



A New Model For Age-Size Structure of a Population

Author(s): James W. Sinko and William Streifer

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Without a great deal of data on potential competitors, this type of control would be indistinguishable operationally from limitation through the utilization of a resource in critical supply, since the requirement for competition is the existence of such a resource. In this connection, it should be noted that in addition to the 2,801 specimens of Variety 2 extracted from field samples by electromigration, and the 595 specimens of Variety 2 calculated to have remained after electromigration, one sample contained Variety 4 of *Paramecium aurelia*. The sample was found positive a week after the extraction process, all three isolates being identified as Variety 4. Since the observation was made before any experimentation on the habitat, it seems likely that this was a case of a natural introduction. No more specimens of Variety 4 were collected in the habitat at any of the 53 subsequent samplings over the next 19 months, and it is evident that Variety 4 failed to establish itself. In this habitat, then, it may be concluded tentatively that competition from closely related species is not a factor determining the abundance of Variety 2. There is an obvious need for field experimentation on this point.

The evidence against other possible methods whereby the abundance of paramecia might be determined, together with the positive evidence that has been presented for control by the food supply, combine to make a convincing case for the latter. If similar conclusions can be drawn for those habitats where more than one variety can be found together, such situations should be fruitful for studies on natural competition and the methods by which competing species coexist.

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A NEW MODEL FOR AGE-SIZE STRUCTURE OF A POPULATION

JAMES W. SINKO* AND WILLIAM STREIFER

Electrical Engineering Department, University of Rochester, Rochester, New York 14627

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Abstract. An equation describing the dynamics of single species populations is derived. The model allows for variations in the physiological characteristics of animals of different ages and sizes. An analytical solution which holds under certain specific conditions is found. It is shown that Von Foerster's equation, the logistic equation and other prior models are special cases of the new model.

INTRODUCTION

Nearly all attempts to construct mathematical models of single species populations have assumed that all animals are physiologically identical regardless of size or age. Numerous ecologists, noting that a population of neonates generally

behaves differently than one of adults, have suggested that mathematical models would be more realistic if they incorporated dependence on age (Leslie 1948; Smith 1952; Cole 1957). As early as 1931 Bailey postulated a model for predator-prey relationships which distinguished animals in a population by their ages. His model leads to integro-differential equations which have not been

* Present address: Stanford Research Institute, Menlo Park, California 94025.

solved to date. Lewis (1942) and Leslie (1945) independently constructed an algebraic model which describes both the population size and age distribution. Von Foerster (1959) derived a partial differential equation to describe the age structure and size of a cellular population. Hoyle (1963) proposed this same equation in a discussion of the human population. As shown below, these three models are closely related.

Frank (1960) applied Leslie's algebraic model to laboratory populations of *Daphnia pulex* and found this model to be unsatisfactory. He discovered that under conditions of overcrowding many abnormally small animals would survive rather than fewer individuals of normal size. Thus the model predicted considerably smaller populations than actually occurred. Frank concluded that "biomass" might be a more meaningful measure of population than total number of individuals. Slobodkin (1954) experimentally studied a number of laboratory populations of *Daphnia obtusa*. He found that age or size alone was not sufficient to characterize the physiological behavior of an animal. Slobodkin concludes that "age and size taken together can be considered to define a class of physiologically identical animals until proven to the contrary." In the following we derive and discuss a model which includes both age and size.

$$\frac{\partial \eta(t, a, m)}{\partial t} + \frac{\partial \eta(t, a, m)}{\partial a} + \frac{\partial}{\partial m} [g(t, a, m) \eta(t, a, m)] = -D(t, a, m) \eta(t, a, m), \quad (2)$$

where the function $g(t, a, m)$ is the average rate of growth for an animal of age a and mass m at time t ,

$$g(t, a, m) = \frac{dm}{dt} = \frac{dm}{da}, \quad (3)$$

and the function $D(t, a, m)$ is the death rate for animals of age a and mass m at time t . The integral

$$\int_{m_0}^{m_1} \int_{a_0}^{a_1} D(t, a, m) \eta(t, a, m) da dm$$

is equal to the rate at which animals between ages (a_0, a_1) and masses (m_0, m_1) die. It should be noted that the functions g and D generally depend on other factors such as food supply, total biomass and total numbers in the population.

In order for the mathematical problem to be well set¹ one must specify boundary conditions for equation (2), i.e. the age-mass distribution of the original animals at time zero, $\alpha(a, m)$, and density of newborn, $\beta(t, m)$, i.e.

