# RANDOM PROCESS THEORY IN ECOLOGICAL AND ENVIRONMENTAL MODELLING

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# Random Process Theory in Ecological and Environmental Modelling

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#### Summary

This paper deals with applications of random process theory to ecological and environmental modelling. We first present some elements of this theory that were developed by Kolmogorov, Harries and others, and then show how the theory can be applied to dynamics of a population passing through different phases of development. The paper next deals with the problem of consecutive food removal from a medium in which some food consumer exists, and with some environmental problems. In the last section we touch on the question of simultaneous impact of different pollutants on the organism (or living organ).

#### 1. Elements of random process theory

Let us consider a particle that after a period of time t creates  $\mathbf{n}_1$  particles of second generation instead of itself.

Each second-generation particle can produce  $n_2$  particles of third generation and so on. Such processes are very common in atomic physics and biology. The probability of the appearance of one, two, three, and more particles in the next generation is  $p^{(1)}$ ,  $p^{(2)}$ ,  $p^{(3)}$ ,... $p^{(n)}$  respectively, where  $\sum_{i=0}^{\infty} p^{(i)} = 1$ 

and i is the number of particles in the next generation that replace the single particle.

Let us introduce the special probability function f(z), which can be written as:

$$f(z) = \sum_{i=1}^{\infty} p^{(i)}z^{(i)} \quad \text{under } |z| \leq 1$$
(1)

or

$$f(0) = P^{(0)}$$
 under  $z = 0$  (2)

Here z is a new variable. Function f(z) is very useful for calculating the main characteristics of random processes which occur in physics and biology. We discuss it briefly in sections 2 and 3. The number of particles m appearing in the next generation from one particle can be calculated by the relation

$$m = \sum_{i=1}^{\infty} i p^{(i)}$$
(3)

We can use function f(z) for the same purpose. Using the differentiation of (1), we receive:

$$\frac{\partial f(z)}{\partial z} = \sum_{i=1}^{\infty} i p^{(i)} z^{i-1}$$
(4)

With z = 1 right-hand side of equation (4) becomes equal to equation (3), so that m can be calculated:

$$m = \frac{\partial f(z)}{\partial z} \bigg|_{z = 1}$$
 (5)

Variance  $\sigma^2$  can be also calculated with the help of function f(z). Normally  $\sigma^2$  is calculated as follows:

$$\sigma^{2} = \sum_{i=0}^{\infty} (i-m)^{2} p^{(i)} = \sum_{i=1}^{\infty} i^{2} p^{(i)} - 2m \sum_{i=1}^{\infty} i p^{(i)} + m^{2}$$

$$= \sum_{i=1}^{\infty} i^2 p^{(i)} - m^2$$

$$i=1$$
(6)

Using function f(z), we have

$$\frac{\partial^2 f(z)}{\partial z^2} = \sum_{i=1}^{\infty} i(i-1)p^{(i)}z^{i-2} =$$

Again taking z = 1, we can rewrite the expression as:

$$= \sum_{i=1}^{\infty} i(i-1)p^{(i)} = \sum_{i=1}^{\infty} i^{2}p^{(i)} - \sum_{i=1}^{\infty} ip^{(i)} = \sum_{i=1}^{\infty} i^{2}p^{(i)} - m$$

$$i=1 \qquad i=1 \qquad i=1$$

We obtain

$$\sum_{i=1}^{\infty} i^{2} p^{(i)} = \frac{\partial^{2} f(z)}{\partial z^{2}} + m$$

$$z = 1$$
(7)

Using equation (7), we can rewrite equation (6) as

$$\sigma^2 = \frac{\sigma^2 f(z)}{\partial z^2} \bigg|_{z = 1} + m - m^2$$
(8)

If we have K generations, the special function should be presented in the form  $F_k(z)$ , where k is the number of generations.

$$F_{k} = f(f(...f(z)...))$$
(9)

For the third generation, for example, we have

$$F_3(z) = f(f(f(z)))$$

Taking into consideration equations (5) and (8) it is easy to obtain  $m_3$  and  $\sigma_3$  for the third generation.

$$m_3 = \frac{\partial F_3(z)}{\partial z} z = 1$$
 (10)

$$\sigma_3^2 = \frac{\partial F_3(z)}{\partial z} \bigg|_{z = 1} + m_3 - m_3^2$$
(11)

The probability of the disappearance of particles in the third generation will be  $p_3^{(0)} = F_3(z) \Big|_{z=0}$  .

