2.3/K, though the numbers 1/α, and 1/K can do just as well. In the clearest known natural waters* these distances 4/α and 2.3/K are believed to be less than 230 feet and 340 feet respectively. In the first numerical example given in paragraph B.2 the distances were found to be 4/α = 55 feet and 2.3/K = 85 feet; in the second, 4/α = 9.3 feet and 2.3/K = 13.5 feet.

1.10 Applications of Hydrologic Optics to the Food-Chain Problem in the Sea

In this section we shall discuss, from the point of view of radiative transfer theory, the problem of food-chain relations in the ocean. The theory of food-chain relations attempts to describe, in quantitative terms, the distribution in time and space, within a given oceanic region, of the food supply of the main animal populations of that region. The food supply is an essentially self-sustaining collection of biological organisms, inorganic matter, and radiant energy. Aside from radiant energy, the chain consists principally of the following four links: nutrients (e.g., phosphate), phytoplankton, herbivores, and predators. This set of interacting organisms is arranged so that each item in the list constitutes the food of the next item in the list, and in this sense forms a *food-chain* in an oceanic region. This food-chain is initiated and sustained by solar radiant energy penetrating into the sea. The radiant energy sustains the photosynthesis within the phytoplankton and the life processes of the herbivores and predators. Furthermore, the continued decomposition into nutrient material of each of the last three links in the chain also contributes to its maintenance. Thus, any complete theory of food-chain relations in the ocean must take into explicit account, among other things, the role of radiant energy in the food-chain relations. A survey of the present state of the theory (ref. [265]) indicates that the systematic inclusion of radiant energy terms into the food-chain relation has been avoided because of the additional difficulties attendant on such an inclusion in an already complex theory. In the present discussion, it will be shown how the general inclusion of radiant energy terms into the description of the food-chain relations can be carried out in such a way that the attendant increase in the complexity of the theory will not render the result altogether impracticable. Furthermore, it will be shown that the resultant formulations point to some novel, detailed descriptions of the depth distributions of the light field in a region containing the members of the food-chain. By doing so, the main purpose of the discussion will be fulfilled, namely, to round out the classical Volterra prey-predator equations [309] which describe

---

*Probable values: α = 0.017 per foot = 0.056 per meter
K = 0.0067 per foot
= 0.022 per meter at 480 millimicrons

Compare this α with that in Table 1 of Sec. 1.6.

food-chain relations, by including one more equation which specifically--and in a manner uniform with the other equations--incorporates the photons of the light field into the list of interacting members of the the food-chain. The manner in which light particles can generally be considered as "prey" or "predator" will become clear as the discussion proceeds.

The General Exponential Law of Change

The simple differential law:

$$\frac{dA}{dt} = KA \qquad (1)$$

has been found to describe a wide variety of natural phenomena, among which are: growth of yeast cultures and bacterial cultures, decay of radioactive substances, growth and decay of animal populations, damped or resonating oscillations of mechanical and electrical systems, and the darkening of light fields with depth in scattering-absorbing media, to name a few. Up until now we have been concerned in this work principally with the latter use of the exponential law. As we shall see in the latter stages of this discussion, we may very well view (1), under suitable interpretations, as the alpha and the omega--that is, the beginning and the end--of the general theory of the food-chain relations. However, for the present, we view (1) as the ostensibly simple equation it appears to be, with constant coefficient K, and thereby obtain the general solution of (1) in the form:

$$A(t) = A(0)e^{Kt} \qquad (2)$$

where A(t) is the amount at time t of the entity under consideration. When K is positive, then there is growth of A(t); when K is negative, there is decay of A(t), as time t increases.