¹ See Sinko (1968) for a verification of the existence of solutions for equation (2).

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THE DENSITY EQUATION

We begin by introducing a density function $\eta(t, a, m)$ which depends on t time, a age, and m , a variable which may represent mass, volume, length, caloric content, or any other physical attribute which characterizes the physiological behavior of an individual animal. The total number of animals between ages (a_0, a_1) and masses (m_0, m_1) at time t is given by

$$\int_{m_0}^{m_1} \int_{a_0}^{a_1} \eta(t, a, m) da dm. \quad (1)$$

If a_0 and m_0 are chosen to be zero, and a_1 and m_1 infinity, the integral (1) yields the total number of animals in the population. Other quantities of interest such as average age, average mass, etc. are obtainable from a knowledge of $\eta(t, a, m)$, e.g. the total biomass is given by

$$\int_0^\infty \int_0^\infty m \eta(t, a, m) da dm.$$

As shown in the Appendix, the age-mass density function $\eta(t, a, m)$ satisfies the partial differential equation

$$\alpha(a, m) = \eta(0, a, m) \quad (4)$$

$$\beta(t, m) = \eta(t, 0, m). \quad (5)$$

In many situations $\beta(t, m)$ is given by

$$\beta(t, m) = \int_0^\infty \int_0^\infty f(t, a, m', m) \eta(t, a, m') da dm', \quad (6)$$

where $f(t, a, m', m) dm$ is the rate at which animals of mass m' and age a give birth to neonates with masses between m and $m + dm$. The mathematical problem is complicated by the fact that the boundary condition (6) is dependent upon the density function itself. Thus, since β , D and g vary with η , the model incorporates "density dependent factors" as suggested by Nicholson (1957) and Slobodkin (1961).

In certain special cases it is possible to find an analytic solution of equation (2). Let g be a function of t and a only and let D be independent of η so that equation (2) becomes

$$\frac{\partial \eta}{\partial t} + \frac{\partial \eta}{\partial a} + g(t, a) \frac{\partial \eta}{\partial m} = -D(t, a, m) \eta. \quad (7)$$

Since equation (7) is linear, it is equivalent to the

following system of three ordinary differential equations (see Courant and Hilbert 1962, p. 70)

$$dt = da = \frac{dm}{g(t, a)} = \frac{d\eta}{-D(t, a, m)\eta} \quad (8)$$

The solution of the left-hand equation of (8) is

$$a = \begin{cases} t + a_i & a > t \\ t - t_0 & a < t, \end{cases} \quad (9)$$

where a_i is the initial age of an original animal (i.e. its age at time 0) and t_0 is the time of birth of a new animal. Inserting the values of a from equation (9) into $g(t, a)$ yields

$$\ln \eta = \begin{cases} - \int_0^t D[t', t' + a_i] \int_0^{t'} g(t'', t'' + a_i) dt'' + m_i] dt' + \ln[\alpha(a_i, m_i)], & a > t \\ - \int_{t_0}^t D[t', t' - t_0] \int_{t_0}^{t'} g(t'', t'' - t_0) dt'' + m_0] dt' + \ln[\beta(t_0, m_0)], & a < t, \end{cases} \quad (11)$$

where t' and t'' are variables of integration, and α and β are the initial age-mass distribution and the density of newborn, respectively. By taking the exponential of equation (11) and employing the relations

$$\begin{matrix} a_i = a - t & a > t \\ t_0 = t - a & a < t \end{matrix}$$

$$(\eta t, a, m) = \begin{cases} \alpha[a - t, m - \int_0^t g(t', t' + a - t) dt'] \times \exp \left\{ - \int_0^t D[t', t' + a - t, m - \int_{t'}^t g(t'', t'' + a - t) dt''] dt' \right\}, & a > t \\ \beta[t - a, m - \int_{t-a}^t g(t', t' - t + a) dt'] \times \exp \left\{ - \int_{t-a}^t D[t', t' - t + a, m - \int_{t'}^t g(t'', t'' - t + a) dt''] dt' \right\}, & a < t. \end{cases} \quad (12)$$

With the functions α , β , g and D specified, equation (12) completely describes the ages and masses of all animals in the population.