All expressions written above reflect the simplest situation, but the same principles can be applied to processes where the special function has to be changed in time, in space, or from one generation to another. In such cases:

$$F_k(z) = f_1(f_2(f_3...F_k(z)...))$$
 (12)

It is possible also to consider situations where particles produce a wide spectrum of different particles of different generations.

It is important to note that the particles exist independently of each other.

# 2. Dynamics of population at different stages of development

Normally, in investigating dynamic processes in nature, one is faced with the problem of the quantity of a population (animals, microbes, particles, etc.) and of its quality. Any organism during its existence has several stages of development in which its quality changes. Every cell has some implicit stages of development before dividing into two. Before appearing as a butterfly, the eggs of the forest pest have been small larvae, large larvae, pupae and adult females.

We will now show how the theory can be applied to population dynamics modelling for organisms going through different development stages.

Let us take special probability transfer function  $f_j(z)$ , for an organism which entered the j development stage from the j - l stage. Going from one stage to another, the organism (animal, microbe, particle etc.) can survive (with probability g)

or die (with probability p).

Taking into consideration equation (1), we can write

$$f(z) = p^{(0)}z^{0} + p^{(1)}z^{1} + p^{(2)}z^{2} + p^{(3)}z^{3} + \dots$$
 (13)

In the case of a development stage where we have only two probabilities:  $p^{(0)} = q$  , and  $p^{(1)} = p$  , we can rewrite (13)

$$f(z) = q + pz \tag{14}$$

If in phase j = 0 we have  $m_0$  organisms to each of which equation (14) can be applied, the special function for the first development stage can be expressed as:

$$f_1(z) = (q_1 + p_1 z)^{m_0}$$
 (15)

Using relations (5), (8), and (2) it is possible to calculate all the important values characterizing the population in the first development stage (mean, variance and probability of disappearance of population).

$$m_1 = \frac{\partial f(z)}{\partial z} \bigg|_{z = 1} = m_0 (q_1 + p_1 z)^{m_0 - 1} p_1 \bigg|_{z = 1} = m_0 p_1$$
 (16)

$$\sigma_{1}^{2} = \frac{\partial^{2} f(z)}{\partial z^{2}} \bigg|_{z = 1} + m_{1} - m_{1}^{2} = m_{0}(m_{0} - 1)p_{1}^{2} + m_{0}p_{1} - (m_{0}p_{1})^{2}$$

$$= m_{o} p_{1} (1 - p_{1}) = m_{o} p_{1} q_{1}$$
 (17)

$$p_1^{(0)} = (q_1)^{m_0}$$
 (18)

The coefficient of variation  $\rho_1$  can be calculated as

$$\rho_{1} = \sqrt{\frac{\sigma^{2}}{m_{1}^{2}}} = \sqrt{\frac{m_{o}^{p} 1^{q} 1}{m_{o}^{p} 1^{2}}} = \sqrt{\frac{q_{1}}{m_{o}^{p} 1}} = \sqrt{\frac{q_{1}}{m_{o}^{p} 1}} = \sqrt{\frac{q_{1}}{m_{o}^{p} 1}}$$
(19)

We consider a very simple example:  $m_0 = 20$ ,  $p_1 = 0.8$ ,  $q_1 = 0.2$ , and find four main characteristics of a population in the first development stage:

$$m_1 = 20 \times 0.8 = 16$$

$$\sigma_1^2 = 20 \times 0.8 \times 0.2 = 3.2$$

$$p_1^{(0)} = (0.2)^{20} \approx 10^{-13}$$

$$\rho_1 = \frac{1}{\sqrt{20}} \times \sqrt{\frac{0.2}{0.8}} \approx 0.1 \approx 10\%$$

This technique becomes more productive in the case of several development stages. Here the special function can be written in the following form:

$$F_{j}(z) = \left[q_{1} + p_{1}(q_{2} + p_{2}(q_{3} + \dots p_{j-1}(q_{j} + p_{j}z)\dots))\right]^{m_{0}}$$

Opening the brackets and rearranging, we have

$$F_{j}(z) = \begin{bmatrix} j & k-1 \\ \sum q_{k} & \sum_{e=1}^{j} p_{e} + \sum_{k=1}^{j} p_{k}z \end{bmatrix}^{m_{0}}$$

