti and Mazanov (1970) for certain insect populations:

$$\frac{dN(t)}{dt} = \alpha N(t-T) \quad (5)$$

where $N(t)$ is the number of adults at time t , α is the rate of egg production per adult, and T is the duration of the egg stage.

Equation (5) points up a difficulty inherent in eq. (2), (3), and (4). Certain specific, reasonably well-fixed, discrete delays often are important aspects of pure-birth processes. Equations (2) and (4) are designed to deal with a continuum of age dependence and thus a continuum of time delays, and eq. (3) is designed to provide a discrete approximation to that continuum. When discrete delays such as gestation periods, nonreproductive lactation periods, and ovulation intervals are to be incorporated in a model, equations designed for a continuum of delays are neither economical nor especially revealing. On the other hand, a delay such as any of those mentioned above generally exhibits a stochastic nature, and representing it as a single number may be a gross

¹Research sponsored by the Joint Services Electronics Program, contract F44620-71-C-0087 and the National Science Foundation, grant GK-3845. (Manuscript received December 28, 1971; accepted March 24, 1972.)

²Sinko and Streifer (1969, 1971) have modified this equation to include mass as a third independent variable, thus incorporating size as well as age.

simplification. However, in most models of population dynamics, random variables are reduced to their mean values; for example, in eq. (2), $\alpha(\gamma)$ usually is defined to be the mean value of natality for a given age γ . One is no less justified in similarly considering the means of discrete delays.

In this note I shall discuss two methods of modeling natality so that discrete delays are retained explicitly. One distinct advantage of these formulations is that one often can deduce from them directly the relationships between the delays (or their mean values) and the biotic potential (innate reproductive capability) of the species involved. Furthermore, these formulations lend themselves rather readily to block diagrams and are therefore easily visualized and quite heuristic. Another advantage, in contradistinction to the Leslie-Lewis formulation, is that this method allows direct use of unequal time delays (equivalent to age classes of unequal lengths) without the implicit assumption of a stable age distribution. A major disadvantage (with respect to eq. (1) and (3)) is that they include continuous delay lines and therefore inherently do not have a finite number of state variables. They are not as difficult in this respect as eq. (2) and (4), however.

MODELING DISCRETE DELAYS

The von Foerster equation provides a dynamic picture of the process of aging in a population. In the form of eq. (4), where death and migration terms have been eliminated, it describes a very simple flow process such as one might find along a conveyor belt moving at constant speed or through a telephone wire carrying messages at a constant speed. Material or messages are loaded at the input end and flow smoothly along a route toward some destination. A string of material or messages thus is distributed over the route, and at any point along the route one finds, unaltered, the material or messages that were loaded at some time in the past. We can lump all such flow processes into the general category of pure "delay lines," which introduce time delays into their

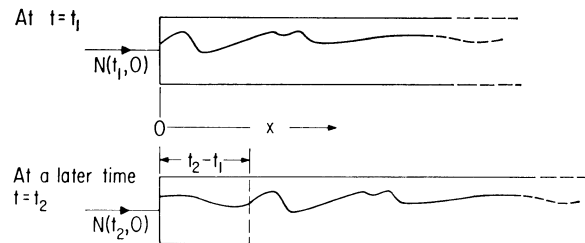


FIG. 1. Von Foerster's dynamic concept of a deathless population. The open-ended rectangles represent a delay line, along which waveforms travel without changing shape or amplitude. In this case, the waveforms $N(t, x)$ represent population density, and distance along the delay line represents age (x). The velocity of travel is one.

input functions but do not otherwise alter them. Equation (4) describes a delay line whose input is the density of newborns (number per unit time) and along which moves a waveform (population density given in individuals per unit age) that does not change shape as it advances (Fig. 1). In its more complete form, with death and migration terms, the equation becomes

$$\frac{\partial N}{\partial t} + \frac{\partial N}{\partial x} + \delta N + rN = 0 \quad (4a)$$

where δ is the death rate and r is the migration rate. This equation does not describe a pure delay line; migration and death will alter the waveform as it advances. The equation was derived from a basic conservation principle: at any age other than zero, the number of individuals is changed only by three processes: aging, death, and migration (von Foerster

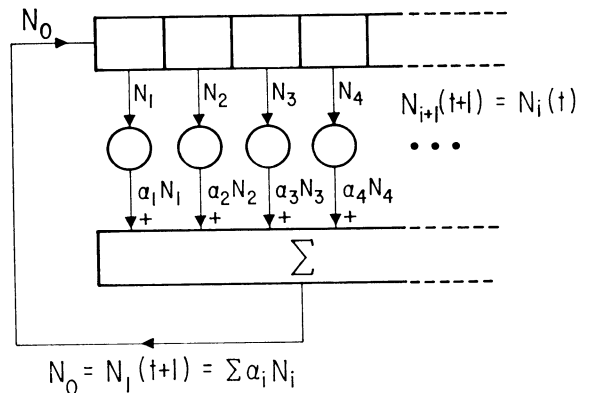


FIG. 2. A discrete (segmented) version of the delay line of Fig. 1, with the input (births) determined by the weighted sums of the delay-line contents. The open sequence of rectangles represents the delay line; the circles represent scalars that apply weighting factors (α 's) to the contents of the delay-line segments; and the long, open rectangle is an adder that sums the weighted contents.

1959). In the renewal equation (2) that generates the input function, $N(t, 0)$, to the delay line of Fig. 1, the contents of the line are sampled continuously along its length. This is most easily diagrammed (Fig. 2) from the discrete approximation represented by eq. (3), where the delay line is segmented and the density function in each segment integrated to yield a single number.

In the case of a single, discrete delay, one may reduce the number of terminals on the delay line to two, one input and one output. Furthermore, with such delays it is most convenient to convert the usual principles of conservation of numbers to an equivalent principle of "continuity" of the flow from section to section of the delay line, completely analogous, for example, to the continuity principle applied to flow processes in fluid mechanics. Rather than con-

sidering the number of individuals at a particular age, we shall consider the rate at which individuals pass through a particular age. Thus, for example, if we happen to be ignoring death, we shall apply our conservation principle by demanding that the rate at which individuals emerge from a 2-year delay is precisely equal to the rate at which they entered 2 years ago. In other words, the rate of emergence of 2-year-olds today equals the birth rate precisely 2 years ago. By applying the conservation principle in this manner we shall be able to construct with ease very heuristic systems diagrams of our population models.