The assumption that g and D do not depend upon η is somewhat restrictive because it does not allow the population to be limited by "density effects" other than by a reduction in fecundity. If the population were food limited, the rate of growth of an individual animal, g , would depend on η or some function of η . Similarly, if the population were limited by an increased death rate caused by accumulating metabolites or increasing physical encounters between individuals, D would in some way depend on η . If the number of neonates entering the population is controlled by some outside source, such as the experimenter, $\beta(t, m)$ is known and equation (12) gives the complete solution of equation (7). However, if the neonates result from births within the population $\beta(t, m)$ must be determined from equation (6). The solution for η in the region $a > t$ will still be known, but in the region $a < t$, $\beta(t, m)$ will

$$m = \begin{cases} \int_0^t g(t', t' + a_i) dt' + m_i, & a > t \\ \int_{t_0}^t g(t', t' - t_0) dt' + m_0, & a < t, \end{cases} \quad (10)$$

where t' is a variable of integration, m_i is the initial mass of an original animal and m_0 is the mass of some neonate at time t_0 . By substituting equations (9) and (10) into $D(t, a, m)$ and integrating, we obtain

$$\begin{aligned} m_i &= m - \int_0^t g(t', t' + a - t) dt' & a > t \\ m_0 &= m - \int_{t_0}^t g(t', t' - t + a) dt' & a < t \end{aligned}$$

we find

depend upon an integral of η . Thus we obtain an integral equation for η whose solution is, in general, difficult to find analytically.

An equation similar to equation (2) has recently been proposed by Oldfield (1966) for cell populations. His equation has three variables, one of which would normally represent age, and the other two are used to represent physical properties of the cells such as mass or electrical resistivity of the cell membrane. Oldfield defines "rate functions," which correspond to the growth function g in equation (2), in such a way that they can depend only on time and the variable they determine. If this were done in equation (2), g would be a function of t and m only. It should be pointed out that the equation he presents holds if more general rate functions are used. [There is a trivial sign error in Oldfield's equation (7) which affects the remainder of his paper.]

By following the method Oldfield uses to obtain his solution, one can find an analytic solution of equation (2) in the special case when:

- (1) g is a function of t and m only.
- (2) D is not a function of η .
- (3) Each animal has the same maximum lifespan, and at the end of this lifespan the animal cleaves into two identical neonates.
- (4) A neonate has the same value of m as its parent.

It is obvious that m cannot represent mass in this case because of the fourth assumption. It may be possible to use m to represent some property such as the ratio of nitrogen content to total dry mass.

No doubt other analytic solutions can be found, but it is likely that they too will place serious restrictions on the population. Numerical solutions are probably necessary to solve equations used to describe more realistic situations. Nevertheless, the analytic solutions are useful for checking numerical calculations and determining basic dependencies. Numerical solutions for *Daphnia pulex* and *Dugesia tigrina* have been obtained and are being prepared for publication.

$$\left. \frac{\partial n}{\partial t} + \frac{\partial n}{\partial a} + g(t, a, m) \eta(t, a, m) \right|_0 = - \int_0^{\infty} D(t, a, m) \eta(t, a, m) dm. \quad (15)$$

Now letting $D(t, a)$ be the mass averaged death rate of all animals age a at time t ,

$$D(t, a) = \frac{\int_0^{\infty} D(t, a, m) \eta(t, a, m) dm}{\int_0^{\infty} \eta(t, a, m) dm}$$

and noting that $\eta(t, a, 0) = \eta(t, a, \infty) = 0$, i.e. there are no animals of zero or infinite mass, we observe that equation (15) is identical to equation (13), Von Foerster's equation. Thus the rigorous derivation of equation (2) presented in the Appendix also serves as a derivation of equation (13). There appears to be no other rigorous derivation of this equation in the literature, even though its application to cell populations has been actively investigated in the last few years (Von Foerster 1959; Trucco 1965a, b; Oldfield 1966).

A number of models describing animal populations (Bailey 1931; Lewis 1942; Leslie 1945) are related to equation (13) as shown below. If in Bailey's model we let the number of parasites be zero, we obtain the following equations for the host population²

$$n(t, a) = l(a) B(t - a) \quad (16)$$

² Bailey's notation has been changed in the interests of uniformity.

