

## Modeling Dynamics and Spatial Aggregation of Biological Populations by Stochastic Networks

KONSTANTIN BOROVKOV & DIETMAR PFEIFER & HANS-PETER BÄUMER

With 2 Text-Figures

### Abstract

[BOROVKOV, K. & PFEIFER, D. & BÄUMER, H.-P. (1996): Modeling dynamics and spatial aggregation of biological populations by stochastic networks. – *Senckenbergiana marit.*, 27: (3/6): 129–136, 2 figs.; Frankfurt a. M.]

A mathematical model of an open stochastic network is presented which can be used to describe dynamics of a biological population, consisting of individuals of several species. The variables in the model are the numbers of individuals within disjoint observation windows, so that in a sense the model describes a ‘macroscopic’ behaviour of the population instead of dealing with individual behaviour of its members (i.e. their exact locations, what is the case when one exploits e.g. a point process model). Our approach allows to model quantitatively both immigration-emigration and (for some species and to some extent) reproduction processes, and also the simplest forms of interaction between individuals.

The model can easily be implemented as a computer program for simulation studies. Moreover, its remarkable feature is that (under natural conditions) there exists an equilibrium distribution of the process in the model, which is given by a simple explicit formula. Varying parameters of the model, one gets the whole spectrum of different equilibrium distributions, which provide rather good possibilities for fitting experimental data. In particular, the model (under a natural choice of parameters) exhibits the same peculiar variance-to-expectation relationships, as is usually discovered in experimental data sets.

### Kurzfassung

[BOROVKOV, K. & PFEIFER, D. & BÄUMER, H.-P. (1996): Dynamik und räumliche Aggregation biologischer Populationen als Modell eines stochastischen Netzwerks. – *Senckenbergiana marit.*, 27: (3/6): 129–136, 2 Abb.; Frankfurt a. M.]

Ein mathematisches Modell eines offenen stochastischen Netzwerks wird vorgestellt, das sich dazu eignet, die Dynamik und räumliche Aggregation einer biologischen Population zu beschreiben, die sich aus Individuen verschiedener koexistierender Arten zusammensetzt. Variablen im Modell sind die Abundanzen dieser Arten in disjunkten Beobachtungsgebieten. Die Kenntnis der exakten Aufenthaltsorte der Individuen in einem solchen Beobachtungsgebiet zu einem Beobachtungszeitpunkt ist nicht erforderlich, wie dies im Fall einer Modellierung als stochastischer Punktprozess vorauszusetzen wäre. Das Modell gestattet, Immigration sowie Emigration, aber auch einfachste Formen der Interaktion von Organismen in einem Beobachtungsgebiet quantitativ zu beschreiben. Eine wichtige Eigenschaft des Modells besteht darin, daß (unter naheliegenden Bedingungen) die Verteilungsfunktion im stochastischen Gleichgewicht des Prozesses existiert und sich explizit angeben läßt. Bemerkenswert ist ferner, daß unter sehr einfachen Annahmen das Modell Varianz-Erwartungswert-Relationen liefert, wie sie häufig in biologischen und ökologischen Fallstudien beobachtet werden. Der Transfer des mathematischen Modells in den Quellcode eines

### Authors' addresses:

KONSTANTIN BOROVKOV, Department of Statistics, University of Melbourne, Parkville 3052, Melbourne, Australia. – DIETMAR PFEIFER, Institut für Mathematische Stochastik, Universität Hamburg, Bundesstr. 55, D-20146 Hamburg, Germany. – HANS-PETER BÄUMER, HRZ-Angewandte Statistik, Carl von Ossietzky Universität Oldenburg, Postfach 2503, D-26111 Oldenburg, Germany.

Programms und damit auf diskrete Strukturen wirft keine grundlegenden Probleme auf. Daten und substanzwissenschaftliche Informationen, die erforderlich sind, um Simulationsstudien auf Rechnern durchzuführen, werden in anderem Kontext spezifiziert und am Beispiel der Prädation von Watvögeln erläutert werden.