Introducing the notations

$$A_{j} = \sum_{k=1}^{j} q_{k} \prod_{e=1}^{k-1} p_{e}$$

and

$$B_{j} = \prod_{k=1}^{j} p_{k}$$

we have the following equation

$$F_{j}(z) = \begin{bmatrix} A_{j} + B_{j}z \end{bmatrix}^{m_{0}}$$

which is practically the same as equation (15) for the first development stage. Following relations (15), (17), (18), (19), we can calculate mean  $(M_j)$ , variance  $(D_j^2)$ , probability of disappearance of population  $(p_j^{(0)})$  and coefficient of variation  $(R_j)$  in the j development stage.

$$M_{j} = M_{O}B_{j} \tag{20}$$

$$D_{j}^{2} = M_{O}B_{j}A_{j} \tag{21}$$

$$R_{j} = \frac{1}{\sqrt{m_{o}}} \sqrt{\frac{A_{i}}{B_{i}}}$$
 (22)

$$p_{j}^{(0)} = F_{j}(z) \begin{vmatrix} z & 0 & 0 \\ z & 0 & 0 \end{vmatrix}$$
 (23)

This mathematical treatment provides all the relevant information on the dynamics of population at different development stages.

### 3. Pollutant distribution in environmental spheres

The formulas developed above can be applied to the distribution of pollutants in environmental spheres. Let us suppose that hundreds of small clouds of poison were released in some region of the atmosphere. Each cloud consists of ten grams of poison, which completely disappears from the atmosphere in ten days: twenty clouds (20%) have been degraded by sunlight in arid areas, and eighty clouds (80%) have been washed from the atmosphere by the rains in humid areas.

The special function for the atmosphere can be written following (15) as:  $\left[f_1(z) = 0.2 + 0.8z\right]^{100}$ .

In the hydrosphere during thirty days, the poison clouds were completely mineralized (with probability 0.3) and the rest were absorbed by plankton (probability 0.7). For the hydrosphere we can write the special function as:  $f_2(z) = 0.3 + 0.7z$ . During the next twenty-day period some poison clouds were degraded in accordance with plankton mortality (probability 0.6), and the rest absorbed by fish together with plankton. For the plankton we have:  $f_3(z) = 0.6 + 0.4z$ .

Let us suppose that after fifty days a portion of poison has left the fish (probability 0.9) or been accepted by people's bodies with fish meat (probability 0.1).

 $f_4(z) = 0.9 + 0.1z$  (This assumption may be considered an unrealistic one.)

All cycles take 110 days to be completed. It is of interest to find the quantity of poison accepted by people at the end of that time.

The special function to the end of the fourth environmental sphere (fish) or to the beginning of the fifth (people) will be as follows:

$$F_4(z) = f_1(f_2(f_3(f_4(z)))) = [0.2 + 0.8(0.3 + 0.7(0.6 + 0.4(0.9 + 0.1z))]^{100} = [0.9776 + 0.0224z]^{100}.$$

Using (20), (21), (22), (23) we can calculate the mean, variance, probability of disappearance of poison before reaching the fifth sphere, and coefficient of variation:

$$M_4 = \frac{\partial F_4(z)}{\partial z} \bigg|_{z = 1} = 100 \left[0.9776 + 0.0224z\right]^{99} 0.0224 \bigg|_{z = 1}$$

$$= 2.24 \text{ clouds}$$

This means that 22.4 grams of the poison should be in people's bodies.

$$D_4^2 = \frac{\partial^2 F(z)}{\partial z^2} \bigg|_{z=1} + m - m^2 = 100.99 \left[ 0.9776 + 90224z \right]^{98}$$

$$\times (0.0224)^2 \bigg|_{z=1} + 2.24 - (2.24)^2 = 100.99 (0.0224)^2$$

$$+ 2.24 - (2.24)^2 = 2.23$$

$$P_4^{(0)} = [0.9776]^{100} \approx 0.05$$

$$R_4 = \sqrt{\frac{D_4^2}{M_4^2}} = \sqrt{\frac{2.23}{(2.24)^2}} \approx \frac{1}{1.5} \approx 0.66 \text{ cloud } \approx 7 \text{ gramms of poison}$$

The calculations suggest that normally after 110 days 22.4  $\pm$  7 grams of poison will reach people. The probability that no poison at all will reach people is very low (~ 0.05).