The description of natural growth and decay processes summarized in (1) and (2) is known as the *exponential law* and pertains as it stands basically to isolated and relatively simple systems. When the systems are no longer isolated or no longer simple in internal structure, then (1) is replaced by a correspondingly modified equation. For example, by removing the isolation restriction, two new features appear: a source term A_η may be added to the right side of (1); and the possibility arises of a non-constant growth rate term K. From the present point of view, the inclusion of a source term A_η presents no essential modification of the equation (1), and so will not be studied in this discussion. However, the practical and theoretical possibilities inherent in a non-constant growth rate term K are endless, and some of them hold the key to the solution of the general problem of the food-chain relation; some of these possibilities will now be considered.

The Volterra Prey-Predator Equations

A theory of food-chains can be made to rest in the classical equations postulated by Volterra [309] which govern the evolution in time of the number P of prey and number A of predators feeding on the prey. Thus, for example, if P is the number of plants and A the number of animals in a symbiotic relation, then their evolution in time may be governed by general equations of the form:

$$\frac{dP}{dt} = K_P P \tag{3}$$

$$\frac{dA}{dt} = K_A A \tag{4}$$

where we have written

$$\text{"}K_P\text{"} \quad \text{for} \quad p\text{-}bA \tag{5}$$

and

$$\text{"}K_A\text{"} \quad \text{for} \quad cP\text{-}a \quad . \tag{6}$$

That is, the growth rate term K_P for the prey is the sum of the intrinsic growth rate p for the prey population and the interaction decay term -bA, where b is a coupling constant between the populations of A and P. Similarly a is the coefficient of decay of the predator population, and c is the coupling constant between A and P in this instance. The coupling constants b and c are usually taken as equal or as connected by some given relation.

Now each equation (3), (4) is of the general type as (1) and, assuming K_P and K_A known as functions of time along with the initial values P(0) and A(0) of P and A, are directly integrable:

$$A(t) = A(0) \exp\left\{\int_0^t K_A(t')\ dt'\right\}$$

$$P(t) = P(0) \exp\left\{\int_0^t K_P(t')\ dt'\right\}$$

However, equations (3) and (4) are generally coupled (i.e., $b \neq 0$ and $c \neq 0$) so that the preceding solutions, while formally correct, are of no immediate practical use, since knowledge of K_P and K_A is tantamount to knowledge of P and A themselves.

The equations (3) and (4), despite their analytically unpleasant nonlinear coupling, form a workable starting point in the quantitative description of the food-chain relation.

It is clear, however, that the equations as they stand describe only the herbivore and predator components of the chain and so cannot adequately describe the complete food-chain relation as defined above. The other members of the chain, namely the phytoplankton and the nutrients (which also constitute a prey-predator pair), along with the radiant energy, are excluded from (3), (4).

The General Food-Chain Equations

We turn now to a formulation of the Volterra-type prey-predator equations which goes beyond that of (3), (4) and which takes into account the interactions of all five members of the food-chain relation. To keep the geometric and physical variables down to a comfortable minimum at the outset, we shall assume that all quantities of the chain depend on depth and time only, over the oceanic region of interest. Thus let:

$U(z,t)$	be the radiant density (radiant energy per unit volume) at depth z, time t
$P(z,t)$	be the number of *phytoplankton* per unit volume at depth z, time t
$B(z,t)$	be the number of *herbivores* per unit volume at depth z, time t
$C(z,t)$	be the number of *carnivores* per unit volume at depth z, time t
$N(z,t)$	be the amount of *nutrient* per unit volume at depth z, time t

We postulate a food-chain ordering among the members of the food-chain, and which is schematically summarized below:

	C	B	P	N	U
C	0	+	+	±	+
B	-	0	+	±	+
P	-	-	0	±	+
N	±	±	±	0	±
U	-	-	-	-	0

(7)

This ordering is to be interpreted as follows: consider the carnivore row. Carnivores in the present hierarchy are understood to grow at the expense of most other members of the chain (hence the + signs in the row). Herbivores, on the other hand, grow at the expense of phytoplankton, nutrients and radiant energy (hence + signs) but are preyed upon by carnivores (hence - sign). The zero entries indicate that in the present model, members of the chain do not increase or decrease at the expense of their own numbers. (In mathematical terms the food-chain ordering relation in (7) is an irreflexive, asymmetric, transitive relation.) The double signs (±) in the nutrient row indicate that at times, N may increase(+) in the direct presence of the other members and at other times may decrease (-) in the direct presence of the other members.

