THE SIZE OF WATER MASSES CONTAINING PLANKTON BLOOMS[1]

By

HENRY KIERSTEAD[2]

Brown University
Providence, Rhode Island

AND

L. BASIL SLOBODKIN

Bingham Oceanographic Laboratory
Yale University
New Haven, Connecticut

ABSTRACT

If a phytoplankton population is assumed to be increasing logarithmically in a mass of water surrounded by water which is unsuitable for the survival of the population, it can be shown that there is a minimum critical size for the water mass below which no increase in concentration of phytoplankton can occur. In a one-dimensional water mass with leakage at both ends, this size, after a time of the order of $L^2/\pi^2 D$, is given by

$$L_c = \pi\sqrt{\frac{D}{K}},$$

where L_c is the length of the water mass, D the diffusion, and K the rate of increase of the population. The corresponding size in a cylindrical water mass is given by

$$R_c = 2.4048\sqrt{\frac{D}{K}},$$

where R_c is the radius of the water mass.

Any unispecific phytoplankton population can be considered as living in some water mass characterized by suitable values of such properties as temperature, salinity, dissolved oxygen, and dissolved nutrients. If this water mass were completely isolated from the surrounding water it should be possible to analyze the growth of the population in terms of one of the equations which have been developed for laboratory populations (Smith, 1952).

[1] The authors wish to express their gratitude to Mr. Henry Stommel for his advice and encouragement.

[2] Present address: Argonne National Laboratory, P. O. Box 5207, Chicago, Illinois.

As a matter of fact, any mass of physiologically suitable water will mix, at its borders, with unsuitable water. For a species with restricted physiological tolerances it is quite likely that large masses of suitable water will rarely occur. It is of interest, therefore, to determine whether or not there exists a minimum water mass size below which no increase of phytoplankton concentration is possible.

In the simplest analysis the population growth in a diffusing water mass can be expressed as

$$\frac{dN}{dt} = (K - \lambda) N , \tag{1}$$

where K is the growth rate per unit population, λN the rate of loss by diffusion, and N the total number of organisms in the water mass. The simple condition for population increase is $(K > \lambda)$. This does not take into account the size of water mass or the distribution of organisms. A more precise analysis of the leakage λ has been made.

We consider for simplicity the one-dimensional problem of a long narrow body of water limited on the two sides by natural boundaries. We assume further that there is a region of length L and transverse cross-sectional area A in which the effective diffusivity D remains constant. We assume that, outside this region, the diffusivity becomes large or that the water is physiologically unsuitable for the organism. Either condition requires that the concentration of organisms drop to zero at the ends of the region. We can neglect transverse diffusion and consider the concentration c to be a function of the longitudinal position only. Let one end be at $x = 0$ and the other at $x = L$. If the organism did not multiply, we would require the solution of the diffusion equation (Churchill, 1941: 19):

$$\frac{\partial c}{\partial t} = D \frac{\partial^2 c}{\partial x^2} , \tag{2}$$

in which t is time. But reproduction must be accounted for by adding a linear growth term to (2). We have then,

$$\frac{\partial c}{\partial t} = D \frac{\partial^2 c}{\partial x^2} + Kc . \tag{3}$$

We seek solutions of (3) which vanish at $x = 0$ and $X = L$ and which correspond to any given initial distribution of organisms, which we can write as

$$c = g(t) \text{ when } t = 0. \tag{4}$$

If we introduce the new variable,

$$f = ce^{-kt} , \tag{5}$$

we find by substitution in (3) that f must satisfy the equation

$$\frac{\partial f}{\partial x} = D \frac{\partial^2 f}{\partial x^2}, \tag{6}$$

which is the ordinary diffusion equation; f must also satisfy the same initial and boundary conditions as c. The solution of (6) for these boundary conditions is known to be (Churchill, 1941: 104)[3]

$$f = \sum_{n=1}^{\infty} B_n \sin n\pi \frac{x}{L} e^{-n^2\pi^2 D/L^2 t}, \tag{7}$$

where

$$B_n = \frac{2}{L} \int_0^L g(x) \sin n\pi \frac{x}{L} dx. \tag{8}$$

Thus the constants B_n ($n = 1, 2, 3, \ldots$) depend on the form of the initial distribution. Our principal conclusions will not depend on the exact values of these constants. Due to the symmetry properties of the sine functions in (8), the even-numbered terms in (7) will vanish if the initial distribution is symmetric with respect to the plane $x = L/2$; in any event, as we shall see, the values of N and λ will depend only on the odd-numbered terms. Substituting (5) into (7), we obtain an expression for the concentration at any position and time:

$$c = \sum_{n=1}^{\infty} B_n \sin n\pi \frac{x}{L} e^{(k-n^2\pi^2 D/L^2) t}. \tag{9}$$

It should be noted that the different terms in the series have different functional dependence on the time. In particular, the terms for which $(K - n^2\pi^2 D/L^2)$ is negative will decrease with time and will eventually become negligibly small.