It is interesting to note that using the Newton binomial theorem we can calculate probability  $(p^{(i)})$  for people to receive different amounts of poison:

$$p_4^{(i)} = (0.9776)^{100-i} c_{100}^{i} (0.0224)^{i}$$

where

$$c_{100}^{i} = \frac{100 \times 99 \times 98 \times \dots (100 - i)^{i}}{i!}$$

and i = number of clouds.

Calculation gives us the following values:

$$p_4^{(0)} \approx 0.05$$
 ;  $p_4^{(1)} \approx 0.13$  ;  $p_4^{(2)} \approx 0.15$  ;

$$p_4^{(3)} \approx 0.10$$
;  $p_4^{(4)} \approx 0.06$ ;  $p_4^{(5)} \approx 0.03$ ;

$$p_4^{(6)} \approx 0.02$$
 and etc.

### 4. Consecutive substrate removal by microbial population

Let us consider some microbial population in a completely mixed reaction tank with an organic substrate of concentration s. From a biological point ov view, any cell can be in an active (1) or in a passive (2) state when it digests the food molecules or waits for interaction with them. The time needed for transferring the cell from one condition to another ( $\Delta$ t) is very short:  $\Delta$ t <<  $\Delta$ T where  $\Delta$ T is the interval of time for doubling the population of microbes. The probability for changing state 1 into state 2 is  $P_{12}$ , for keeping the same state  $P_{11}$ ,  $P_{22}$ , and for returning to the initial condition  $P_{21}$ .

For time interval  $\Delta t$  we can use the transfer probability matrix

$$P = \begin{vmatrix} P_{11} & P_{12} \\ P_{21} & P_{22} \end{vmatrix}$$

For time interval t =  $k\Delta t$  we should use matrix P, k times. From the theory it is known that with  $k \rightarrow \infty$ , matrix  $p^k \rightarrow \hat{p}$ , where

$$\hat{P} = \begin{bmatrix} \frac{P_{21}}{P_{12} + P_{21}} & \frac{P_{12}}{P_{12} + P_{21}} \\ \frac{P_{21}}{P_{12} + P_{21}} & \frac{P_{12}}{P_{12} + P_{21}} \end{bmatrix}$$

This property of matrix  $P^k |_{k \longrightarrow \infty}$  can be easily demonstrated by a simple example.

Let 
$$P = \begin{pmatrix} \frac{1}{4} & \frac{3}{4} \\ \frac{1}{2} & \frac{1}{2} \end{pmatrix}$$
 be the initial matrix.

Then 
$$P^2 = \begin{vmatrix} \frac{7}{16} & \frac{9}{16} \\ \frac{6}{16} & \frac{10}{16} \end{vmatrix}$$
 and  $P^4 = \begin{vmatrix} \frac{103}{255} & \frac{153}{256} \\ \frac{102}{256} & \frac{154}{256} \end{vmatrix} \approx \begin{vmatrix} \frac{2}{5} & \frac{3}{5} \\ \frac{2}{5} & \frac{3}{5} \end{vmatrix}$ .

Multiplication of matrix P soon (after four or five steps) provides a matrix practically equal to  $\hat{p}$ . Transposed matrix  $(\hat{p})^*$  can be used to calculate the number of active  $m_{\infty}^{(1)}$  and passive  $m_{\infty}^{(2)}$  microbes:

$$\begin{vmatrix} m_{\infty}^{(1)} \\ m_{\infty}^{(2)} \end{vmatrix} = (\hat{p})^* \times \begin{vmatrix} m_{0}^{(1)} \\ m_{0}^{(2)} \end{vmatrix}$$

Or we can rewrite it as:

$$m_{\infty}^{(1)} = \frac{P_{21}}{P_{12} + P_{21}} (m_{0}^{(1)} + m_{0}^{(2)})$$

$$m_{\infty}^{(2)} = \frac{P_{12}}{P_{12} + P_{21}} (m_{O}^{(1)} + m_{O}^{(2)})$$

It is interesting to note that in period t = k $\Delta$ t the number of active and passive microbes does not depend on the initial number (m<sub>0</sub><sup>(1)</sup>; m<sub>0</sub><sup>(2)</sup>), but on values of P<sub>12</sub> and P<sub>21</sub>. But practically, P<sub>12</sub> and P<sub>21</sub> are functions of organic substrate concentration S; when S is high enough P<sub>22</sub> >> P<sub>12</sub>, and then m<sub>∞</sub><sup>(1)</sup> >> m<sub>∞</sub><sup>(2)</sup>. We assume P<sub>21</sub> =  $\lambda$ S and P<sub>12</sub> =  $\beta$  where  $\lambda$  and  $\beta$ 

are some constants. ( $\lambda$  should be so chosen that if  $S \longrightarrow \infty$ ,  $P_{21} \longrightarrow 1$ .) We then have :

$$\frac{P_{21}}{P_{12} + P_{21}} = \frac{\lambda S}{\lambda S + \beta} = \frac{S}{S + \frac{\beta}{\lambda}}$$