Consider, for example, a population of idealized bacteria, each of which undergoes fission every 10 min. Using classical approaches, we could describe this population rather simply with either eq. (1) or eq. (3):

$$\frac{dN}{dt} = \alpha N; \alpha = [(\log 2)/10] \tag{6}$$

or

$$N_t = 2N_{t-10}, \tag{7}$$

the unit of time in each case being 1 min. On the other hand, if the process of fission is sufficiently continuous or if the population is sufficiently large that we can define a continuous rate of fission at any time, then we can say that the rate of fission now is precisely twice the rate of fission 10 min ago. We may represent this view diagrammatically as shown in Fig.

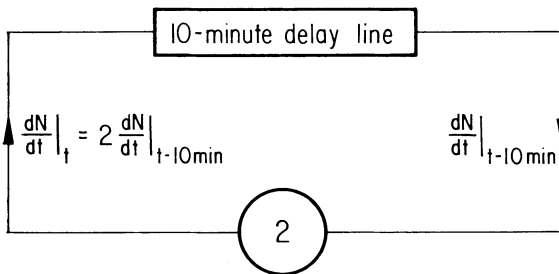


FIG. 3. A delay-line model of an idealized fission process. In this case the fission interval is 10 min.

3. The current products of fission enter a 10-min delay. On emerging from this delay, they immediately undergo fission again. Therefore, we may write a third equation to describe the population:

$$\frac{dN}{dt} \Big|_t = 2 \frac{dN}{dt} \Big|_{t-10} \tag{8}$$

For contrast, a diagrammatic representation of eq. (6) is presented in Fig. 4. The major distinction between the two representations is the replacement of the integrator in the classic model by a delay line. When one computes the appropriate value of α ($= \log 2/10$), he begins to suspect that the model of Fig. 3 is the more fundamental representation. This suspi-

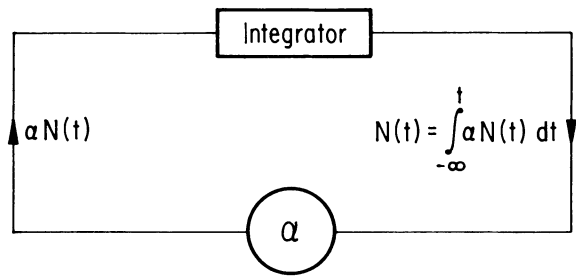


FIG. 4. The classic model for the idealized fission process of Fig. 3.

cion is confirmed when populations with several discrete delays, such as those of mammals, are considered. The relationship between α and the various delays becomes an end result of modeling rather than a starting point.

While it may be a more fundamental representation than eq. (6), eq. (8) also has somewhat more complicated solutions, which are difficult to express precisely in closed form. One can discuss this difference conveniently in terms of Fig. 3 and 4. The system of Fig. 4 has a single state variable, $N(t)$. If $N(t)$ is known for any single value of time, the behavior of the system can be predicted precisely for all time. It is simply

$$N(t) = N_0 e^{\alpha t}.$$

In order to predict completely the behavior of the system of Fig. 3, one must know the entire contents of the delay line at some moment in time. In other words, one must know the form of the function $N(t)$ over a complete 10-min span. Just as the initial value of N is constrained to be positive for eq. (6), the slope of $N(t)$ over the specified segment for eq. (8) is constrained to be greater than or equal to zero (assuming no death or migration). In serving as a boundary condition, this segment of $N(t)$ carries information about the proportion of the initial population participating in fission. Since we initially assumed that every bacterium participated, we must conclude that in this case our boundary conditions are compensating for a deficit in our model. Such a deficit is not present in the classic difference equation (eq. (7)). However, this form is no more fundamental nor useful than that of eq. (6) when several delays are involved.

Even when the contents of the delay line are specified at some point in time, it is difficult to express the future (or past) behavior of the system of Fig. 3 in analytical form. On the other hand, in this particular example it is not difficult to construct the behavior graphically. One simply draws the known segment of $N(t)$, then repeats it for successive 10-min intervals, amplifying it successively by factors of 2 (see Fig. 5).

From the known segment of $N(t)$, one also can

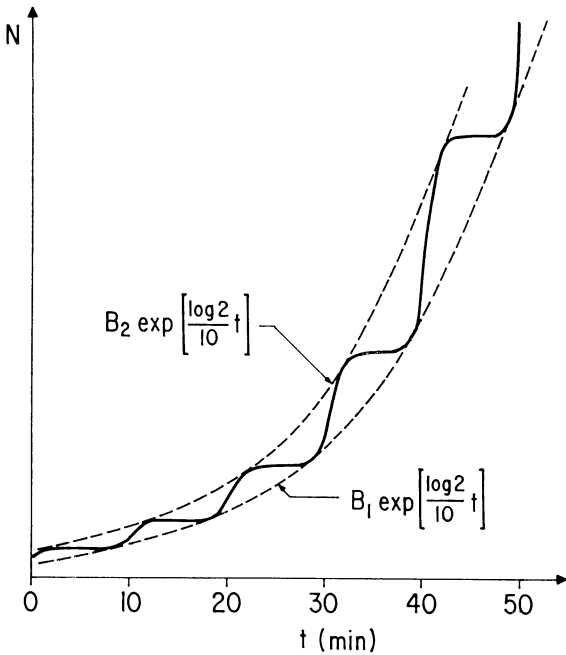


FIG. 5. One of many growth curves for the model of Fig. 3. Ordinate, population; abscissa, time.

find two exponential functions (as shown in Fig. 5) that precisely bound the behavior of the population. These functions have the form

$$A + B_1 \exp[\alpha t]$$

and $\alpha = \frac{\log 2}{10}$

$$A + B_2 \exp[\alpha t]$$

where the unit of time again is 1 min, and $A = 0$ if all of the initial population participates in fission. One can approximate the behavior of the system of Fig. 4 rather well with any function of the form

$$A + B \exp[\alpha t], \alpha = \frac{\log 2}{10}$$

where B lies between B_1 and B_2 . Such a Malthusean approximation will intersect the actual behavior every 10 min and will never be an error by more than 100%. Malthusean approximations with values of α that differ from $(\log 2)/10$, on the other hand, will diverge progressively from the actual behavior and the maximum error will increase without limit. The exponential coefficient of the nondiverging Malthusean approximation can be found by substituting $e^{\alpha t}$ into eq. (8):

$$\alpha e^{\alpha t} = 2\alpha e^{\alpha(t+10)}$$

from which

$$\alpha = \frac{\log 2}{10}.$$

This value of α , then, can be taken as a long-term

average measure of the innate reproductive capability of the species represented by eq. (6) or the system of Fig. 3. Therefore, as is often done, we shall define α to be the biotic potential of that species.

