A THEORETICAL TREATMENT OF UNSTRUCTURED FOOD WEBS

G. D. LANGE AND A. C. HURLEY[1]

ABSTRACT

In a recent paper, Isaacs has proposed a model for an unstructured food web in which the interconnections are so diverse that all heterotrophs in the system can be treated as if they were at the same average trophic position. This paper recasts the original model in terms of a 3 × 3 matrix using three empirical constants. In this form, the model can be easily generalized to one having nine constants and reflecting a more realistic view of the interactions among levels of a community.

Recent papers by Isaacs (1972, 1973) proposed an alternative to trophic level schemes for representing interactions among species. He termed this an unstructured food web and proposed a "matrix"[2] technique (Isaacs 1972) for evaluating the equilibrium distribution of energy (or matter) which would result from these interactions. In this paper we propose an alternative formulation of Isaacs' model which utilizes classical matrix and operator techniques.

SERIES APPROACH

Isaacs' model was originally proposed to account for Young's data (Young 1970) from the Gulf of California which indicated that cesium was not found concentrated in ratios one would expect from a simple food chain. Isaacs assumes that the principal interconnections in the marine food web are so diverse that all heterotrophs in the system (from microorganisms to vertebrates) can be treated as if they derived their food from a common source that is only coarsely differentiated. Therefore, the heterotrophs can all be treated as if they were at the same average trophic position. In this unstructured food web, Isaacs visualizes four levels of matter or energy: 1) source, 2) living tissue, 3) nonliving but retrievable matter, and 4) irretrievable matter. The source is assumed to be phytoplankton which is added to the system at a constant rate. The living matter consists of all heterotrophs, while the dead retrievable matter may consist of such sources of carbon as organic detritus or dissolved organic matter. The irretrievable component is that matter (or energy) which is forever lost to the system through such processes as respiratory combustion or mineralization. The "unstructured" nature of the food web comes from a set of coefficients which represent movement of material between these groups. The transitions are not in a trophic level line. Rather, groups two and three interact bilaterally and groups three and four can receive from other levels bypassing intermediates.

Isaacs calculates the final steady state values for the total living and dead material by summing two infinite series. To obtain these series, he introduces a "matrix" which is designed to aid in the formulation of each of the terms. The series take the form:

$$\begin{aligned} M'_t = {} & M_0 K_1 + M_0 K_1 (K_1 + K_3) \\ & + M_0 K_1 [K_1 (K_1 + K_3) + K_3 (K_1 + K_3)] \\ & + M_0 K_1 [K_1 (K_1 + K_3)^2 + K_3 (K_1 + K_3)^2] \\ & + \ldots = \frac{M_0 K_1}{1 - (K_1 + K_3)} = \frac{M_0 K_1}{K_2} \end{aligned}$$

$$\begin{aligned} M''_t = {} & M_0 K_3 + M_0 K_3 (K_1 + K_3) \\ & + M_0 K_3 [K_1 (K_1 + K_3) + K_3 (K_1 + K_3)] \\ & + M_0 K_3 [K_1 (K_1 + K_3)^2 + K_3 (K_1 + K_3)^2] \\ & + \ldots = \frac{M_0 K_3}{1 - (K_1 + K_3)} = \frac{M_0 K_3}{K_2} \end{aligned}$$

where M_0 = increment of initial input periodically introduced into the

[1]Department of Neurosciences, School of Medicine, and Marine Neurobiology Unit, Scripps Institution of Oceanography, University of California San Diego, La Jolla, CA 92037.

[2]We have enclosed Isaacs' use of the word "matrix" in quotes because he has used the word in a common rather than in the standard mathematical sense. When the word appears without quotes in this text we are using it in the standard sense of a rectangular array of elements which operates on column vectors from the left to produce new column vectors.

Manuscript accepted June 1974.
FISHERY BULLETIN: VOL. 73, NO. 2, 1975.

system at intervals equal to the time taken by one average step in the food web,

M'_t = total quantity of material in living tissue (level two),

M''_t = total in nonliving recoverable material (level three),

K_1 = a coefficient of conversion of matter (or energy) in food into living tissue,

K_2 = a coefficient of conversion of matter (or energy) in food into irretrievable form (e.g., by respiratory combustion or mineralization), and

K_3 = a coefficient of conversion of matter (or energy) in food into nonliving but retrievable form (e.g., organic detritus or dissolved organic matter).

Restrictions on coefficients are:

$$K_1 + K_2 + K_3 = 1,$$
$$0 < K_i < 1, \text{ where } i = 1, 2, \text{ or } 3.$$

MATRIX APPROACH

In our representation of the unstructured food web, source, living tissue, and nonliving but retrievable matter are taken to be components in a vector in a three-dimensional space. This vector can be written

$$\overline{w} = \begin{pmatrix} w_1 \\ w_2 \\ w_3 \end{pmatrix}$$

where w_1 is the amount of matter (or energy) present in phytoplankton, w_2 is the amount present in heterotrophs, and w_3 is the amount present in retrievable dead material. The fourth level (loss) is the difference between the total input and the material present in the three other levels.