## Introduction

The motivation of the present paper was to find an appropriate mathematical model, suitable for describing the dynamics of some open biological populations, whose members exhibit rather simple forms of behaviour. More exactly, one of the problems was to model spatial patterns of benthic micro- and macrofauna and their mutual dependence, especially with respect to aggregation effects (see EKSCHEMITT (1993) for a general discussion or REISE (1985) for a more specific treatment), including the time-space patterns in the behaviour of certain bird species (wader predators). Therefore, desirable features of the model one should look for are as follows.

(i) *Relative simplicity of the model.* We mean by this not only that the mathematical relations defining the model should not be too complicated. Another important aspect is that the model must admit of a reasonable implementation as a computer program to be used in simulation studies.

(ii) *Existence of exact results and explicit formulae.* This does not follow automatically from (i), of course. A limit theorem, showing the existence of, say, limiting probability distributions of the process, and especially explicit expressions for these distributions are of great importance both for theoretical and practical inference from the model.

(iii) However, the most crucial property is certainly *the fitting of data.* This is the most serious criterion for choosing a model. The availability of the equilibrium distribution of the process (cf. (ii) above) plays an important role here, too.

A straightforward approach to modeling dynamics of a population of the sort we are interested in could look as follows. Suppose that the observed area is represented by a bounded region  $\Omega \subset \mathbb{R}^2$ , and the position of the  $n$ -th individual (particle) from our (homogeneous for a while) population  $P$  at time  $t \geq 0$  is given by a point  $X_n(t) \in \Omega$ . The total number of particles (the size of  $P$ ) is given by an integer-valued random variable  $N(t)$ . Thus our population  $P$  can be represented as a random vector  $\xi(t)$  with a random number of components:

$$\xi(t) = (X_1(t), \dots, X_{N(t)}(t)), \quad t \geq 0,$$

each component  $X_i(t)$  being itself two-dimensional. The particles are moving, they are leaving the region  $\Omega$  (emigration), and other ones are coming in from outside of  $\Omega$  (immigration), thus changing the total number  $N(t)$  of particles. To describe the movement, which is supposed to be 'chaotic', one usually assumes that  $X_n(t)$  is a *Brownian motion process*, that is a continuous process with independent increments:

$$X_n(t_2) - X_n(t_1) \quad \text{and} \quad X_n(t_4) - X_n(t_3)$$

are independent for  $t_1 \leq t_2 \leq t_3 \leq t_4$ , such that  $X_n(t) - X_n(s)$  has a bivariate normal distribution with probability density function

$$\frac{1}{2\pi\sigma^2} \exp\left(-\frac{(x-a(t-s))^2}{2\sigma^2}\right), \quad x \in \mathbb{R}^2,$$

$a \in \mathbb{R}^2$  being the *drift* and  $\sigma^2 > 0$  the *dispersion coefficient* of the process. The drift  $a$  is a measure for the local average rate of displacement (which is zero, if there is no systematic trend in location of particles). The second coefficient reflects the intensity of the 'chaotic' component of the movement (the 'temperature' of the system).

Further, the birth-and-death phenomena are described usually by assuming that in fact  $X_n(t)$  is a *branching Brownian motion process*. That is, after some random time  $\tau$ , the  $n$ -th particle disappears at the position  $X_n(\tau)$  (death) or there appear instead of it  $k > 1$  new particles, evolving then independently of each other (their trajectories after the time of birth are independent Brownian motion processes with common initial value  $X_n(\tau)$ ), and so on. The emigration and immigration processes can also be described in frames of this model. An attempt to describe an interaction between particles introduces further serious complications. Even in a simple situation the mathematical theory of such processes is rather complex, and the simulation of them is not a simple task.

A somewhat more suitable version of such a 'detailed' description is possible in the form of the so-called *point processes*. That is, a population  $P$  is represented by a time-dependent point process

$$\xi_t = \sum_n \varepsilon_{X_n(t)}, \quad t \geq 0,$$

where  $\varepsilon_x$  is the *Dirac-measure* concentrated in  $x \in \Omega$ . A discussion of such models can be found e.g. in PFEIFER et al. (1992).