The population will then be unable to maintain itself against diffusion unless there is at least one term in the series for which

$$K - n^2\pi^2 \frac{D}{L^2} \geqslant 0. \tag{10}$$

Since the smallest value of n is one,[4] a necessary condition for maintenance of the population is

$$K \geqslant \pi^2 \frac{D}{L^2}. \tag{11}$$

[3] We shall assume that all infinite series used in this paper converge properly for $t > 0$, $0 \leqslant x \leqslant L$. A detailed investigation of their convergence properties shows that this is the case for all situations of physical interest.

[4] This would not be true if $B_1 = 0$. However, $\sin \pi x/L$ is positive throughout the interval $0 > x > L$, and in any real population $g(x)$ cannot be negative and must therefore be greater than zero somewhere. Hence the integral in (8) is necessarily positive.

For given values of D and K, there is a critical length given by

$$L_c = \pi \sqrt{\frac{D}{K}}, \tag{12}$$

such that a population will increase if $L > L_c$, decrease if $L < L_c$, and will remain static if $L = L_c$. Of course the situation is exactly analogous to the situation in a chain-reacting pile.

Going back to equation (9), we can calculate the total number of organisms by integration:

$$N = A \int_0^L c \, dx = \frac{2AL}{\pi} \sum_{n=0}^{\infty} \frac{B_{2n+1}}{2n+1} e^{[k-(2n+1)^2 \pi^2 D/L^2] t}, \tag{13}$$

the terms with even n vanishing on account of their symmetry. The net number of organisms diffusing in the forward direction past any plane in unit time is given by

$$n(x, t) = -AD \frac{\partial c}{\partial x} = -AD \frac{\pi}{L} \sum_{n=1}^{\infty} n B_n \cos n\pi \frac{x}{L} e^{(k-n^2\pi^2 D/L^2) t}. \tag{14}$$

The number lost from the system per unit time by diffusion through the end boundaries $x = 0$ and $x = L$ is

$$n(L, t) - n(0, t) = 2AD \frac{\pi}{L} \sum_{n=0}^{\infty} (2n+1) B_{2n+1} e^{[k-(2n+1)^2 \pi^2 D/L^2] t}. \tag{15}$$

It is useful to define the 'leakage' λ as

$$\lambda = \frac{n(L, t) - n(0, t)}{N}. \tag{16}$$

Then

$$\lambda = \frac{\pi^2 D}{L^2} \frac{\sum_{n=0}^{\infty} (2n+1) B_{(2n+1)} e^{[k-(2n+1)^2 \pi^2 D/L^2] t}}{\sum_{n=0}^{\infty} \frac{B_{2n+1}}{2n+1} e^{[k-(2n+1)^2 \pi^2 D/L^2] t}}. \tag{17}$$

$$= \frac{\pi^2 D}{L^2} \frac{\sum_{n=0}^{\infty} (2n+1) B_{2n+1} e^{-4n(n+1) \pi^2 D/L^2 t}}{\sum_{n=0}^{\infty} \frac{B_{2n+1}}{2n+1} e^{-4n(n+1) \pi^2 D/L^2 t}}. \tag{18}$$

By differentiating (13) with respect to time, we find

$$\frac{1}{N}\frac{dN}{dt} = K - \frac{\pi^2 D}{L^2}\,\frac{\sum_{n=0}^{\infty}(2n+1)\,B_{2n+1}\,e^{[k-(2n+1)^2\pi^2 D/L^2]\,t}}{\sum_{n=0}^{\infty}\frac{B_{2n+1}}{2n+1}\,e^{[k-(2n+1)^2\pi^2 D/L^2]\,t}}\,, \tag{19}$$