These values can be considered as a coefficient which can help us to calculate part of the microbial population which will be in an active state  $(m_{\infty}^{(1)})$  after a period of  $5\Delta t$  or  $6\Delta t$ . Remember that the entire microbe population is  $(m_{O}^{(1)} + m_{O}^{(2)})$ . It grows at a rate  $\mu(s)$ ,

$$\mu(s) = \hat{\mu} \frac{dS}{K+S},$$

where  $\hat{\mu}$  = growth rate of a population under optimal conditions, i.e. the concentration of organic substrate is high enough to put the whole microbial population into the active state, and  $K = \frac{\beta}{\lambda}$ . Here we obtain a relation between  $\mu$  (s),  $\hat{\mu}$  and S which was found experimentally by Monod.

In more general cases, we can write

$$\mu(S) = \hat{\mu} \Psi(S) \tag{24}$$

where

$$\Psi(o) = 0; \quad \lim \Psi(S) = 1$$

$$S \longrightarrow \infty$$

Considering n organic substrates with concentrations of  $s_1$ ,  $s_2 \dots s_n$  we can use the approach described above. Let us

suppose that the substrate subscripts reflect the likelihood of the organic substrate to be a food for the microbial population. A cell can be active to one of n substrates and passive to all the others, or be passive to all of them. We thus have n+1 states for microbes. Let us assume that microbes can only pass to adjacent substrates in a sequence  $S_1, S_2, \ldots S_n$ , or vice versa. (This is the only restricting condition, which sometimes is hardly realistic.) Then the probability matrix will be:

$$P_{11} \quad P_{12} \quad O \quad \cdots \quad P_{21} \quad P_{22} \quad P_{23} \quad O \quad \cdots \quad P_{32} \quad P_{33} \quad P_{34} \quad O \quad \cdots \quad P_{n,n-1} \quad P_{nn} \quad P_{n,n+1} \quad \cdots \quad P_{n+1,n} \quad P_{(n+1)} \quad (n+1)$$

Matrix  $P \xrightarrow{k} \hat{P}$  under  $K \longrightarrow \infty$ . K is again the number of time steps  $\Delta t$ .

$$\hat{P} = \begin{bmatrix} a_{1}, a_{2}, \dots a_{n}, a_{n+1} \\ a_{1}, a_{2}, \dots a_{n}, a_{n+1} \\ \dots \\ a_{1}, a_{2}, \dots a_{n}, a_{n+1} \end{bmatrix}$$

Here

$$a_{1} = \frac{P_{21}}{P_{12} + P_{21}}$$

$$a_{2} = \frac{P_{12}}{P_{12} + P_{21}} \frac{P_{32}}{P_{23} + P_{32}}$$

$$a_{3} = \frac{P_{12}}{P_{12} + P_{21}} \frac{P_{23}}{P_{23} + P_{32}} \frac{P_{43}}{P_{34} + P_{43}}$$

$$a_{n} = \frac{P_{12}}{P_{12} + P_{21}} \cdots \frac{P_{n-1,n}}{P_{n-1,n} + P_{n,n-1}}$$

a<sub>1</sub> is the part of population which is active for substrate 1, but passive for all other substrates, a<sub>2</sub> the part of the population active for substrate 2 but passive for all other substrates, and so on.