However, in practice we are not so much interested in a detailed description of the population, giving exact locations of the individuals. Often one deals only with a number of disjoint observation windows  $W_1, \dots, W_j$  and the counts of 'particles' observed in these windows:

$$n_j = \text{number of individuals from } P \text{ in } W_j,$$

and the data consist only of these window counts. Firstly, there is usually no need in knowing the detailed position of each member of the population. The most important aspects of the modeling are the trends in dynamics, allocations of the individuals at different sites etc. Secondly, both collecting and processing such detailed data is much

more expensive. Thus the variables of interest are the 'macroscopic' characteristics  $n_j$ , describing a subdivision of  $P$  into subpopulations at sites  $W_j$ .

In the present paper, we consider a relatively simple stochastic network model, which can be employed in de-

scribing dynamics of a population in terms of the variables  $n_j$ . This model has (under an easily verifiable condition) an equilibrium distribution, admitting simple explicit expressions. Implementing the model as a computer program for simulation studies also creates no serious difficulties.

## The Network Model

We now start with a formal description of the network model  $N$ . It includes a finite set  $J = \{1, 2, \dots, J\}$ , whose elements are called *nodes*, and a finite set of *particle classes*  $C = \{c_1, c_2, \dots, c_N\}$ . There are moving 'units' in the network  $N$ , which are called *particles* (these represent individuals in modeling biological populations). Each particle in the network belongs to one class  $c$  in  $C$  and is, at each given time  $t$ , at one of the nodes from  $J$ . The total number of all particles of class  $c$  at node  $j$  at time  $t$  we denote by  $n_j^{(c)} = n_j^{(c)}(t)$ ,  $t \geq 0$ , and the total number of all particles at node  $j$  is denoted by

$$n_j = n_j(t) = \sum_{c \in \mathcal{C}} n_j^{(c)}.$$

Moreover, the particles are allowed to enter and leave the network, the latter is said in such case to be *open*. The arrival streams of particles of different classes  $c$  from outside the network at nodes  $j \in J$  are described by independent *Poisson processes*  $\pi_j^{(c)}(t)$ ,  $t \geq 0$ . That is, all the processes  $\pi_j^{(c)}$ ,  $j \in J$ ,  $c \in C$ , are mutually independent, and, for fixed  $j$  and  $c$ , the integer-valued process  $\pi_j^{(c)}(t)$  has independent increments and

$$P(\pi_j^{(c)}(t) = k) = \exp(-a_j^{(c)}t) \frac{(a_j^{(c)}t)^k}{k!}, \quad k = 0, 1, 2, \dots, t \geq 0,$$

the parameter  $a_j^{(c)} \geq 0$  is called the *intensity* of the process  $\pi_j^{(c)}$ .

The assumption on the Poisson nature of arrival streams is a usual one reflecting the fact that the sum of a large number of weakly dependent integer-valued inputs that are zeros with high probabilities is 'almost Poissonian' in distribution. Suppose for a moment that our nodes (observation windows) are only few from a larger 'closed' set  $J_0$  of such nodes, and the particles can move via all these nodes, too (not leaving this large set  $J_0$ ). Then, provided the 'departure streams' are more or less steady and are 'evenly' distributed between all the nodes (this corresponds to the condition that the entries of the routing matrix  $\Lambda^{(c)}$  to be defined below are uniformly small), the arrival streams from the 'unobserved' nodes  $j \in J_0 \setminus J$  at the 'observed' ones (from  $J$ ) will be approximately Poissonian and independent (for more details see e.g. POLLETT (1986)).