RELATION TO OTHER MODELS

Equation (2) includes Von Foerster's equation (see also Hoyle 1963),

$$\frac{\partial n}{\partial t} + \frac{\partial n}{\partial a} = -D(t, a) n(t, a), \quad (13)$$

as a special case. Here, $n(t, a)$ is an age density function given by

$$n(t, a) = \int_0^{\infty} \eta(t, a, m) dm. \quad (14)$$

The number of animals at time t with ages between a_0 and a_1 is

$$\int_{a_0}^{a_1} n(t, a) da,$$

and the total number of animals in the population is found by setting $a_0 = 0$ and $a_1 = \infty$. We integrate equation (2) with respect to m and employ the definition (14) to obtain

$$B(t) = \int_0^{\infty} b(a) n(t, a) da, \quad (17)$$

where $n(t, a)$ is the same age density function that appears in the Von Foerster's equation, $l(a)$ is the fraction of animals surviving to age a , $B(t)$ is the total rate at which neonates enter the population at time t , and $b(a)$ is the rate at which an animal of age a bears young. To understand equation (16) note that $n(t, a) da$ animals are the survivors of $B(t - a) da$ neonates born in the interval $(t - a - da, t - a)$. Equation (17) is obvious. Taking the partial derivatives of equation (16) with respect to t and a and adding them yields

$$\frac{\partial n(t, a)}{\partial t} + \frac{\partial n(t, a)}{\partial a} = B(t - a) \frac{dl(a)}{da}.$$

We note that $B(t - a)$ is equivalent to $n(t - a, 0)$ and that

$$l(a) = \frac{n(t, a)}{n(t - a, 0)}.$$

Thus

$$\frac{\partial n(t, a)}{\partial t} + \frac{\partial n(t, a)}{\partial a} = \frac{1}{l(a)} \frac{dl(a)}{da} n(t, a). \quad (18)$$

It is well known (see Lotka 1925) that

$$D(a) = - \frac{1}{l(a)} \frac{dl(a)}{da}, \quad (19)$$

where $D(a)$ is the death rate of animals of age a . Equations (18) and (19) yield

$$\frac{\partial n(t, a)}{\partial t} + \frac{\partial n(t, a)}{\partial a} = -D(a) n(t, a). \quad (20)$$

Thus we see Bailey's model reduces to Von Foerster's equation when D depends only on age. Equation (17) is the same as that proposed by Hoyle (1963) as a boundary condition for equation (13).

The model proposed independently by Lewis (1942) and Leslie (1945) is a discrete or difference equation representation of population dynamics. In the limit they reduce to equations (13) and (17). We generalize Leslie's birth and death functions so that they are time dependent and modify his notation to conform with that employed herein. Let Δ be a time increment and define $n_{\Delta}(t, a)$ as the number of animals at time t with ages between a and $a + \Delta$. $D_{\Delta}(t, a)$ is the probability that an animal of age $(a, a + \Delta)$ at time t will die³ in the time interval $(t, t + \Delta)$, and $b_{\Delta}(t, a)$ is the number of newborn in the time in-

terval $(t, t + \Delta)$ per animal of age $(a, a + \Delta)$ at time t . If the maximum lifespan of an animal is $k \cdot \Delta$, the equations

$$n_{\Delta}(t + \Delta, a + \Delta) - n_{\Delta}(t, a) = -D_{\Delta}(t, a) n_{\Delta}(t, a) \quad (21)$$

$$n_{\Delta}(t + \Delta, 0) = \sum_{i=1}^k b_{\Delta}(t, i \cdot \Delta) n_{\Delta}(t, i \cdot \Delta) \quad (22)$$

follow directly from the definitions of $D_{\Delta}(t, a)$ and $b_{\Delta}(t, a)$. From the definition of $n(t, a)$ given above

$$n_{\Delta}(t, a) = \int_a^{a+\Delta} n(t, a') da', \quad (23)$$

where a' is a variable of integration. Implicit in equation (21) is the fact that time and age advance at the same rate, i.e.

$$\frac{dt}{da} = 1. \quad (24)$$

Upon substituting equation (23) in equation (21) and dividing by Δ we obtain

$$\int_a^{a+\Delta} \frac{n(t + \Delta, a' + \Delta) - n(t, a')}{\Delta} da' = -\frac{D_{\Delta}(t, a)}{\Delta} \int_a^{a+\Delta} n(t, a') da'$$

which by application of the mean value theorem for integrals becomes

$$\frac{n(t + \Delta, \theta + \Delta) - n(t, \theta)}{\Delta} = -\frac{D_{\Delta}(t, a)}{\Delta} n(t, \theta), \quad a < \theta \leq a + \Delta. \quad (25)$$

In the limit as Δ goes to zero the left-hand side of equation (25) becomes the total derivative of n with respect to t and

$$\lim_{\Delta \rightarrow 0} \frac{D_{\Delta}(t, a)}{\Delta} = D(t, a),$$

the death rate for animals of age a . Thus equation (25) becomes

$$\frac{dn(t, a)}{da} = -D(t, a) n(t, a). \quad (26)$$

Equations (24) and (26) can be combined into

$$dt = da = \frac{dn}{-D(t, a)n}. \quad (27)$$

This system of ordinary differential equations is equivalent to Von Foerster's partial differential equation by the theory of characteristics (see Courant and Hilbert 1962; Sneddon 1957).