and, introducing (17),

$$\frac{1}{N}\frac{dN}{dt} = K - \lambda\,, \tag{20}$$

which is identical to (1). The over-all growth of the population can be described therefore by (1) with λ defined by (18). In general λ will be a function of time, but after a time of the order of magnitude of $L^2/8\pi^2 D$, the first terms in the two series in (18) will be the only ones of importance. We have then

$$\lambda \simeq \pi^2\frac{D}{L^2} \text{ if } t \gg L^2/8\pi^2 D\,. \tag{21}$$

The generality of these results can be seen by considering a different geometrical model. Let the region of constant diffusion coefficient be a cylinder of radius R and depth h bounded on all sides by physiologically unsuitable water; also assume cylindrical symmetry. Equation (2) must then be replaced by

$$\frac{\partial c}{\partial t} = \frac{D}{r}\frac{\partial}{\partial r}\left(\frac{1}{r}\frac{\partial c}{\partial r}\right), \tag{2'}$$

and a similar modification must be made in (3) and (6). Solving the modified equations in the same manner as the original ones, we find (Churchill, 1951: 166)

$$c = \sum_{n=1}^{\infty} E_n\,J_0\left(\beta_n\frac{r}{R}\right)e^{(k-\beta_n^2 D/R^2)\,t}\,, \tag{9'}$$

where J_0 is a Bessel function of the first kind and order zero, where the β_n's are the roots of the equation

$$J_0(\beta_n) = 0$$

numbered in order of increasing magnitude, and where

$$E_n = \frac{2}{[R\,J_1(\beta_n)]^2}\int_0^R r\,g(r)\,J_0\left(\beta_n\frac{r}{R}\right)dr\,. \tag{8'}$$

J_1 is the Bessel function of order one and $g(r)$ is the initial distribution as before. The first few β_n's and the corresponding values of $J_1(\beta_n)$ are listed in Table I (Jahnke and Emde, 1945: 166) along with the values of $n\pi$ for comparison (for large n, B_n approaches $((n - \frac{1}{4})\pi)$. Equations (11), (12), (18), and (21) become

TABLE I.—Comparison of the Coefficients in Series (9) and (9′)

n	$n\pi$	β_n	$J_1(\beta_n)$
1	3.1416	2.4048	+0.5191
2	6.2832	5.5201	−0.3403
3	9.4248	8.6537	+0.2715
4	12.5664	11.7915	−0.2325
5	15.7080	14.9309	+0.2065
6	18.8496	18.0711	−0.1877

$$K \geqq \frac{2 \cdot 4048^2 D}{R^2}, \tag{11′}$$

$$R_c = 2.4048 \sqrt{\frac{D}{K}}, \tag{12′}$$

$$N = 2\pi h \int_0^R rc\, dr = 2\pi h\, R^2 \sum_{n=1}^{\infty} J_1(\beta_n) \frac{E_n}{\beta_n} e^{k - \beta_n^2 D/R^2 t}, \tag{13′}$$

$$\lambda = \frac{D}{R^2} \frac{\sum_{n=1}^{\infty} \beta_n J_1(\beta_n)\, E_n\, e^{(\beta_1^2 - \beta_n^2) D/R^2 t}}{\sum_{n=1}^{\infty} J_1(\beta_n) \frac{E_n}{\beta_n} e^{(\beta_1^2 - \beta_n^2) D/R^2 t}}, \tag{18′}$$

$$\lambda \simeq 2 \cdot 4048^2 \frac{D}{R^2} \text{ if } t \gg \frac{R^2}{25D}, \tag{21′}$$

while equation (20) remains the same.

Solutions for other models are easily derived, but the results are essentially the same as those presented here. The numerical constants in equations (11), (12), and (21) are somewhat different in different models, but they are always of the same order of magnitude.

We conclude, therefore, that a population in a finite region can support itself against diffusion only if its reproductive rate exceeds the leakage, which is of the order of magnitude of the ratio of the diffusivity to the square of the extent of the region in the direction of most rapid diffusion.

Churchill, R. V.
1941. Fourier series
York. 206 pp
Jahnke, E. and F. Emd
1945. Tables of funct
Smith, F. E.
1952. Experimental
33 (4): 441–45(

REFERENCES

CHURCHILL, R. V.
1941. Fourier series and boundary value problems. McGraw-Hill, Inc., New York. 206 pp.

JAHNKE, E. AND F. EMDE
1945. Tables of functions. 4th Ed. Dover, New York. 306 pp.

SMITH, F. E.
1952. Experimental methods in population dynamics, a critique. Ecology, *33* (4): 441–450.