 $x \frac{P_{n+1,n}}{P_{n,n+1} + P_{n+1,n}}$ 

If we know from experiments all  $\mu_{\bf i}(S_{\bf i})$ , where  $\mu_{\bf i}(S_{\bf i})=\hat{\mu}$ ,  $\Psi_{\bf i}(S_{\bf i})$ , we can calculate all  $\Psi_{\bf i}(S_{\bf i})$ . Taking into consideration that the number of active cells for substrate i can be written as:

$$\frac{P_{i+1,i}(S_{i})}{P_{i,i+1}(S_{i}) + P_{i+1,i}(S_{i})} = \Psi_{i}(S_{i})$$

and that

$$\frac{P_{i,i+1}}{P_{i,i+1} + P_{i+1,i}} = 1 - \frac{P_{i+1,i}}{P_{i,i+1} + P_{i+1,i}} = 1 - \Psi_{i}(S_{i}) ,$$

we can rewrite matrix  $\hat{P}$  utilizing function  $\Psi_{i}(S_{i})$ . Then we have

$$a_{1} = \Psi_{1}(S_{1})$$

$$a_{2} = \begin{bmatrix} 1 - \Psi_{1}(S_{1}) \end{bmatrix} \Psi_{2}(S_{2})$$

$$a_{3} = \begin{bmatrix} 1 - \Psi_{1}(S_{1}) \end{bmatrix} \begin{bmatrix} 1 - \Psi_{2}(S_{2}) \end{bmatrix} \Psi_{3}(S_{3})$$

$$\dots$$

$$a_{n} = \begin{bmatrix} 1 - \Psi_{1}(S_{1}) \end{bmatrix} \begin{bmatrix} 1 - \Psi_{2}(S_{2}) \end{bmatrix} \dots \begin{bmatrix} 1 - \Psi_{n-1}(S_{n-1}) \end{bmatrix}$$

$$\times \Psi_{n}(S_{n})$$

Here  $\Psi_i$  is the ratio of the active cell population for substrate i to the number of cells active for substrates i, i + l...n. The growth rate of the microbial population in the different organic substrates i = 1,2,3...n normally is known from experiments, in contrast to probability  $P_{12}$ ,  $P_{22}$ , etc. Now we can calculate the total growth rate of the microbial population in the mixture of n organic substrates which have corresponding concentrations  $S_1$ ,  $S_2$ ,  $S_3$ ...  $S_n$ .

$$\mu(S_{1}, S_{2}, S_{3}, \dots S_{n}) = \hat{\mu}_{1} a_{1} + \hat{\mu}_{2} a_{2} + \dots + \hat{\mu}_{n} a_{n} = \hat{\mu}_{1} \Psi_{1}(S_{1})$$

$$+ \hat{\mu}_{2} \left[ 1 - \Psi_{1}(S_{1}) \right] \Psi_{2}(S_{2}) + \dots + \hat{\mu}_{n} \left[ 1 - \Psi_{1}(S_{1}) \right]$$

$$\times \left[ 1 - \Psi_{2}(S_{2}) \right] \dots \left[ 1 - \Psi_{n-1}(S_{n-1}) \right] \Psi_{n}(S_{n}) = \sum_{i=1}^{n} \hat{\mu}_{i} \Psi_{i}(S_{i})$$

$$\times \left[ 1 - \Psi_{2}(S_{2}) \right] \dots \left[ 1 - \Psi_{n-1}(S_{n-1}) \right] \Psi_{n}(S_{n}) = \sum_{i=1}^{n} \hat{\mu}_{i} \Psi_{i}(S_{i})$$

$$\times \left[ 1 - \Psi_{2}(S_{2}) \right] \dots \left[ 1 - \Psi_{n}(S_{n}) \right] \qquad (25)$$

Taking into consideration (24) it is possible to rewrite (25) as

$$\mu(S_{1}, S_{2}, S_{3}, ... S_{n}) = \sum_{i=1}^{n} \mu_{i}(S_{i}) \begin{bmatrix} i-1 \\ j=0 \end{bmatrix} \begin{bmatrix} 1 - \frac{\mu_{j}(S_{j})}{\hat{\mu}_{j}} \end{bmatrix}$$
(26)

The relation (26) allows us to outline the consecutive substrates removal by the microbial population and to find the total growth rate of the population in the mixture of substrates, using only experimental values  $\hat{\mu}_i$  and  $\mu_i(S_i)$ . If  $S_1 >> S_2 >> \dots >> S_n$ , the function  $\Psi_1(S_1) \approx 1$ , but  $\begin{bmatrix} 1 - \Psi_1(S_1) \end{bmatrix} \approx 0$ . In this case we shall have  $\mu(S_1, S_2, \dots, S_n) \approx \hat{\mu}_1 \Psi_1(S_1)$ . If all values  $S_1$ ,  $S_2$ ,  $S_3$ ... $S_n$  are high enough the microbial population grow first with growth rate  $\hat{\mu}_1$ , utilizing mostly substrate 1, then with growth rate  $\hat{\mu}_2$ , utilizing substrate 2 and so on

If  $S_1 \approx S_2 \approx \ldots \approx S_4 \approx 0$ , the total growth rate  $\mu(S_1, S_2, \ldots S_n) \approx 0$ . (In this section, we assume a rate of change of concentration  $S_1, S_2, \ldots S_n$  much smaller than that of the occupancy level of the state.)