Certain studies of Frank (1960) and Slobodkin (1953) are also noteworthy. Frank used Leslie's model, with b_{Δ} and p_{Δ} (and thus D_{Δ}) dependent upon the total number of animals, in an

³ Leslie uses $p_{\Delta}(t, a)$, the probability an animal will survive in a time interval of length Δ ,

$$D_{\Delta}(t, a) = 1 - p_{\Delta}(t, a).$$

unsuccessful attempt to describe *Daphnia pulex* populations. Frank then generalized the model by adding equations to find the mass⁴ of individual animals and the biomass of the population; he let b_{Δ} and D_{Δ} depend on biomass. The mass of the animals is determined by using the equations

$$m(t + \Delta, a + \Delta) = m(t, a) + g_{\Delta}[M(t), a] \quad (28)$$

$$m(t, 0) = m_0 \quad (29)$$

where g_{Δ} is the increase in mass⁵ in the time Δ for an animal of age a maintained in a population with biomass $M(t)$

$$M(t) = \sum_{i=1}^k n(t, i \cdot \Delta) m(t, i \cdot \Delta).$$

We now divide equation (28) by Δ and take the limit as Δ goes to zero

⁴ Frank actually used volume for his criteria. The use of mass rather than volume does not constitute an essential change in Frank's model.

⁵ Frank uses the ratio of an animal's mass at time $t + \Delta$ to its mass at time t , $s_{\Delta}[M(t), a]$, to describe an animals growth. The two functions are related by

$$s_{\Delta}[M(t), a] = 1 + \frac{g_{\Delta}[M(t), a]}{m(t, a)}.$$

$$\lim_{\Delta \rightarrow 0} \frac{m(t + \Delta, a + \Delta) - m(t, a)}{\Delta} = \lim_{\Delta \rightarrow 0} \frac{g_{\Delta}[M(t), a]}{\Delta}.$$

The left-hand side is the total derivative of m with respect to t , and the right-hand side becomes the rate of growth g as defined above

$$\frac{dm}{dt} = g[M(t), a]. \quad (30)$$

Equations (27) and (30) resemble the system of equations (8), which determines solutions for $\eta(t, a, m)$. However in Frank's model at any given time all animals of a given age have the same mass. In our equation (2) there is a distribution of masses among animals of the same age.

Slobodkin (1953) has also proposed an algebra of population growth in which the animals are divided into different size and age categories. He defines a function, which depends on the age, size, and population density, to describe both the growth of animals and the number of deaths in a time increment. For any given age-size category the function will assume one of three values which correspond to all the animals in that age-size category; increasing in size to the next largest size category, remaining the same size, or dying. Slobodkin's ternary formulation and equation (2) differ. The latter allows a fraction of the animals in any age-size category to die in a given time increment and allows the mass of any animal to change at a rate dictated by environmental and physiological factors.

A very simple and extensively studied mathematical model for animal populations is the logistic equation of Verhulst (1838) and Pearl and Reed (1920). The logistic equation can be derived from Von Foerster's equation by integrating equation (13) with respect to age from zero to infinity to obtain

$$\frac{dN(t)}{dt} = n(t, 0) - \int_0^{\infty} D(t, a) n(t, a) da, \quad (31)$$

where $N(t)$ is the total number of animals. Since $dN(t)/dt$ is the total rate of change in the population, and the integral is the rate at which animals leave the population, $n(t, 0)$ must be the rate at which animals enter the population

$$n(t, 0) = \int_0^{\infty} b(t, a) n(t, a) da.$$

If the birth rate $b(t, a)$ is a constant,

$$n(t, 0) = bN(t)$$

and if

$$D(t, a) = d + \frac{r_0 N(t)}{K},$$

where d is the "intrinsic rate of death," equation (31) becomes the logistic equation,

$$\frac{dN(t)}{dt} = r_0 N(t) \left[1 - \frac{N(t)}{K} \right],$$

where K is the "equilibrium population size" and $r_0 = b - d$ is the "intrinsic rate of increase." Thus the logistic equation is a very special case of Von Foerster's equation, and in showing this we have illustrated some of the weaknesses of the logistic equation (see also Leslie 1948; Smith 1952). The intrinsic birth and death rates have been assumed independent of age, hardly a realistic assumption. We have also assumed that as density increases, the birth rate does not change and the death rate increases equally for animals of all ages. It should be pointed out that in certain special cases logistic growth can occur without the above assumptions; however, other severe restrictions must be placed on the population. For example Lotka (1931) and Leslie (1948) have specified initial age distributions in such a way that logistic growth occurs for certain birth and death rates.