DELAY LINE MODELS THAT LEAD TO DIFFERENTIAL-DIFFERENCE EQUATIONS

In probably their simplest application to vertebrate populations, delay lines can be used to represent the mean time (T_1) between birth and the initiation of offspring production and the mean duration (T_2) of the productive period. If one ignores age-dependent fecundity and assumes that the rate of production of new females, \dot{N}_{pf} , is directly proportional to the total number of productive adult females, N_{pf} , he can write

$$\dot{N}_{pf} = kN_{pf}. \tag{9}$$

Assuming no deaths,

$$N_{pf} = \int_{t-(T_1+T_2)}^{t-T_1} \dot{N}_{pf} dt. \tag{10}$$

Substituting eq. (9) into eq. (10) and decomposing the integral, one obtains

$$N_{pf} = k \int_{-\infty}^{t-T_1} N_{pf} dt - k \int_{-\infty}^{t-(T_1+T_2)} N_{pf} dt. \tag{11}$$

Differentiating both sides with respect to t leads to a simple differential difference form of eq. (9).

$$\frac{dN_{pf}}{dt} = k[N_{pf}(t - T_1) - N_{pf}(t - T_1 - T_2)]. \tag{11a}$$

Substituting $e^{\alpha t}$ for N_{pf} in eq. (11) or (11a), one can find the Malthusean approximation and a transcendental equation relating the biotic potential, α , implicitly to T_1 and T_2 :

$$\alpha = k e^{-\alpha T_1} (1 - e^{-\alpha T_2}). \tag{12}$$

One also can construct a systems diagram directly from eq. (11) with its decomposed integral. However, a simpler, but completely equivalent diagram (Fig. 6) can be constructed directly from simple considerations of conservation and continuity. In the absence of death, the rate at which the population of productive females changes is completely determined by two terms—the rate of addition of newly maturing females (i.e., the rate at which females emerge from delay T_1) and the rate of removal of sexually senescent females (i.e., the rate at which females emerge from delay T_2). The delay line T_2 contains all the productive females and the integrator simply provides a running total of that delay line's contents. The scalar k relates the total number of productive females to the rate of production of new

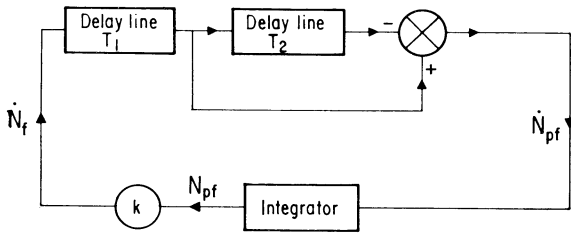


FIG. 6. A delay-line model of natality in an idealized deathless vertebrate population, \dot{N}_f is the present birth-rate of females; N_{pf} is the total number of sexually productive females; T_1 is time from birth to sexual maturity; T_2 is the duration of sexual productivity.

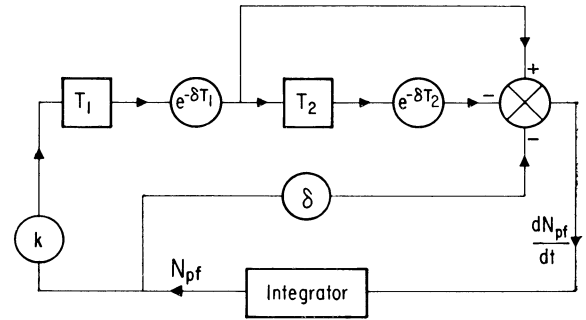


FIG. 7. The model of Fig. 6 with a nonselective death process added. The poisson death rate is δ (individuals per individual unit time).

females, which then enter delay T_1 . The characteristic differential-difference equation (11a) can be found by direct analysis of the system diagram, beginning at the right of the summing point.

The effects of an ideal, nonselective (i.e., Poisson) death process can be added rather simply to the model. If the fractional death rate is δ deaths per individual per unit time, then one can account for the deaths in each time delay, T , by introducing a survivorship scalar, $e^{-\delta T}$, in series with it. Thus the rate at which surviving individuals emerge from a delay T is $e^{-\delta T}$ times the rate at which they entered it T time units ago. The rate of change of productive females now has three components: the rate of addition of young females surviving to maturity:

$$(e^{-\delta T_1}) \dot{N}_f(t - T_1) ,$$

the rate of subtraction of females surviving to sexual senescence:

$$(e^{-\delta(T_1+T_2)}) \dot{N}_f(t - T_1 - T_2) ,$$

and the rate of attrition due to death:

$$\delta N_{pf}(t) .$$

These processes are represented in the systems diagram of Fig. 7. Beginning at the right of the summing point in this figure, one easily can write the characteristic differential-difference equation for the system:

$$\frac{dN_{pf}}{dt} = e^{-\delta T_1} N_{pf}(t - T_1) - e^{-\delta(T_1+T_2)} N_{pf}(t - T_1 - T_2) - \delta N_{pf}(t) . \quad (13)$$

The transcendental equation for the biotic potential becomes

$$\alpha = (e^{-\delta T_1}) e^{-\alpha T_1} - (e^{-\delta(T_1+T_2)}) e^{-\alpha(T_1+T_2)} - \delta . \quad (13a)$$

Systems models, such as those of Fig. 6 and 7, that contain both delay lines and integrators in any loop inherently lead to differential-difference equations. The two population models of Fig. 6 and 7 led to differential-difference equations of the retarded

type (Bellman and Cooke 1963, Hale 1971). This will be a common result in population models whose dynamic properties are determined both by discrete delays and by mass-action phenomena. (The models of Fig. 6 and 7 contain two first-order mass-action phenomena: a first-order natality process and a first-order death process.) Many population systems are represented most naturally by models that incorporate mass action; and when delays also are important in such systems, then models often lead to retarded differential-difference equations (see Wangersky and Cunningham 1956, Tognetti and Mazanov 1970). Such equations generally are extremely difficult to manage analytically.

