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COMMISSION OF THE EUROPEAN COMMUNITIES

A MATHEMATICAL MODEL FOR THE EVOLUTION OF ZOOPLANKTON POPULATIONS

by

H. HEMBD

1972

Joint Nuclear Research Centre
Ispra Establishment - Italy

Nuclear Study

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ABSTRACT

In the framework of ecology a deterministic model to describe the evolution of zooplankton (copepods) populations in lakes has been developed. Balance equations are derived relating the observed concentrations of copepods to production rates and mortality. These demographic parameters are to serve as indicators of water-environment conditions. Numerical studies are in progress.

KEYWORDS

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SURVIVAL TIME
TIME DEPENDENCE
QUANTITY RATIO

CONTENTS

The zooplankton populations, especially the different species of copepods (Eudiaptomus, Cyclops) are considered to be suitable and sensitive biological detectors for the control of the water quality in lakes and of the consequences of the inputs from the environment. On the basis of long term observations done by Ravera and coworkers [1] of the populations of copepods in the subalpine lakes (Lago Maggiore, Lago di Osmate and presently Lago di Lugano) a mathematical model has been constructed describing the evolution of the different stages of species as a function of productivity and mortality. For the application of the model in its present version a time series of observations of the population must be given and the times of development of every stage (= maximal possible lifetime) must be known. Then the demographic parameters like productivity and mortality are calculated. The variation of these parameters from period to period gives a measure for the variation of the ecological conditions in a lake.

The Model

The model describes the evolution of the populations in two time scales, one scale is the physical time or observation time t, the second one counts the age s of an individuum. Clearly, $0 \leq s \leq \tau_i$, if τ_i is the time of development of stage i. We denote the number of individuals of stage i per unit volume at time t, having an age between s and $s+\Delta s$ by $N_i(t,s)\ \Delta s$. The mortality or the percentage of individuals that die out or get lost per unit time be $q_i(t,s)$. We can write down a balance equation, expressing the fact that the number density or concentration of individuals of stage i at time $t+\Delta t$ with age $s+\Delta s$ is equal to the concentration at a time step $\Delta t = \Delta s$ before, diminished by the fraction that has died out.

$$N_i(t+\Delta t, s+\Delta s) = N_i(t,s)\,[1 - q_i(t,s)\,\Delta s] \tag{1}$$

This change of concentration is illustrated in Fig. 1. The history of an individuum proceeds along a diagonal from the bottom (s = 0, "newborn" inviduals) to the top (s = τ_i , maturity). By taylor expansion of Eq. (1) we state that the concentration satisfies the following differential equation

$$\frac{\partial N_i(t,s)}{\partial t} + \frac{\partial N_i(t,s)}{\partial s} = -q_i(t,s)\,N_i(t,s) \tag{2}$$

Its solution is

$$N_i(t,s) = f(s-t)\,\exp\left[-\int_0^s q_i(s'-s+t,s')\,ds'\right] \tag{3}$$

with an arbitrary function f. This function can be determined from an initial state. For s = 0 we have $N_i(t,0) = f(-t)$. Hence

$$N_i(t+s,s) = N_i(t,0)\cdot Q_i(t,s) \tag{4}$$

where

$$Q_i(t,s) = \exp\left[-\int_0^s q_i(s'+t,s')\,ds'\right] \tag{5}$$

is the probability that an individuum of state i and born at time t will not die out before attaining the age s at time t+s. Obviously $Q(t,s=0) \equiv 1$.

The individuals that have passed the complete time of development τ_i in stage i are assumed to change then immediately into the next stage (i+1) of their metamorphosis. In the next stage the begin with age zero:

$$N_{i+1}(t,0) = N_i(t,\tau_i) \tag{6}$$

The leakage due to mortality is compensated by the productivity of the adults in the last stage i = n. The adults may produce eggs during their whole lifetime, not only at the end of the stage. If p(t,s)ds is the number of eggs produced at time t by an adult of age s in the time interval ds, the concentration of new eggs $N_1(t,s=0)$ at time t is given as the sum (integral) of the contribution of the adults of any age:

$$N_1(t,0) = \int_0^{\tau_n} N_n(t,s')\, p(t,s')\, ds' \qquad (7)$$

The three processes of "aging", "passage of stage" and "production", expressed by Eqs. (4), (6) and (7) describe completely the evolution of the populations in any stage.