The food-chain ordering associated with each pair of the food-chain is given a quantitative measure by assigning interaction functions to each pair of members of the chain. Thus to the pair (C,B) we assign a function K_{CB} which on the basis of the food-chain ordering relation tabulated above, is positive for all z and t. Similarly to (C,P) we assign the interaction function K_{CP} which is also positive-valued. Continuing in this way we assign to the pair (U,N) the function K_{UN} which is negative-valued for all z,t. The functions K_{CC}, K_{BB}, etc. are all zero-valued, and K_{NC} may be positive, zero or negative-valued for various z, and t.

Once a food-chain ordering has been established and the 20 non zero interaction functions have been assigned, the Volterra interaction equations can be written down:

$$\left.\begin{aligned}
\frac{dC}{dt} &= K_C C \\
\frac{dB}{dt} &= K_B B \\
\frac{dP}{dt} &= K_P P \\
\frac{dN}{dt} &= K_N N \\
\frac{dU}{dt} &= K_U U
\end{aligned}\right\} \qquad (8)$$

where we have written

$$\left.\begin{aligned}
&\text{"}K_C\text{"} \quad \text{for} \quad k_C + K_{CB}B + K_{CP}P + K_{CN}N + K_{CU}U \\
&\text{"}K_B\text{"} \quad \text{for} \quad k_B + K_{BC}C + K_{BP}P + K_{BN}N + K_{BU}U \\
&\text{"}K_P\text{"} \quad \text{for} \quad k_P + K_{PC}C + K_{PB}B + K_{PN}N + K_{PU}U \\
&\text{"}K_N\text{"} \quad \text{for} \quad k_N + K_{NC}C + K_{NB}B + K_{NP}P + K_{NU}U \\
&\text{"}K_U\text{"} \quad \text{for} \quad k_U + K_{UC}C + K_{UB}B + K_{UP}P + K_{UN}N
\end{aligned}\right\} \qquad (9)$$

The five functions $k_C, \ldots, k_U$ are inherent growth-decay rates, which are operative independently of the presence of other members of the chain. Furthermore, the differentiation operator d/dt in (8) is a total derivative operator, i.e., we have written

$$\text{"}d/dt\text{"} \quad \text{for} \quad \partial/\partial t + v(\partial/\partial z) \tag{10}$$

where in each case v is an averaged speed of propagation in the z direction. In the case of U it is the speed of light. In the case of C and B, it is variable with time and space according to the vertical movements of the animals. In the case of P and N, v represents rate of rising and sinking, plus eddy diffusion rates. The theoretical basis for the equation governing U in (8) which is one of the novel features of (8), rests in the general theory of K-functions for directly observable radiometric quantities as developed in Chapter 9 below. For practical purposes, one may, however, use (7) of Sec. 1.4 with each side divided by v (recall (5) of Sec. 1.1).

Once the interaction functions are known and the initial states C(z,0), K(z,0),...,U(z,0) are known over all depths z in the region of interest, the system (8) is in principle solvable by iteration techniques. Thus, for example, by writing

$$\text{"}\mathbf{A}\text{"} \quad \text{for} \quad (C, B, P, N, U) \tag{11}$$

and

$$\text{"}\mathbf{K}\text{"} \quad \text{for} \quad \begin{bmatrix} K_C & & & 0 \\ & K_B & & \\ & & \ddots & \\ 0 & & & K_U \end{bmatrix} \tag{12}$$

The system (8) becomes transformed into the vector equation:

$$\boxed{\frac{d\mathbf{A}}{dt} = \mathbf{A}\,\mathbf{K}} \tag{13}$$

which may be solved by any of several modern iteration techniques (see, e.g., [23]) using large scale computers. It is therefore no longer necessary to limit the generality of a food-chain theory because of the possible intractability of the analytic solution procedure (e.g., the impossibility of obtaining closed forms for the integrations).