# 5. Consecutive prey removal by predators

Let us now consider x as the predator population and  $S_i$  as the prey number in a fixed area of inhabitance. Symbol "i" reflects the priority of the prey as a food for the predator. If the growth rate of the predator population depends only on the prey population, equation (25) can be used without change.

It is more convenient to use differential equations for the predator population x and for different kinds of prey  $S_1$ ,  $S_2$ ,  $S_n$ , as follows:

$$\dot{\mathbf{x}} = \mathbf{x} \sum_{\mathbf{i}=1}^{n} \mu_{\mathbf{i}}(\mathbf{S}_{\mathbf{i}}) \begin{bmatrix} \mathbf{i}-1 \\ \mathbf{j} \end{bmatrix} \begin{bmatrix} \mathbf{1} - \frac{\mu_{\mathbf{j}}(\mathbf{S}_{\mathbf{j}})}{\hat{\mu}_{\mathbf{j}}} \end{bmatrix}$$

$$\dot{s}_1 = \frac{1}{y_1} x \mu_1 (S_1)$$

$$\dot{s}_2 = -\frac{1}{2} x \mu_2 (s_2) \left[ 1 - \frac{\mu_1 (s_1)}{\hat{\mu}_1} \right]$$

$$\dot{s}_{n} = -\frac{1}{y_{n}} x \mu_{n}(s_{n}) \left[ 1 - \frac{\mu_{1}(s_{1})}{\hat{\mu}_{1}} \right] \left[ 1 - \frac{\mu_{2}(s_{2})}{\hat{\mu}_{2}} \right] \cdots \left[ 1 - \frac{\mu_{n-1}(s_{n-1})}{\hat{\mu}_{n-1}} \right]$$

Here y ,  $y_2, \dots y_n$  are special coefficients for different kinds of prey.

Some functions reflecting the rate of prey birth and death, and processes of migration, can be included in this system of differential equations. In simple cases when only two types

of prey exist, we have

$$\mu_1(S_1) = \hat{\mu}_1 \frac{S_1}{k_1 + S_1}; \quad \mu_2(S_2) = \hat{\mu}_2 \frac{S_2}{k_2 + S_2}$$

The differential equations will be:

$$\dot{x} = x \left[ \hat{\mu} \frac{S_1}{k_1 + S_1} + k_1 \hat{\mu}_2 \frac{S_2}{(k_1 + S_1)(k_2 + S_2)} \right]$$

$$\dot{s}_1 = -\frac{1}{y_1} \times \hat{\mu}_1 \frac{s_1}{k_1 + s_1}$$

$$\dot{s}_2 = -\frac{1}{y_2} x k_1 \hat{\mu}_2 \frac{s_2}{(k_1 + s_1)(k_2 + s_2)}$$

The ratio of change in two kinds of predator population will be:

$$\frac{s_1}{s_2} = \frac{y_2 \hat{\mu}_1}{y_1 \hat{\mu}_2 k_1} \frac{s_1 (k_2 + s_2)}{s_2}$$

If  $S_1 > S_2$ , we have  $S_1 > S_2$ : the predator in the long run destroys mostly his preferred prey population.

If  $S_1 < S_2$ , we have  $\dot{S}_1 \approx \dot{S}_2$  or  $\dot{S}_1 < \dot{S}_2$ ; and if  $S_1 \approx S_2 \approx 0$ , we have  $\dot{S}_1 \approx \dot{S}_2$  or  $\dot{S}_1 > \dot{S}_2$ .

# 6. Simultaneous impact of different pollutants on a living organism

In this section we will discuss the possibility of applying random process theory to modelling the processes that take place in living bodies. This topic is attractive to modellers and very important to practice. The process of treating the body with medicine or poisoning it with some matter can be

divided into two stages. The first is the distribution of poison through the different organs (or spheres) of the living body; the second the accumulation of poison in some organs, destroying this organ and so causing death.