System Equations

Equations for the initial states (s = 0) of the stages (i = 2,3,...,n) can be related to $N_1(t,0)$ (i.e. the productivity) by successive application of Eqs. (6) and (7). With Eq. (6) we perform $N_i(t+\tau_1+\tau_2+\cdots\tau_{i-1}, 0) = N_{i-1}(t+\tau_1+\tau_2+\cdots+\tau_{i-1}, \tau_{i-1})$. According to relation (4) this is equal to $N_{i-1}(t+\tau_1+\ldots+\tau_{i-2}, 0)\cdot Q_{i-1}(t+\tau_1+\ldots+\tau_{i-2}, \tau_{i-1})$. Reducing further in the same way we obtain

$$N_i(t+T_{i-1}, 0) = Q_{i-1}(t+T_{i-2}, \tau_{i-1})\, Q_{i-2}(t+T_{i-3}, \tau_{i-2})\cdot \qquad (8)$$

$$\cdots Q_2(t+T_1, \tau_2)\, Q_1(t,\tau_1)\, N_1(t,0)$$

where

$$T_k \equiv \tau_1 + \tau_2 + \cdots + \tau_k \qquad (9)$$

and $N_1(t,0)$ is given by Eq. (7). If $N_n(t,0)$ were known for a whole cycle, i.e. for the time range $0 \leq t \leq T_n$, then $N_i(t,0)$ (i = 1,2,...) would be known for all time. The distribution function $N_i(t,s)$ can be obtained from (8) via relation (4) with t replaced by t-s:

$$N_i(t+T_{i-1}, s) = N_i(t+T_{i-1}-s, 0)\, Q_i(t+T_{i-1}-s, s) = \qquad (10)$$

$$= Q_1(t-s,\tau_1)\cdots Q_{i-1}(t+T_{i-2}-s, \tau_{i-1})\, Q_i(t+T_{i-1}-s, s)\int_0^{\tau_n} N_n(t-s,s')\, p(t-s,s')\, ds'$$

In practice it is difficult to measure the concentrations resolved with respect to the age s. What is generally observed are the integral concentrations

$$y_i(t) = \int_0^{\tau_i} N_i(t,s)\,ds \tag{11}$$

denoting the number of individuals of any age at time t in stage i per unit volume of water. In order to rewrite the balance equations (10) for the integral data it is consequent to introduce the average production rate (average over all ages) at time t

$$\bar{p}(t) = \int_0^{\tau_n} N_n(t,s')\,p(t,s')\,ds' \Big/ \int_0^{\tau_n} N_n(t,s')\,ds' \tag{12}$$

After integration the system of equations (10) passes into the following system for the $y_i(t)$

$$y_i(t+T_{i-1}) = \int_0^{\tau_i} Q_1(t-s,\tau_1)\cdots Q_i(t+T_{i-1}-s,s)\,\bar{p}(t-s)\,y_n(t-s)\,ds \tag{13}$$

(i = 1,2,...,n)

Approximations

It seems reasonable to assume that the changes of the "survival proabilities" $Q_i(t,s)$ as a function of the time t of observation is negligible compared to the changes with respect to s during the time interval of length τ_i in which stage i is developing.

Replacing t by t + τ_i and applying the mean value theorem we may rewrite Eqs. (13) in the form

$$y_i(t+T_i) = Q_1(t+\tau_1-s_i,\tau_1)\cdots Q_{i-1}(t+T_{i-1}-s_i,\tau_{i-1})\cdot \int_0^{\tau_i} Q_i(t+T_i-s_i,s)\,\bar{p}(t+\tau_i-s)\,y_n(t+\tau_i-s)\,ds \tag{14}$$

(i = 1,2,...,n)

where $0 \le s_i \le \tau_i$. According to the weak dependence of the $Q_i(t,s)$ on the first variable the factors in front of the integral sign of Eq. (14) are nearly constant

$$Q_k(t+T_k-s_i, \tau_k) \approx Q_k(T_k, \tau_k); \quad (k=1,2,\ldots,n) \tag{15}$$

This is true at least within observation intervals not too large with respect to the τ_k.

In order to reduce the influence of the errors of the observation data y_i to the desired demographic parameters p and Q_i the time averages of Eqs. (17) will be considered too. We introduce the following mean values

$$\frac{1}{t^*}\int_0^{t^*} y_i(t+T_i)\,dt \equiv \langle T_i | y_i | T_i + t^* \rangle \tag{16}$$

For t^* sufficiently large we obtain from Eq. (14) by integration and a further application of the mean value theorem

$$\langle T_i | y_i | T_i + t^* \rangle = \langle 0 | \bar{p} y_n | \tau_i + t^* \rangle\, Q_1(t_1,\tau_1) \cdots Q_{i-1}(t_{i-1},\tau_{i-1}) \cdot \int_0^{\tau_i} Q_i(t_i,s)\,ds \quad (i=1,2,\ldots,n) \tag{17}$$

The reference times t_k satisfy

$$T_{k-1} \le t_k \le T_k + t^*. \tag{18}$$

$Q_k(t_k, \tau_k)$ is the fraction of individuals of stage k and at time t_k that actually will stay in the population all the time of development τ_k and then pass into the next stage. The quantity

$$\int_0^{\tau_i} Q_i(t_i,s)\,ds = \bar{s}_i \tag{19}$$

can be considered, in the sense of relation (4), as the mean lifetime of those individuals that are found at time t_i at the beginning of stage i.