The matrix operator controlling movement of material from one level to another, using Isaacs' coefficients, takes the form:

$$A = \begin{pmatrix} 1 & 0 & 0 \\ K_1 & K_1 & K_1 \\ K_3 & K_3 & K_3 \end{pmatrix}$$

Each K represents the proportion of material transferred between the levels appropriate to its position in a time equivalent to one application of the matrix.

As Isaacs points out, three constants may not be sufficient. It is probably not reasonable to assume, for example, that all matter is converted to living tissue with the same coefficient of conversion or that both living and dead matter have the same conversion factor to irretrievable form. One advantage of our method is that it can be generalized to a more complex form. This cannot easily be done with Isaacs' original method because crossterms in the K's rule out viewing the steady state values as simple geometric series. The generalized form of the matrix for an unstructured food web with these additional coefficients is:

$$A = \begin{pmatrix} 1 & 0 & 0 \\ k_1 & k_4 & k_7 \\ k_2 & k_5 & k_8 \end{pmatrix}$$

where k_1 = conversion factor from source to living,

k_2 = conversion factor from source to dead retrievable,

k_3 = conversion factor from source to inrretrievable,

k_4 = conversion factor from living to living,

k_5 = conversion factor from living to dead retrievable,

k_6 = conversion factor from living to irretrievable,

k_7 = conversion factor from dead to living,

k_8 = conversion factor from dead to dead retrievable, and

k_9 = conversion factor from dead to irretrievable.

In this case,

$$k_1 + k_2 + k_3 = 1$$
$$k_4 + k_5 + k_6 = 1$$
$$k_7 + k_8 + k_9 = 1$$
$$0 < k_i < 1, \text{ where } i = 1 \text{ to } 9.$$

When this matrix acts upon the state vector $\overline{w}$ the result is somewhat more complex:

$$A\overline{w} = \begin{pmatrix} 1 & 0 & 0 \\ k_1 & k_4 & k_7 \\ k_2 & k_5 & k_8 \end{pmatrix} \begin{pmatrix} w_1 \\ w_2 \\ w_3 \end{pmatrix} = \begin{pmatrix} w_1 \\ k_1 w_1 + k_4 w_2 + k_7 w_3 \\ k_2 w_1 + k_5 w_2 + k_8 w_3 \end{pmatrix}.$$

Steady State Results

The eigenvectors and eigenvalves of a matrix fully characterize its properties. For the matrix representing the Isaacs assumptions the following eigenvalues (λ's) and eigenvectors ($\bar{u}$'s) can be obtained:

$$\lambda_1 = 1 \qquad \lambda_2 = K_1 + K_3 \qquad \lambda_3 = 0$$

$$u_1 = \begin{pmatrix} 1 \\ \frac{K_1}{K_2} \\ \frac{K_3}{K_2} \end{pmatrix} \quad u_2 = \begin{pmatrix} 0 \\ \frac{K_1}{K_2} \\ \frac{K_3}{K_2} \end{pmatrix} \quad u_3 = \begin{pmatrix} 0 \\ 1 \\ -1 \end{pmatrix}.$$

Any initial state of the system (e.g., $\overline{w}$) can be written as a weighted sum of the eigenvectors

$$\overline{w} = c_1\overline{u}_1 + c_2\overline{u}_2 + c_3\overline{u}_3.$$

If we now apply A n times to this vector we obtain

$$A^n\overline{w} = c_1\lambda_1^n\overline{u}_1 + c_2\lambda_2^n\overline{u}_2 + c_3\lambda_3^n\overline{u}_3.$$

After a sufficient time (n very large), the second and third term will vanish, leaving an expression for the final state of the system:

$$\lim_{n\to\infty} A^n\overline{w} = c_1\overline{u}_1.$$

In Isaacs' terms $c_1 = M_0$ and the limiting values for the second and third compartments are M'_t and M''_t respectively. Therefore

$$M'_t = M_0 K_1/K_2$$
$$M''_t = M_0 K_3/K_2$$

which is exactly Isaacs' result.

For the nine constant model, there is also always a steady state distribution of matter in the system. By finding the eigenvector corresponding to an eigenvalue of one, we can obtain the following steady state values of M'_t (total quantity of material in living matter) and M''_t (total in nonliving recoverable material) in terms of a constant input M_0:

$$M'_t = \frac{-k_1(k_8-1) + k_2k_7}{(k_4-1)(k_8-1) - k_5k_7} M_0$$

$$M''_t = \frac{-k_2(k_4-1) + k_5k_1}{(k_4-1)(k_8-1) - k_5k_7} M_0.$$

Trophic Level Equations

In addition to values for total amounts of living and retrievable dead matter, Isaacs develops equations for general trophic levels. His equations can be generated by our approach if our original matrix is broken down into component parts and then applied to the steady state vector. For example, let us consider Isaacs' case (Isaacs 1973) of a subset of trophic levels which are complete and mutually exclusive. He considers strict herbivores, detrital feeders, and full predators to be such a subset.