DELAY-LINE MODELS THAT LEAD TO SIMPLE LINEAR DIFFERENCE EQUATIONS

If one looks into the fine structure of the natality process, one generally finds discrete processes with fixed delays. Thus, for example, it often is more natural to discuss a reproductive interval than a reproductive rate. The latter is only approximated by the reciprocal of the former; and in some cases, such as that of binary fission, the approximation is rather gross. One can model such reproductive intervals quite naturally and easily with delay lines. As an example, consider a population of idealized fin whales. On reaching sexual maturity (at age T_1), a female whale becomes pregnant, producing one calf at the end of her first gestation period (T_G) and becoming pregnant again at the end of her nonreproductive lactation period (T_L). She continues this process as long as she survives, producing one calf every T_L plus T_G years. Half the calves born at any given time are female. The proportion of female calves surviving to become sexually mature adults is γ_1 . (This factor may include the effects of infant mortality due to deaths of lactating females.) The survivorships for pregnant and lactating females are γ_G and γ_L respectively. With simple bookkeeping (conservation) one easily can construct an appropriate systems diagram (Fig. 8) from the verbal model. Beginning at the

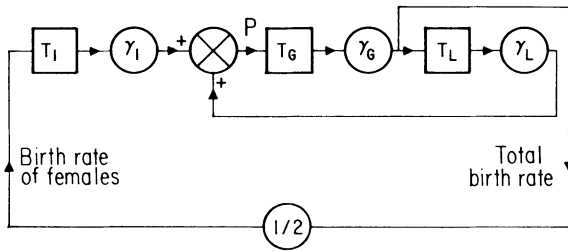


FIG. 8. A very simple model of fin-whale natality (see text for details).

left in Fig. 8, one requires a delay of T_1 and a survivorship scalar γ_1 between the rate of production of newborn females and the rate at which maturing females are added to the productive population. The rate of addition of maturing females is summed with the rate at which already-productive females are completing lactation, the sum representing the present rate of impregnation. Between impregnation and birth, a gestation delay of T_G and a survivorship scalar γ_G are required. The total birth rate is divided by 2 to yield the rate of production of females, which is the input to the first delay line, T_1 . After giving birth, the females are delayed by T_L and scaled by γ_L before reentering the reproductive pool and becoming pregnant again. From the diagram one can write a characteristic difference equation, the exponential solution of which will yield the biotic potential of the idealized whale population. For convenience, we can write the equation in terms of the output of the summer (i.e., the rate of impregnation P):

$$P = (1/2)\gamma_1\gamma_G P(t - T_G - T_1) + \gamma_G\gamma_L P(t - T_G - T_L). \quad (14a)$$

Substituting e^{at} for P , one finds

$$1 = (1/2)\gamma_1\gamma_G e^{-a(T_G+T_1)} + \gamma_G\gamma_L e^{-a(T_G+T_L)}, \quad (14b)$$

which is a transcendental expression giving the biotic potential implicitly in terms of the delays and survivorships.

One might wish to include even more fine structure of natality in the model. For example, adult females that are neither pregnant nor lactating do not automatically and instantaneously become pregnant. Therefore the ovulation interval becomes a potentially important factor. Again, one can model this with delay lines. Consider the same baleen whale population, but with an ovulation interval T_0 and a probability β of impregnation at any given ovulation. This leads to the systems diagram of Fig. 9. Baleen whales (and most other groups of mammals) show seasonal variation in fecundity, rate of impregnation, or both. This can be incorporated in the scalar β by making it time dependent. Finally, there is some evidence (Laws 1961) that nulliparous baleen whales have ovulation intervals of as much as a year, while

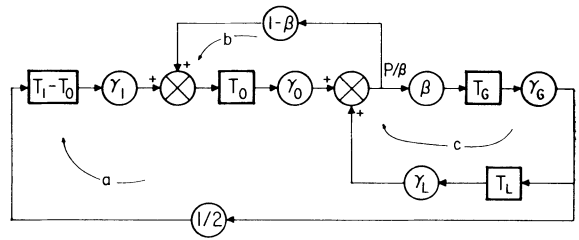


FIG. 9. A slightly more complete model of fin-whale natality. P represents the rate of impregnation (see text for remaining details).

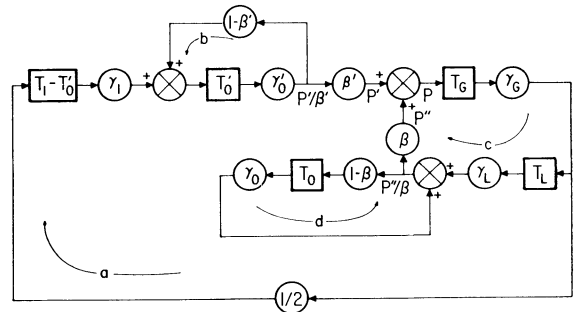


FIG. 10. An even more complete model of fin-whale natality. T'_0 represents the ovulation interval for nulliparous whales, and β' is the probability of impregnation of an ovulating nulliparous whale (see text for remaining details).

the ovulation interval of primiparous and multiparous females generally is 1 month. This dichotomy can be included in the model quite easily, as shown in Fig. 10. Characteristic difference equations can be obtained easily for the systems of Fig. 9 and 10. In the case of Fig. 9, we must sum the effects of three loops:

$$(1/\beta)P(t) = \beta\gamma_G(1/2)\gamma_1\gamma_0 \frac{P(t - T_G - T_1)}{\beta} + (1 - \beta)\gamma_0 \frac{P(t - T_0)}{\beta} + \beta\gamma_G\gamma_L \frac{P(t - T_G - T_L)}{\beta} \quad (15)$$

where the first term on the right represents loop a ; the second term represents loop b ; and the third term represents loop c . The corresponding transcendental equation for the biotic potential is

$$1 = (1/2)\gamma_1\gamma_0\gamma_G\beta e^{-a(T_G+T_1)} + \gamma_0(1 - \beta)e^{-aT_0} + \gamma_G\gamma_L\beta e^{-a(T_G+T_L)}.$$