An Illustration of the Food-Chain Theory with A Radiant Energy Term

As a simple illustration of the general theory outlined above, let us consider a three-member food-chain consisting of phytoplankton, herbivores, and radiant energy. Hence we will study the effect of adding to the classical prey-predator equations (3), (4), another equation which specifically includes radiant energy in the prey-predator interactions. The following discussion is actually independent of the number of members in the food-chain, so that a reader following the general line of argument developed below may extend the arguments and their results to arbitrarily large food-chains.

The General Three-Term Equations

The requisite equations for the present illustration are:

$$\frac{dU}{dt} = (k_U + K_{UB}B + K_{UP}P)U \quad \text{(photons)} \tag{14}$$

$$\frac{dB}{dt} = (k_B + K_{BP}P + K_{BU}U)B \quad \text{(herbivores)} \tag{15}$$

$$\frac{dP}{dt} = (k_P + K_{PB}B + K_{PU}U)P \quad \text{(phytoplankton)} \tag{16}$$

The Quasi-Steady State Equations

We shall be interested for the present in a *quasi-steady state solution of the preceding system* of equations. By 'quasi-steady state' we mean that the time rates of change of the magnitudes of P and B are negligible compared to that of U, so that the light field U adjusts to and settles down to steady state almost instantly in accordance to the prevailing spatial distributions of P and B at time t. Therefore, in (14) we may drop the time derivative and consider only change of U in depth for fixed t and adjust the definitions of the K-functions to absorb the speed constant v; and in (15) and (16) we may drop the spatial derivatives, and consider only the change of B and P in time for a fixed depth z:

$$\frac{dU}{dz} = (k_U + K_{UB}B + K_{UP}P)U \tag{17}$$

$$\frac{\partial B}{\partial t} = (k_B + K_{BP}P + K_{BU}U)B \tag{18}$$

$$\frac{\partial P}{\partial t} = (k_P + K_{PB}B + K_{PU}U)P \tag{19}$$

This set of equations like the general equations, is readily solvable in principle for given arbitrary constants k_U, K_{UB}, etc., and initial conditions. The steady state spatial distributions of U, P, B are of especial interest, and we shall devote the remainder of this section to the study of these distributions.

The Equilibrium Solutions

When $\partial B/\partial t = 0$ for every z at a given time t, the existing spatial distribution of B is called the *equilibrium population* and denoted by "B_q"; similarly for P. The equilibrium populations of P or B are readily characterized in terms of the spatial distribution of the radiant energy. Thus from (18) we have:

$$\frac{\partial B_q}{\partial t} = 0$$

which implies

$$k_B + K_{BP}P_q + K_{BU}U = 0$$

so that

$$\boxed{P_q = -(k_B + K_{BU}U)/K_{BP}} \qquad (20)$$

Similarly from (19), for steady state:

$$\frac{\partial P_q}{\partial t} = 0$$

so that

$$k_P + K_{PB}B_q + K_{PU}U = 0$$

whence

$$\boxed{B_q = -(k_P + K_{PU}U)/K_{PB}} \qquad (21)$$

Equations (20) and (21) show that if the steady state radiant energy distribution U is known, the equilibrium P and B distributions are determinable over the range of depths of interest.

We now show that the relations (20) and (21) together with (17) uniquely determine the steady state radiant energy distribution through the medium so that P_q and B_q are uniquely determinable, in turn. Substituting P_q and B_q as given by (20) and (21) into (17), and rearranging, we have:

$$\frac{dU}{dz} = \left\{k_U - \frac{K_{UB}}{K_{PB}}(k_P + K_{PU}U) - \frac{K_{UP}}{K_{BP}}(k_B + K_{BU}U)\right\}U$$