Our original matrix A can be written in the following way

$$A = A_{S+R} + A_H + A_D + A_P$$

where $$A_{S+R} = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 0 & 0 \\ K_3 & K_3 & K_3 \end{pmatrix}$$

$$A_H = \begin{pmatrix} 0 & 0 & 0 \\ K_1 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}$$

$$A_D = \begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & K_1 \\ 0 & 0 & 0 \end{pmatrix}$$

$$A_P = \begin{pmatrix} 0 & 0 & 0 \\ 0 & K_1 & 0 \\ 0 & 0 & 0 \end{pmatrix}$$

A_{S+R} = matrix responsible for the biomass in source and the retrievable dead matter,
A_H = matrix responsible for biomass in herbivores,
A_D = matrix responsible for biomass in detrital feeders, and
A_P = matrix responsible for biomass in predators.

To obtain the potential biomass for each of the trophic levels, we take the appropriate matrix times the steady state vector. Thus, the equation for the potential biomass of herbivores is obtained from

$$A_H\bar{u}_1 = \begin{pmatrix} 0 & 0 & 0 \\ K_1 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix} \begin{pmatrix} M_0 \\ \frac{M_0K_1}{K_2} \\ \frac{M_0K_3}{K_2} \end{pmatrix} = \begin{pmatrix} 0 \\ M_0K_1 \\ 0 \end{pmatrix}.$$

Similarly, for detrital feeders

$$A_D \bar{u}_1 = \begin{pmatrix} 0 \\ \dfrac{M_0 K_1 K_3}{K_2} \\ 0 \end{pmatrix}$$

and for predators

$$A_P \bar{u}_1 = \begin{pmatrix} 0 \\ \dfrac{M_0 K_1^2}{K_2} \\ 0 \end{pmatrix}.$$

All of Isaacs' other equations for trophic level potential biomasses or fluxes can be obtained in a similar manner.

Equations for the potential biomass of trophic levels can also be calculated for the generalized model. This is done in a manner similar to that described in the previous section.

Strict herbivores (feeding on source):

$$M_m = M_0 k_1.$$

Omnivores (feeding on source, living and retrievable dead):

$$M_v = M_0 \left(\frac{-k_1 (k_8 - 1) + k_2 k_7}{(k_4 - 1)(k_8 - 1) - k_5 k_7} \right)$$

$$= k_1 M_0 + k_4 M'_t + k_7 M''_t.$$

Particle feeders (feeding on source and retrievable dead):

$$M_\mu = M_0 \left(\frac{k_1 (k_4 - 1)(k_8 - 1) + k_2 k_7 (1 - k_4)}{(k_4 - 1)(k_8 - 1) - k_5 k_7} \right)$$

$$= k_1 M_0 + k_7 M''_t.$$

Detrital feeders (feeding on retrievable dead):

$$M_d = M_0 \left(\frac{-k_2 k_7 k_4 + k_2 k_7 + k_1 k_5 k_7}{(k_4 - 1)(k_8 - 1) - k_5 k_7} \right)$$

$$= k_7 M''_t.$$

Full predators (feeding on living):

$$M_P = M_0 \left(\frac{-k_4 k_1 (k_8 - 1) + k_4 k_2 k_7}{(k_4 - 1)(k_8 - 1) - k_5 k_7} \right)$$

$$= k_4 M'_t.$$

Nonherbivorous omnivores (feeding on living and retrievable dead):

$$M_n = M_0 \left(\frac{-k_4 k_1 k_8 + k_1 k_4 + k_2 k_7 + k_1 k_5 k_7}{(k_4 - 1)(k_8 - 1) - k_5 k_7} \right)$$

$$= k_4 M'_t + k_7 M''_t.$$

ACKNOWLEDGMENTS

This work was partially supported by Public Health Service Grant NS-09342. We would like to thank the following people for reading the manuscript and making valuable comments: J. D. Isaacs, G. Wick, J. Enright, P. Hartline, and M. Mullin. Thanks are also due E. Venrick who brought the problem to our attention and the other students in NS 242 who patiently allowed us to work out the model as a classroom example.

LITERATURE CITED

ISAACS, J. D.

1972. Unstructured marine food webs and "pollutant analogues." Fish. Bull., U.S. 70:1053-1059.

1973. Potential trophic biomasses and trace-substance concentrations in unstructured marine food webs. Mar. Biol. (Berl.) 22:97-104.

YOUNG, D. R.

1970. The distribution of cesium, rubidium, and potassium in the quasi-marine ecosystem of the Salton Sea. Ph.D. Thesis, Univ. California, San Diego, 234 p.