The system of Fig. 10 is more complicated, having four loops. Analysis proceeds most easily if the rate of impregnation is decomposed into P' and P'' and the effects of loops a and b are summed separately from the effects of c and d . For a and b , we have

$$(1/\beta')P'(t) = (1/2)\gamma_G\gamma_1\gamma'_0 [P'(t - T_G - T_1) + P''(t - T_G - T_1)] + (1 - \beta')\gamma'_0 \frac{P'(t - T'_0)}{\beta'}, \quad (16)$$

and for c and d we have

$$(1/\beta)P''(t) = \gamma_G\gamma_L[P'(t - T_G - T_L) + P''(t - T_G - T_L)] + (1 - \beta)\gamma_0 \frac{P''(t - T_0)}{\beta} \tag{17}$$

Next we can solve eq. (17) for $P'(t)$:

$$\begin{aligned} & \frac{1}{\beta'\beta\gamma_G\gamma_L} P''(t + T_G + T_L) - \frac{1}{\beta'} P''(t) - \frac{1 - \beta}{\beta\beta'} \frac{\gamma_0}{\gamma_G\gamma_L} P''(t - T_0 + T_G + T_L) \\ & = (1/2) \frac{\gamma_1\gamma'_0}{\beta\gamma_L} P''(t + T_L - T_1) - (1/2)\gamma_1\gamma'_0\gamma_G P''(t - T_G - T_1) \\ & - (1/2) \frac{\gamma_1\gamma'_0\gamma_0}{\gamma_L} \frac{1 - \beta}{\beta} P''(t - T_0 - T_1 + T_L) + (1/2)\gamma_1\gamma'_0\gamma_G P''(t - T_G - T_1) \\ & + \frac{(1 - \beta')\gamma'_0}{\beta\beta'\gamma_G\gamma_L} P''(t + T_G + T_L - T'_0) - \frac{(1 - \beta')\gamma'_0}{\beta'} P''(t - T'_0) \\ & - \frac{(1 - \beta')(1 - \beta)}{\beta'} \frac{\gamma_0\gamma'_0}{\gamma_G\gamma_L} P''(t - T_0 - T'_0 + T_G + T_L) \end{aligned} \tag{18}$$

from which one obtains a 10-term transcendental equation for the biotic potential.

Although eq. (14) and (18) may seem rather complicated, they are in fact simple linear difference equations, for which analytical techniques are well established (see Goldberg 1958). In addition to biotic potentials, the various oscillatory modes inherent in the models also can be evaluated by application of these techniques. Returning briefly to simple binary fission, the characteristic equation was

$$\frac{dN}{dt} \Big|_t = 2 \frac{dN}{dt} \Big|_{t - T}$$

(where T is the fission interval). This can be rewritten as follows:

$$\begin{aligned} \text{let } \tau &= \frac{t}{T} \\ \text{and } \frac{dN}{dt} &= x \\ \text{then } x_\tau &= 2x_{\tau-1} \end{aligned} \tag{19}$$

for all nonnegative integral values of τ . The solutions to linear difference equations such as this always take the form

$$x_\tau = m^\tau \tag{20}$$

where m is a root of the characteristic polynomial of the difference equation. The polynomial is found quite easily by collecting all terms of the difference equation on one side and substituting eq. (20). Thus, for eq. (19)

$$\begin{aligned} x_\tau - 2x_{\tau-1} &= 0 \\ m^\tau - 2m^{\tau-1} &= 0 \\ m - 2 &= 0 \\ m &= 2. \end{aligned}$$

$$\begin{aligned} P'(t) &= \frac{1}{\beta\gamma_G\gamma_L} P''(t + T_G + T_L) - P''(t) - \\ & \frac{1 - \beta}{\beta} \frac{\gamma_0}{\gamma_G\gamma_L} P''(t - T_0 + T_G + T_L), \end{aligned}$$

and the solution can be substituted for each P' term in eq. (16):

The solution by this method for simple binary fission becomes

$$\frac{dN}{dt} \Big|_{t_0 + \tau} = 2^\tau \frac{dN}{dt} \Big|_{t_0} \tag{21}$$

where the choice of t_0 is completely arbitrary. Geometrically, this solution represents a sequence of discrete points at integral values of τ . In order to describe the behavior of the equation completely, one would need an infinite sum of such solutions, one for each point on a continuous curve representing dN/dt over a span of T time units.

On the other hand, one can connect with a continuous curve all the points of a single solution of the form of eq. (21). Clearly, one such curve is given by

$$y(t_0 + t) = y(t_0) e^{\left(\frac{\log 2}{T}\right)t} \tag{22}$$

Furthermore, by appropriate choices of t_0 , one can obtain two solutions of this type that form, respectively, the upper and lower bounds of all such solutions intersecting the actual behavior of the system. This is precisely what was done graphically in Fig. 5. However, since these solutions represents dN/dt , they must be integrated to provide the bounds of N . Thus, if

$$y(t_m + t) = y(t_m) e^{\left(\frac{\log 2}{T}\right)t}$$

describes the upper (or lower) bound of all exponential solutions intersecting dN/dt , then

$$\begin{aligned} z(t_m + t) &= \frac{T}{\log 2} y(t_m) e^{\left(\frac{\log 2}{T}\right)t} \\ &= z(t_m) e^{\left(\frac{\log 2}{T}\right)t} \end{aligned}$$

describes the upper (or lower) bound of all exponential solutions intersecting N . Clearly, in the case of simple exponentials, integration does not alter the functional form of the bound. The upper and lower bounds, taken together, form an envelope confining the behavior of the system.

In the case of a linear natality process with more than one delay, the difference-equation solution generally will have oscillatory terms, and these can be incorporated as temporal fine structure in the envelope of the systems behavior. Presumably, in any practical model, each time delay can be expressed as an integer times a common divisor of all the delays (i.e., the common divisor becomes the unit element of an integral domain to which all the delays belong). The order of the resulting difference equation (and its characteristic polynomial) will be given by the longest time delay divided by the greatest unit element T (the greatest common divisor of all delays in the model).