Some authors have suggested that population models would be more realistic if they incorporated time lags (Hutchinson 1948; Cunningham 1954). Frank (1960) impressively demonstrated the need of taking time lags into account by comparing his age-volume model discussed above with and without a time lag in the adjustment of fecundity to new biomasses. The agreement with experimental results was only fair in the model without a time lag, but was very good in the model with a time lag. Time lags can easily be incorporated in equation (2) and in the models discussed in this section.

APPENDIX

The derivation of equation (2)

Let $\Delta m(t + \Delta t, a, m, \Delta t)$ be the average increase in mass of an animal of age a and mass m in the time interval $(t, t + \Delta t)$. Let $N(t)$ be the total number of animals characterized by points inside the rectangle formed by the solid line in Figure 1 at time t

$$N(t) = \int_{a_0}^{a_1} \int_{m_0}^{m_1} \eta(t, a, m) dm da. \quad (A-1)$$

The points a_0 , a_1 , m_0 and m_1 are arbitrary.

We now determine the change in $N(t)$ in the time interval $(t, t + \Delta t)$. At time t the area surrounded by the broken line contains all of the animals which will contribute to $N(t + \Delta t)$, provided they do not die. To find $N(t + \Delta t) - N(t)$ we take the number of animals moving into the rectangle formed by the solid line (those in areas

1 and 3) and subtract animals moving out (those in areas 2 and 4) and also subtract those who

would have contributed to $N(t + \Delta t)$ had they not died in the time interval $(t, t + \Delta t)$:

$$\begin{aligned}
 N(t + \Delta t) - N(t) = & \int_{a_0 - \Delta t}^{a_0} \int_{m_0 - \Delta m(t + \Delta t, a + \Delta t, m_0, \Delta t)}^{m_1 - \Delta m(t + \Delta t, a + \Delta t, m_1, \Delta t)} \eta(t, a, m) dm da \\
 & - \int_{a_1 - \Delta t}^{a_1} \int_{m_0 - \Delta m(t + \Delta t, a + \Delta t, m_0, \Delta t)}^{m_1 - \Delta m(t + \Delta t, a + \Delta t, m_1, \Delta t)} \eta(t, a, m) dm da \\
 & + \int_{a_0}^{a_1} \int_{m_0 - \Delta m(t + \Delta t, a + \Delta t, m_0, \Delta t)}^{m_0} \eta(t, a, m) dm da \\
 & - \int_{a_0}^{a_1} \int_{m_1 - \Delta m(t + \Delta t, a + \Delta t, m_1, \Delta t)}^{m_1} \eta(t, a, m) dm da \\
 & - \int_t^{t + \Delta t} \int_{a_0 - \Delta t - t + \tau}^{a_1 - \Delta t - t + \tau} \int_{m_0 - \Delta m(t + \Delta t, a + \Delta t, m_0, t + \Delta t - \tau)}^{m_1 - \Delta m(t + \Delta t, a + \Delta t, m_1, t + \Delta t - \tau)} \eta(\tau, a, m) D(\tau, a, m) dm da d\tau.
 \end{aligned} \quad (A-2)$$

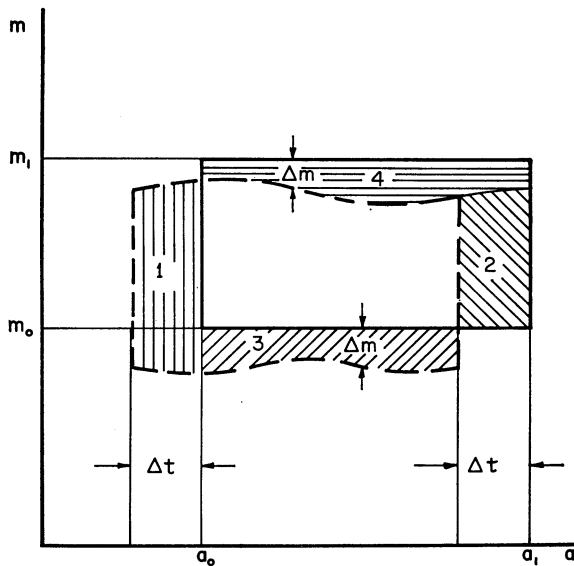


FIG. 1. Population members in the rectangle at time $t + \Delta t$ were in the area surrounded by the broken line at time t .