That is:

$$\boxed{\frac{dU}{dz} = aU + bU^2} \qquad (22)$$

where we have written:

$$\text{"a"} \quad \text{for} \quad k_U - \left(k_P \frac{K_{UB}}{K_{PB}} + k_B \frac{K_{UP}}{K_{BP}} \right) \tag{23}$$

and

$$\text{"b"} \quad \text{for} \quad - \left(\frac{K_{UB}K_{PU}}{K_{PB}} + \frac{K_{UP}K_{BU}}{K_{BP}} \right) \tag{24}$$

If "U(0)" denotes the initial value of U at some fiducial depth (here $z = 0$), then (22) resolves into:

$$\boxed{U(z) = \frac{aU(0)e^{az}}{-bU(0)e^{az} + [bU(0) + a]}} \tag{25}$$

This solution may now be used in (20) and (21) to obtain detailed descriptions of the depth distribution of the steady state populations of P and B. The solution (25) exhibits some interesting mathematical properties for various choices of a and b. For $b = 0$, we have simple exponential growth ($a > 0$) or decay ($a < 0$). For $a = 0$, by a limiting argument, we have

$$U(z) = \frac{U(0)}{1-bU(0)z} \quad .$$

Some General Properties of Equilibrium Solutions

The equilibrium solutions found above have several interesting practical properties, one of which we isolate for particular attention here. This is the property of predicting a possible band of depths below the ocean surface outside of which the P and B populations cannot exist. To find the limits of this band of depths, we return to equations (20) and (21) and require that $P_q \geq 0$ and $B_q \geq 0$. These conditions merely state that real distributions of phytoplankton and herbivores must not have negative populations. The non negativity condition applied to (20) yields:

$$-(k_B + K_{BU}U)/K_{BP} \geq 0$$

From the interaction table (7) we find that $K_{BP} \geq 0$, so that

$$k_B + K_{BU}U \leq 0$$

whence

$$U \leq -k_B/K_{BU}$$

Similarly, from (21) with the help of the nonnegativity condition we find:

$$U \geq -k_P / K_{PU}$$

Hence a necessary condition for the existence of steady state P and B equilibrium distributions at depth z is that

$$\boxed{-k_P/K_{PU} \leq U(z) \leq -k_B/K_{BU}} \qquad (26)$$

It is to be noted that (26) are *necessary* conditions (i.e., *if* a band exists, *then* it must be such that (26) holds) and not sufficient conditions, except insofar as the steps can be retraced from (26) to (20) and (21). This can be done if K_{PB} and K_{BP} are strictly negative and strictly positive, respectively, and if the left side of (26) is indeed less than the right side.

Now according to (25), U(z) is under certain conditions a decreasing function of z (for negative a). Thus if U(0) is greater than $-k_B/K_{BU}$, then (26) shows that no steady state population should exist for depths $z = 0$ down to where $U(z) = -k_B/K_{BU}$. Then there is expected a band of depths within which $P > 0$ and $B > 0$. Since U(z) decreases monotonically, there will be depths below which the left side of (26) no longer holds, so that $P = 0$ and $B = 0$ in those depths. It appears then that the present model can in principle predict a euphotic zone in natural hydrosols in which the food-chain is in a quasi-steady state condition.

We have reached the main goal of the discussion, namely to supplement the classical Volterra prey-predator equations with a third equation governing the flow of radiant energy in the sea, and to briefly explore the consequences of the interactions of the prey-predator-photon system.

<< Table of Contents << Title Page >> Next Page >>

1.11 Future Problems of Hydrologic Optics

The present introductory chapter to hydrologic optics is brought to a close with a small, carefully selected list of important problems which are as yet only partially resolved. The list is deliberately kept small so as not to overwhelm prospective students of the subject with a mass of more or less obvious types of applicational problems they soon would encounter in their own fashion as their studies proceed. Rather, we have selected for presentation and discussion here three archetype problems which, if eventually satisfactorily resolved, would elevate the discipline of hydrologic optics to the level of a mature science which could predict and describe, in the fullest sense of these terms, all aspects of the transfer of radiant energy in the seas, lakes and other natural hydrosols of the world.