Consider a simple population of idealized herring gulls. Beginning at age 3, each adult female annually produces a brood from which n females survive to full fledge (age 2 months) and $n \gamma$ survive to age 3. From the time of full fledge until the end of her life, each female faces a constant probability of death, which can be expressed as a fractional death rate, δ (deaths per bird per year). Employing delay

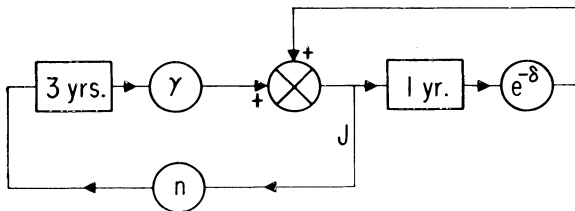


FIG. 11. A delay-line model of an idealized herring-gull population. J is the rate of nesting (see text for remaining details).

lines, one easily arrives at the systems model shown in Fig. 11. The greatest common divisor of the delays is 1 year, and the corresponding difference equation is

$$J_\tau = n\gamma J_{\tau-3} + e^{-\delta} J_{\tau-1} \tag{23}$$

where J is the rate of nesting, τ is an integer in the domain for which 1 year is unity, and

$$\gamma = \exp[-(17/6)\delta].$$

The characteristic equation is

$$(m^3 - e^{-\delta}m^2 - n\gamma) = 0, \tag{24}$$

and the solution to eq. (23) takes the form

$$J_\tau = a_1 m_1^\tau + a_2 m_2^\tau + a_3 m_3^\tau$$

where m_1, m_2 and m_3 are the roots of eq. (24).

By Descartes's rule we know that eq. (24) has at most one (the number of reversals of sign) positive real root. The remaining roots must be negative real

or complex conjugates. The positive real root will represent a growing term if the root is greater than unity, a constant term if the root is equal to unity, or a declining term if the root is less than unity. A negative real root represents oscillation at an apparent frequency of $1/2T$ (i.e., the term n^τ is positive for even τ , negative for odd τ). If the magnitude of the root is greater than unity, the oscillations will grow; if it is equal to unity, the oscillations will remain constant; if the magnitude of the root is less than unity, the oscillations will be damped. The same statements hold for a conjugate pair of complex roots; but the frequency of oscillation will not equal $1/2T$.

Thus J_τ generally will contain one nonoscillatory term and one or two oscillatory terms:

either

$$J_\tau = A|m_1|^\tau + B|m_2|^\tau \cos \pi\tau + C|m_3|^\tau \cos \pi\tau \tag{25a}$$

or

$$J_\tau = A|m_1|^\tau + B|m_2|^\tau \cos(\theta\tau + c) \tag{25b}$$

where $\tau \in \mathbb{Z}^+$;

and, the envelope of J will be given by two equations of the form

$$J_{env} = ae^{at} + be^{\beta t} \cos \pi t + ce^{\gamma t} \cos \pi t \tag{26a}$$

or

$$J_{env} = ae^{at} + be^{\beta t} \cos(\theta t + c). \tag{26b}$$

From the envelope of J alone, we cannot determine the envelope of N (in the sense of a curve that periodically is tangent to the actual solution). However, since J cannot be negative, we can determine the upper and lower bounds of all possible envelopes:

$$N \leq N_{max} = \int_{-\infty}^t (n\gamma J'_{env} - \delta N_{max}) dt \tag{27a}$$

$$N \geq N_{min} = \int_{-\infty}^t (n\gamma J''_{env} - \delta N_{min}) dt \tag{27b}$$

where J'_{env} describes the upper bound of J and J''_{env} describes the lower bound. Evaluation of N_{max} and N_{min} can be achieved quite easily with the aid of Laplace transforms. From (27a), for example,

$$\mathcal{L}(N_{max}) = n\gamma \mathcal{L}(J'_{env}) / (s + \delta) \tag{28}$$

where s is the complex variable of the Laplace transform. The function N_{max} can be found directly from eq. (28). Qualitatively, the effects of the factor $1/(s + \delta)$ on J'_{env} are threefold: (1) The relative amplitudes of the various components (oscillatory and nonoscillatory) are changed, the slower or lower frequency components being favored. (2) The oscillatory components will be shifted in phase (but not in frequency). (3) An additional nonoscillatory term,

$De^{-\delta t}$, will appear. For a quantitative example of these effects, consider the second term in eq. (26b),

$$be^{\beta t} \cos(\theta t + c).$$

The factor $1/(s + \delta)$ converts this term to

$$b'e^{\beta t} \cos(\theta t + c + \Psi) + d'e^{-\delta t} \quad (29a)$$

where

$$b' = \frac{b}{\sqrt{(\delta + \beta)^2 + \theta^2}} \quad (29b)$$

$$\Psi = -\tan^{-1} \frac{\theta}{\delta + \beta}. \quad (29c)$$

Such shifting of amplitude and phase, of course, does not alter the rate constants and frequencies of the various terms; therefore, we can obtain the biotic potential along with the frequencies of various oscillations directly from the solution of eq. (23), or analogous equations from other linear natality models.

RELATIONSHIP TO THE LESLIE MODEL

If we are content to ignore the temporal fine structure embedded in the initial functions (i.e., the initial contents of the delay lines) of the models of the previous section, and instead concentrate on the envelopes and the natural frequencies contained in those envelopes, then we effectively reduce the number of state variables in the models to a finite set. In fact, the dimension k of the state space becomes simply the order of the difference equation, which

can be replaced by a vector state equation consisting of a $k \times k$ state projection matrix and a k -order state vector. In the case of the herring gulls we can write

$$\begin{bmatrix} J_i \\ J_{i-1} \\ J_{i-2} \end{bmatrix}_{i=\tau+1} = \begin{bmatrix} e^{-\delta} & 0 & n\gamma \\ 1 & 0 & 0 \\ 0 & 1 & 0 \end{bmatrix} \begin{bmatrix} J_i \\ J_{i-1} \\ J_{i-2} \end{bmatrix}_{i=\tau}. \quad (30)$$

Because mass action could be ignored and continuity could replace conservation, the elements of the state vector are rates rather than age cohorts.

If, on the other hand, we had taken the mass action approach, the elements of the state vector would be age cohorts and the elements of the state projection matrix would be different.