The respiratory system, blood, brain, nerves and other systems of an organism can be considered as specific spheres through which some part of the poison is consecutively distributed. We face practically the same problem that was considered in section 3: knowing the probability of different organs receiving a part of the poison, one can calculate the amount of poison in different organs at time period t. Of course the calculation becomes more complicated if poison can be circulated among organs. Using the numerical methods and relations discussed in section 2, it is possible to calculate the mean amount and variance of poisons in different organs.

To find the solution of the second stages — the action of poison on the living organism — the formulas of sections 4 and 5 may be used. For this purpose any part (or cell) of the organ must be in one of two conditions: in a normal state, or in a damaged state which reflects the influence of the poison. This picture corresponds to reality. Regeneration processes bring cells back to a normal condition, and poison to a damaged condition. The degree of damage to the organ or body is a function of the number of cells damaged by the poison. Let us take  $\Psi_{\bf i}(S_{\bf i})$  as that part of the cells which is damaged by poison i. Using the technique developed in section 4, we can write the following equation for the case of n types

of poison:

$$Q_{n} = \Psi_{1}(S_{1}) + \begin{bmatrix} 1 - \Psi_{2}(S_{1}) \end{bmatrix} \Psi_{2}(S_{2}) + \begin{bmatrix} 1 - \Psi_{1}(S_{1}) \end{bmatrix} \begin{bmatrix} 1 - \Psi_{2}(S_{2}) \end{bmatrix}$$

$$\times \Psi_{3}(S_{3}) + \begin{bmatrix} 1 - \Psi_{1}(S_{1}) \end{bmatrix} \begin{bmatrix} 1 - \Psi_{2}(S_{2}) \end{bmatrix} \dots \begin{bmatrix} 1 - \Psi_{n-1} \end{bmatrix}$$

$$\times (S_{n-1}) \Psi_{n}(S_{n}) = \sum_{i=1}^{n} \Psi_{i}(S_{i}) \begin{bmatrix} i-1 \\ j=0 \end{bmatrix} \begin{bmatrix} 1 - \Psi_{j}(S_{j}) \end{bmatrix} \tag{27}$$

Here  $\mathbf{Q}_n$  is the total number of cells damaged by 1,2,...n poisons, which have  $\mathbf{S}_1,\mathbf{S}_2,\ldots\mathbf{S}_n$  respective concentration in the organ.

If we have only two types of poison (n = 2), and function  $\Psi_{\bf i}(S_{\bf i})$  is written as  $\Psi_{\bf i}(S_{\bf i}) = \frac{S_{\bf i}}{k_{\bf i} + S_{\bf i}}$ , the equation (27) can be written as:

$$Q_{2} = \frac{s_{1}}{k_{1} + s_{1}} + \frac{s_{2}}{k_{2} + s_{2}} - \frac{s_{1}s_{2}}{(k_{1} + s_{1})(k_{2} + s_{2})}$$

$$= \frac{k_{1}s_{2} + s_{1}s_{2} + k_{2}s_{1}}{(k_{1} + s_{1})(k_{2} + s_{2})}$$
(28)

From this formula we conclude that the total effect is not equal to the sum of influences of different poisons, but somewhat less than this value. For example, if  $\Psi_1 = \Psi_2$  considered as a simple sum or calculated by equation (28). The result of this comparison can be seen in Table 1.

Table 1

$\Psi_1 = \Psi_2$	Ψ <sub>1</sub> + Ψ <sub>2</sub>	Q <sub>2</sub>	
0.1	0.20	0.19	
0.2	0.40	0.36	
0.3	0.60	0.56	
0.4	0.80	0.64	

In the case when  $\Psi_i$  = 0.1, n = 8 we can also compare the value that is a product of multiplication  $n\Psi_i$ , and that which can be received by equation (27).

Table 2

n	2	3	4	5	6 	7	8
n0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8
$Q_{\mathbf{n}}$	0.19	0.27	0.34	0.40	0.46	0.50	0.54

The results are in good agreement with experimental data. It is well known that the total impact of two or three poisons on living bodies is practically equal to their sum if the amount of poison is not high, but becomes less as the amount of poison rises. The total impact of four, five and more poisons on the body has not been properly investigated. Taking into account the result of Table 2, we can predict a relative decrease in impact with increasing number of poisons. From the practical point of view, this result suggests an interesting task for environmental management. If experiments support the calcula-

tions, it could be more desirable in some environmental conditions to have numerous pollutants of low concentration rather than one or two pollutants of high concentration.