For convenience in taking limits below, animals in a small area (not outlined in Fig. 1) have been added and subtracted, for a net result of zero, in the second and third terms on the right hand side of equation (A-2). The term corresponding to deaths is found by integrating over a volume in t, a, m space. The volume is that swept out as t changes by all population members which fall in the rectangle (a_0, a_1) and (m_0, m_1) . In Figure 1 we have shown an increase in mass with t . Were

the food supply inadequate, for example, so that mass diminished with t , the rectangle would lie below the dashed area. Mathematically this is taken into account by the function $g(t, a, m)$.

We now divide equation (A-2) by Δt and take the limit as Δt goes to zero. The left-hand side is simply the definition of the derivative

$$\frac{dN(t)}{dt}.$$

Now consider each term on the right-hand side individually. If $h(t, a, \Delta t)$ is the value of the inside integral, the first term becomes

$$\lim_{\Delta t \rightarrow 0} \frac{1}{\Delta t} \int_{a_0 - \Delta t}^{a_0} h(t, a, \Delta t) da.$$

If Δm and η are continuous functions of their variables, h is a continuous function of its variables we apply the mean value theorem for integrals to obtain.

$$\lim_{\Delta t \rightarrow 0} h(t, \theta, \Delta t) = h(t, a_0, 0) \quad a_0 - \Delta t \leq \theta \leq a_0$$

$$= \int_{m_0}^{m_1} \eta(t, a_0, m) dm,$$

where we have assumed that an animal's mass cannot increase instantaneously, or $\Delta m(t, a, m, 0)$ is zero. The second term can be treated in a similar manner. Applying the mean value theorem for integrals to the inside integral of the third term yields

$$\lim_{\Delta t \rightarrow 0} \int_{a_0}^{a_1} \frac{\Delta m(t + \Delta t, a + \Delta t, m_0, \Delta t)}{\Delta t} \eta(t, a, \theta') da, \quad m_0 - \Delta m(t + \Delta t, a + \Delta t, m_0, \Delta t) \leq \theta' \leq m_0.$$

If the function inside the integral is uniformly continuous in Δt , we can take the limit inside the integral and obtain

$$\int_{a_0}^{a_1} g(t, a, m_0) \eta(t, a, m_0) da.$$

The fourth term can be handled in a similar manner. For the fifth term let $u(t, a, \Delta t, \tau)$ represent the value of the inside integral. Then define

$$v(t, \Delta t, \tau) = \int_{a_0 - \Delta t - t + \tau}^{a_1 - \Delta t - t + \tau} u(t, a, \Delta t, \tau) da.$$

If Δm , η , and D are continuous functions of their variables, u and v will be continuous functions of

their variables and we can apply the mean value theorem for integrals to the fifth term. Thus

$$\lim_{\Delta t \rightarrow 0} \frac{1}{\Delta t} \int_t^{t+\Delta t} v(t, \Delta t, \tau) d\tau = \lim_{\Delta t \rightarrow 0} v(t, \Delta t, \theta''), t \leq \theta'' \leq t + \Delta t$$

$$= v(t, 0, t) = \int_{a_0}^{a_1} u(t, a, 0, t) da, \quad = \int_{a_0}^{a_1} \int_{m_0}^{m_1} \eta(t, a, m) D(t, a, m) dm da.$$

Then dividing equation (A-2) by Δt and taking the limit as Δt goes to zero yields

$$\frac{dN}{dt} = \int_{m_0}^{m_1} \eta(t, a_0, m) dm - \int_{m_0}^{m_1} \eta(t, a_1, m) dm + \int_{a_0}^{a_1} g(t, a, m_0) \eta(t, a, m_0) da - \int_{a_0}^{a_1} g(t, a, m_1) \eta(t, a, m_1) da$$

$$- \int_{a_0}^{a_1} \int_{m_0}^{m_1} \eta(t, a, m) D(t, a, m) dm da. \quad (A-3)$$