Since natality in individual gulls is assumed in the model of Fig. 11 to be precisely annual, it is simplest to formulate the corresponding Leslie matrix by assuming that the entire population is synchronous. Define $t = 0$ to be immediately after egg laying (each nest has a full clutch), and τ is an integer defined by

$$\tau = t/T; T = 1 \text{ year}.$$

The number of eggs, N_0 , at $\tau + 1$ is given by

$$(N_0)_{\tau+1} = n_0 e^{-\delta} [(N_2)_{\tau} + (N_3)_{\tau} + \dots + (N_k)_{\tau}]$$

where $(N_x)_{\tau}$ is the number of x -year-old female gulls alive at τ . The parameter n has been factored into n_0 (the number of female eggs per clutch) and γ_0 (the survivorship of those eggs to full fledge). The resulting state equation is

$$\begin{bmatrix} N_0 \\ N_1 \\ \cdot \\ \cdot \\ \cdot \\ \cdot \\ \cdot \\ \cdot \\ N_k \end{bmatrix}_{\tau+1} = \begin{bmatrix} 0 & 0 & n_0 e^{-\delta} & n_0 e^{-\delta} \\ \gamma' & 0 & 0 & 0 \\ 0 & e^{-\delta} & 0 & 0 \\ 0 & 0 & e^{-\delta} & 0 \\ \cdot & \cdot & \cdot & \cdot \\ 0 & 0 & 0 & \cdot \end{bmatrix} \begin{bmatrix} N_0 \\ N_1 \\ \cdot \\ \cdot \\ \cdot \\ \cdot \\ \cdot \\ \cdot \\ N_k \end{bmatrix}_{\tau} \quad (31)$$

where $\gamma' = \gamma_0 e^{-(5/6)\delta}$.

Owing to the transcendental nature of the model (which was employed as a reasonable convenience rather than a logical necessity), k in the Leslie formulation is not finite. Nonetheless, the characteristic polynomial and eigen values (λ 's) of the matrix are easily found. First, from the method outlined in Pielou (1969: 30) we have

$$\lambda^{k+1} - \gamma' n_0 e^{-2\delta} \lambda^{k-2} - \gamma' n_0 e^{-3\delta} \lambda^{k-3} - \dots - \gamma' n_0 e^{-k\delta} = 0,$$

which can be simplified as follows:

$$\lambda^{k+1} - \gamma' n_0 \lambda^k \sum_{j=2}^k (e^{-\delta} \lambda^{-1})^j = 0$$

$$\lambda - \gamma' n_0 \sum_{j=0}^k (e^{-\delta} \lambda^{-1})^j + \gamma' n_0 + \gamma' n_0 e^{-\delta} \lambda^{-1} = 0$$

$$\lim_{k \rightarrow \infty} \sum_{j=0}^k (e^{-\delta} \lambda^{-1})^j = \frac{1}{1 - e^{-\delta} \lambda^{-1}}$$

$$\lambda - \frac{\gamma' n_0}{1 - e^{-\delta} \lambda^{-1}} + \gamma' n_0 + \gamma' n_0 e^{-\delta} \lambda^{-1} = 0$$

$$\lambda - e^{-\delta} - \gamma' n_0 + \gamma' n_0 - \gamma' n_0 e^{-\delta} \lambda^{-1} + \gamma' n_0 e^{-\delta} \lambda^{-1} - \gamma' n_0 e^{-2\delta} \lambda^{-2} = 0$$

$$\lambda^3 - e^{-\delta} \lambda^2 - n\gamma = 0 \quad (n\gamma = \gamma' n_0 e^{-2\delta}).$$

Thus the Leslie formulation leads to the same characteristic polynomial as the delay-line formulation.

The Leslie matrix is a bit more cumbersome than that of eq. (30); but this is due simply to the transcendental nature of the model. Since the dimension of the state space is three, we could have simplified the Leslie approach by considering only three cohorts N_1, N_2 , and all adults N_A :

$$N_A = \sum_3^{\infty} N_i$$

$$\begin{pmatrix} N_1 \\ N_2 \\ N_A \end{pmatrix}_{\tau+1} = \begin{pmatrix} 0 & 0 & n_0 e^{-\delta} \\ \gamma' & 0 & 0 \\ 0 & e^{-\delta} & e^{-\delta} \end{pmatrix} \begin{pmatrix} N_1 \\ N_2 \\ N_A \end{pmatrix}_{\tau} \quad (32)$$

The characteristic polynomial can be found quite easily by noting that for any eigen value λ , and its corresponding eigen vector,

$$(N_A)_{\tau+1} = \lambda(N_A)_{\tau} = e^{-\delta}(N_2)_{\tau} + e^{-\delta}(N_A)_{\tau},$$

from which

$$(N_A)_{\tau} = \frac{e^{-\delta}}{\lambda - e^{-\delta}} (N_2)_{\tau}$$

and

$$(N_A)_{\tau+1} = \frac{\lambda e^{-\delta}}{\lambda - e^{-\delta}} (N_2)_{\tau}.$$

This allows the matrix to be displayed in the standard Leslie form

$$\begin{pmatrix} 0 & 0 & n_0 e^{-\delta} \\ \gamma' & 0 & 0 \\ 0 & \frac{\lambda e^{-\delta}}{\lambda - e^{-\delta}} & 0 \end{pmatrix}$$

and the characteristic polynomial can be obtained directly (Pielou 1969):

$$\lambda^3 - \frac{\gamma' n_0 e^{-2\delta} \lambda}{\lambda - e^{-\delta}} = 0$$

$$\lambda^4 - e^{-\delta} \lambda^3 - n \gamma \lambda = 0$$

$$\lambda^3 - e^{-\delta} \lambda^2 - n \gamma = 0.$$

Thus, if we assume that natality in the gulls is synchronized, we can develop a simple Leslie formulation that leads to precisely the same characteristic polynomial as the difference equation derived from the delay-line model. If time is considered discrete, both methods lead to a three-dimensional state vector and to projection matrices that are similar and contain simple biological parameters. Thus, if one wishes to consider time as a discrete variable, the two approaches are equally easy and, accepting the assumption of synchronized natality, equally intuitive. This is true of all linear natality models in which the time delays have a common divisor that can serve as the unit element of an integral domain to which all time delays belong.

In the case of the fin-whale model of Fig. 9, however, the greatest common divisor that can serve as a unit element of the time delays is, at most, 1 month (the ovulation interval). Therefore, an algebraic state equation, whether generated by the delay-line or the Leslie approach, will be of awkwardly high degree for analysis. Furthermore, if any of the time delays is carried as a parameter with unspecified value, as it might be in sensitivity studies, then variation of that parameter will lead to variation in the degree structure of the polynomial rather than to variations of its coefficients. In other words, the time-delay parameter is not carried explicitly in the characteristic polynomial of the algebraic state equations. It is carried explicitly, however, in the transcendental characteristic equations (such as eq. (13b) and (14b)) derived directly from the characteristic differential-difference or difference equations of the delay-line models. In this case, therefore, the delay-line model has very distinct advantages, the most important of which is that it allows us to deal simply, directly, and realistically with nonuniform age classes.