If the $Q_k(t_k, s)$ depend weakly on t_k they may again be replaced by $Q_k(T_k, s)$ as in (15). Eq. (17) expresses the fact that the average concentration $y_i(t)$ in stage i observed from $t = T_i$ to $t = T_i + t^*$ is given by the average production rage observed from $t = 0$ to $t = \tau_i + t^*$, times the probability that an individuum has passed successfully all stages from the egg to stage (i-1), times the mean lifetime $\bar{s}_i$ in stage i.

From Eq. (17) for i = 1 we can deduce the average production rate during the time $0 \leq t \leq \tau_1 + t^*$

$$\langle 0 | \bar{p} | \tau_1 + t^* \rangle \, \bar{s}_1 = \langle \tau_1 | y_1 | \tau_1 + t^* \rangle / \langle 0 | y_u | \tau_1 + t^* \rangle \tag{20}$$

Since $\bar{p}$ is the full production rate and $\bar{s}_1$ the mean lifetime of an egg, the quantity of interest is the "effective productivity" $(\bar{p} \cdot \bar{s}_1)$. It is given by the measurable ratio on the r.h.s. of Eq. (20). In this way the ambiguity of a scaling factor between the Q_i and $\bar{p}$ in the homogeneous form of Eq. (14) is removed.

Discretization

Since in praxis the observations are not done continously in time but at discrete time steps of distance Δt of the order of ten days, we substitute t by $k \cdot \Delta t$ and s by $\hat{\ell} \cdot \Delta s$. All processes are measured in the new time unit $\Delta t = \Delta s$. We further introduce $\tau_i = \ell_i \cdot \Delta t$; $T_i = L_i \, \Delta t$. Hence

$$L_i = \ell_1 + \ell_2 + \dots + \ell_i \tag{21}$$

The integrals are replaced by sums and $\bar{p}(t + \tau_i - s) \Delta s$ is replaced by $P(k + \ell_i - \hat{\ell})$. In this way system (14) with the assumption (15) turns over into the discrete system

$$y_i(k + L_i) = \sum_{\hat{\ell}=1}^{\ell_i} G_i(L_i, \hat{\ell}) \, P(k + \ell_i - \hat{\ell}) \, y_u(k + \ell_i - \hat{\ell}) \tag{22}$$

(i = 1,2,...,n)
$(k = 1,2,\dots,K^*)$

where

$$G_i(L_i,\ell) = Q_1(L_1,\ell_1)\cdots Q_{i-1}(L_{i-1},\ell_{i-1})\cdot Q_i(L_i,\ell) \qquad (22')$$

In an analogous way the equations of the time averages (17) are transformed. Instead of (16) we define for K^* sufficiently large

$$\langle L_i | y_i | L_i + K^* \rangle = \frac{1}{K^*}\sum_{k=1}^{K^*} y_i(k+L_i) \qquad (23)$$

and obtain the system

$$\langle L_i | y_i | L_i + K^* \rangle = \langle 0 | P y_n | \ell_i + K^* \rangle \sum_{\ell=0}^{\ell_i} G_i(L_i,\ell) \qquad (24)$$

$$(i = 1,2,\ldots,n)$$

The number of unknowns $G_i(\ell)$ in system (22) is extactly L_n. The vector P(m), $1 \le m \le K^* + \max \ell_i$, could in principle be determined fully. But in view of the fluctuations in the observed data it is more realistic to assume an average productivity given by Eq. (20) and not to rely on a value at every time step. The number of equations is $(n \cdot K^*)$ and generally chosen to be larger than the number of unknowns. The unknown paramters $G_i(\ell)$ are obtained from the condition that the functional consisting of the sum of the squares of the residues of the overdetermined system (22) be a minimum. A computer program has been written that does this minimisation with the aid of a certain strategy [2]. The series of observations $y_i(k)$ and the ℓ_i are input, the parameters P and $G_i(\ell)$ are output of the program. Numerical studies are in progress.

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>
> Alfred Nobel

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