By differentiating equation (A-1) we can obtain a new expression for the left hand side of equation (A-3). The fundamental theorem of integral cal-

culus can be applied to the first and second terms and to the third and fourth terms of the right-hand side to obtain

$$\int_{a_0}^{a_1} \int_{m_0}^{m_1} \frac{\partial \eta(t, a, m)}{\partial t} dm da = \int_{m_0}^{m_1} \int_{a_1}^{a_0} \frac{\partial \eta}{\partial a} da dm + \int_{a_0}^{a_1} \int_{m_1}^{m_0} \frac{\partial (g\eta)}{\partial m} dm da - \int_{a_0}^{a_1} \int_{m_0}^{m_1} \eta D dm da$$

or

$$\int_{a_0}^{a_1} \int_{m_1}^{m_0} \left[\frac{\partial \eta}{\partial t} + \frac{\partial \eta}{\partial a} + \frac{\partial (g\eta)}{\partial m} + \eta D \right] dm da = 0. \quad (A-4)$$

Since a_0 , a_1 , m_0 , and m_1 are arbitrary, the term inside the square brackets must be zero and equation (2) results

$$\frac{\partial \eta}{\partial t} + \frac{\partial \eta}{\partial a} + \frac{\partial (g\eta)}{\partial m} = -D\eta.$$

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PERIPHYTON GROWTH ON ARTIFICIAL SUBSTRATES IN A RADIOACTIVELY CONTAMINATED LAKE¹

ERNEST C. NEAL,² BERNARD C. PATTEN, AND CHARLES E. DEPOE³

*Radiation Ecology Section, Health Physics Division, Oak Ridge National Laboratory,
Oak Ridge, Tennessee*

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Abstract. Periphyton colonization, biomass development and radionuclide accumulation were studied by suspending polyethylene tape vertically for up to 9 weeks in a radioactively contaminated lake. After 2 weeks biomass growth was nearly complete on the upper tape sections, but full development on the deeper sections took longer. Maximum biomass occurred at 25.4-50.8 cm (6-20 in.) depth. Bacterial colonization and slime formation went unobserved. Blue-greens were the initial algal dominants, succeeded by diatoms and filamentous greens. Species succession continued beyond biomass equilibrium, with blue-greens tending to maintain importance in the deeper zones and greens developing best in the upper, lighted regions. Animals were minor constituents.

Radioisotope concentrations equilibrated rapidly in both the artificial substrates and the periphyton biomass. Zinc-65 was concentrated highly by the polyethylene tape, Cs¹³⁷ moderately, and Co⁶⁰ and Ru¹⁰⁶ only slightly or not at all. Ambient concentrations of Zn⁶⁵ in water and periphyton were below detection. The other isotopes contributed about equally (ca. 10-20 dpm/mg) to biomass radioactivity. Biomass activity-densities of Ru¹⁰⁶ and Cs¹³⁷ increased slightly with depth; this pattern was pronounced for Co⁶⁰. Factors considered to account for observed vertical distributions include: different radioisotope concentrations in surface and deep water; a hyperbolic rather than linear relationship between activity-density and biomass; and, in the case of Co⁶⁰, concentration by blue-green algae as an essential element, or by microbiota for use in cobalamin synthesis.

INTRODUCTION

Periphyton comprises an important community of microorganisms occupying submerged surfaces in freshwater and marine environments. Investigations of taxonomic composition and, to a lesser extent, the dynamics of colonization and growth, have involved use of foreign substrates introduced into water. Kinds of materials utilized and specific innovations of technique are reviewed by Cooke (1956). Parameters studied in addition to species composition include biomass (e.g. Butcher 1940; Sládečková 1962), phyt pigments (Grzenda and Brehmer 1960), productivity (Kevern, Wilhm and Van Dyne 1966), and radioisotope accumulation (Williams and Mount 1965; Cushing 1967;

Nelson et al. 1967). Most work has been in streams or rivers with the substrates, usually glass slides, placed on or near the bottom in horizontal or vertical orientation. Substrates also have been suspended, usually near the surface, in standing or slowly flowing waters, but little attention seems to have been given to possible vertical differences in periphyton growth. Bissonette (1930) suspended slide-containing racks vertically to collect marine invertebrates, but algae were not considered. This approach would appear to offer a good means of studying vertical structure and organization of periphyton, as well as how the community develops in time, and it is implemented here by suspending continuous artificial substrates vertically in a radioactively contaminated lake. Objectives of the study are (1) to characterize the vertical and temporal development of periphyton on the substrates, in terms of both species composition and biomass, and (2) to describe the associated accumulation of several radioactive isotopes.

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² Present address: Ohio Dept. of Health, Columbus, Ohio.

³ Visiting investigator. Present address: Dept. of Biology, Northeast Louisiana State College, Monroe, Louisiana.