THE INTEGRAL APPROACH VERSUS THE DIFFERENTIAL APPROACH

In most population models, natality is viewed as a mass-action phenomenon, with the present natality rate taken to be determined either by the total number of sexually productive females or by the weighted sums of the numbers occupying various age classes. This approach, which has been quite successful, is an application of the classical state-variable method; in which the rates of change of state variables are related (by a state-transition matrix) to those variables themselves. Most population models incorporating time delays also have been based on the state-variable approach. In these cases, however, the present rates of change of the state variables are related not to the present values of those variables but to their values at some fixed interval of time prior to the present. Once this has been done, of course, the notion of state variable is no longer particularly useful; and one must think in terms of state functions. Nonetheless, the models generated by this approach can be useful (see Wangersky and Cunningham 1956, Frank 1960, Lefkovitch 1966, Kiefer 1968, Pennyquick, Compton, and Beckingham 1968, Tognetti and Mazanov 1970). In general, these models are characterized by their property of relating the present natality rate either to the total population at some time in the past or to the weighted sum of age cohorts at some time past. Conceptually, using this approach, one converts rates to populations by integration, then delays the products of integration to generate future rates. Since this approach, strictly speaking, is not a state-variable approach, and since continuous systems models generated by this approach can be identified

by the presence of integrators in the loops representing natality, it might well be called an "integral" approach.

In this paper a second approach has been introduced. Here, rather than introducing delays into the population or the population vector, we have introduced them into the rates themselves. Present rates are related to rates at key times in the past rather than to total numbers. In its purest form, this method leads to systems models (Fig. 3, 8, 9, 10) that are completely devoid of integrators in the loops representing natality. Formally, these pure delay models are specific forms of the renewal equation, in which the weighting factor [$\alpha(\gamma)$ in eq. (2)] is a sequence of Dirac delta functions. Because of the lack of integrators in the systems models, this approach might well be called a "differential" approach.

The models of Fig. 6 and 7 represent a hybrid approach. Natality is taken to be a mass-action phenomenon, but the time delays are applied to the rates rather than the populations. Fundamentally, this approach is quite similar to those of Wangersky and Cunningham (1956) and Tognetti and Mazanov (1970). Conceptually, however, it differs in that the time delays are placed ahead of the integrators instead of after them. Formally, the hybrid integral-differential approach represented by Fig. 6. and 7 is a specific form of the renewal equation in which the weighting factor is a sequence of steps.

It is not my intention to propose that either the differential approach or the integral approach is inherently better than the other and therefore leads to more realistic models. I do assert, however, that the two methods differ heuristically, that depending on the circumstances one or the other will be more natural, and that the proper choice therefore will facilitate the modeling of the particular system at hand. Clearly, where dynamics are most easily described in terms of mass action, as of course they often are, the integral approach is indicated. On the other hand, time delays generally (but not always) can be modeled most easily by the differential approach. Where time delays are coupled to mass action, the most natural overall approach may be hybrid, in which case a differential-difference equation will result. Certain linear natality processes, as we have shown, can be modeled with a purely differential approach, in which case simple difference equations result.

LITERATURE CITED

- Bellman, R., and K. L. Cooke. 1963. Differential-difference equations. Academic Press, New York. 462 p.
- Bharucha-Reid, A. T. 1960. Elements of the theory of Markov processes and their applications. McGraw-Hill, New York. 468 p.
- Bronk, B. V., G. J. Dienes, and A. Paskin. 1968. The stochastic theory of cell proliferation. *Biophys. J.* **8**: 1353-1398.
- Feller, W. 1941. On the integral equation of renewal theory. *Ann. Math. Stat.* **12**:243-267.
- Frank, P. W. 1960. Prediction of population growth form in *Daphnia pulex* cultures. *Am. Nat.* **44**:357-372.
- Fredrickson, A. G. 1971. A mathematical theory of age structure in sexual populations: random mating and monogamous marriage models. *Math. Biosci.* **10**:117-143.
- Goldberg, S. 1958. Introduction to difference equations. Wiley, New York. 260 p.
- Goodman, L. A. 1967. On the reconciliation of mathematical theories of population growth. *J. Roy. Stat. Soc. A.* **130**:541-553.
- Hale, J. 1971. Functional differential equations. Springer-Verlag, Berlin. 238 p.
- Keyfitz, N. 1967. Reconciliation of population models, integral equation and partial fraction. *J. Roy. Stat. Soc. A.* **130**:61-83.
- Kiefer, J. 1968. A model of feedback-controlled cell populations. *J. Theoret. Biol.* **18**:263-279.
- Laws, R. M. 1961. Reproduction, growth and age of southern fin whales. *Discovery Rep.* **31**:327-486.
- Lefkovich, L. P. 1966. A population growth model incorporating delayed responses. *Bull. Math. Biophys.* **28**:214-233.
- Parlett, B. 1970. Ergodic properties of populations I: the one sex model. *Theoret. Popul. Biol.* **1**:191-207.
- Pennycuik, C. J., R. M. Compton, and L. Beckingham. 1968. A computer model for simulating the growth of a population or of two interacting populations. *J. Theor. Biol.* **18**:316-329.
- Pielou, E. C. 1969. An introduction to mathematical ecology. Wiley-Interscience, New York. 286 p.
- Sinko, J. W., and W. Streifer 1967. A new model for age-size structure of a population. *Ecology* **48**:910-918.
- . 1969. Applying models incorporating age-size structure of a population to *Daphnia*. *Ecology* **50**:608-615.
- . 1971. A model for populations reproducing by fission. *Ecology* **52**:330-335.
- Tognetti, K. P., and A. Mazanov. 1970. A two-stage population model. *Math. Biosci.* **8**:371-378.
- von Foerster, H. 1959. Some remarks on changing populations, p. 382-407. *In* Frederick S. Stohman [ed.] *The kinetics of cellular proliferation*. Grune and Stratton, New York.
- Wangersky, P. J., and W. J. Cunningham. 1956. On time lags in equations of growth. *Nat. Acad. Sci., Proc.* **42**: 699-702.