The ratio

$$\lambda_{0j}^{(c)} = \frac{a_j^{(c)}}{a^{(c)}}, \quad a^{(c)} = \sum_{j=1}^J a_j^{(c)},$$

is the conditional probability that a particle of class  $c$  arriving at the network arrives in fact at the node  $j$ . Clearly,

$$\sum_{j=1}^J \lambda_{0j}^{(c)} = 1.$$

A particle, arriving at node  $j \in J$  from outside the network, spends there a random time (which depends in general on how many other particles are at the node during its stay and is to be defined later on), and then moves to some other node and so on, or leaves the network (in the latter case we consider the particle to be 'lost' and it never comes back to the network). These movements are described by the *routing matrices*:

$$\Lambda^{(c)} = (\lambda_{jk}^{(c)})_{j,k=1,\dots,J}, \quad c \in \mathcal{C},$$

with non-negative entries  $\lambda_{jk}^{(c)} \geq 0$ , which are the probabilities for a particle of class  $c$  to arrive at node  $k$  immediately after it leaves node  $j$  (thus measuring the 'intrinsic' tendency for a particle of class  $c$  to move from node  $j$  to node  $k$ ), so that for the row sums

$$\sum_{k=1}^J \lambda_{jk}^{(c)} \leq 1.$$

Thus the matrix  $\Lambda^{(c)}$  is *substochastic*. The *defect* in the  $j$ -th row of the matrix  $\Lambda^{(c)}$ , that is the difference

$$\lambda_{j0}^{(c)} = 1 - \sum_{k=1}^J \lambda_{jk}^{(c)} \geq 0,$$

is the probability that, after leaving node  $j$ , a particle of class  $c$  leaves the network  $N$  itself. Our network  $N$  is supposed to be open, so that

$$\max_j \lambda_{j0}^{(c)} > 0, \quad c \in \mathcal{C}.$$

Moreover, we suppose that, for any class  $c$  and any node  $j$ , there exists a sequence of nodes  $i_1 = j, i_2, \dots, i_k, \dots, i_{m-1}, i_m = 0, i_k \in J, 2 \leq k \leq m-1$ , such that

$$(1) \quad \lambda_{i_2 i_1}^{(c)} \cdot \lambda_{i_3 i_2}^{(c)} \cdot \dots \cdot \lambda_{i_m i_{m-1}}^{(c)} > 0.$$

This means, that it is possible for a particle of any class  $c$  eventually to leave the network  $N$  either directly or in-

directly (via a sequence of nodes), at whatever node  $j$  it is now.

Denote by  $r^{(c)}$  the Perron root of the matrix  $\Lambda^{(c)}$  (this is a positive eigenvalue of  $\Lambda^{(c)}$ , such that all other eigenvalues of  $\Lambda^{(c)}$  do not exceed  $r^{(c)}$  in absolute value, see e.g. GANTMACHER (1977), Ch.XIII). The last assumption ensures that

$$r^{(c)} < 1, c \in C,$$

and therefore the matrix

$$I - \Lambda^{(c)}, I \text{ is the unit } J \times J\text{-matrix,}$$

has an inverse one given by

$$(2) \quad (I - \Lambda^{(c)})^{-1} = I + \Lambda^{(c)} + (\Lambda^{(c)})^2 + (\Lambda^{(c)})^3 + \dots,$$

where the series of non-negative matrices on the right hand side converges (since the maximal entry of the  $k$ -th power of  $\Lambda^{(c)}$  does not exceed  $(r^{(c)})^k$ ). Hence, for each  $c \in C$ , there exists a uniquely determined non-negative vector  $Q^{(c)} = (q_1^{(c)}, \dots, q_j^{(c)})$  that satisfies

$$(3) \quad Q^{(c)} = A^{(c)} + Q^{(c)} \Lambda^{(c)},$$

where  $A^{(c)} = (a_1^{(c)}, \dots, a_j^{(c)})$  is the vector of arrival rates. In fact, this vector  $Q^{(c)}$  is given by the convergent series

$$(4) \quad Q^{(c)} = A^{(c)} \sum_{k=0}^{\infty} (\Lambda^{(c)})^k$$

(see (2)). The entry  $q_j^{(c)}$  of  $Q^{(c)}$  can be interpreted as the equilibrium arrival rate for particles of class  $c$  at node  $j$ . In equilibrium (if it exists) the departure rate from node  $j$  should coincide with the arrival rate at this node, and equation (3) is easily seen to be just the *balance equation*. The entry  $q_j^{(c)}$  is positive, if and only if it is possible for a particle of class  $c$  to visit node  $j$ . If  $q_j^{(c)} = 0$ , then, whatever the initial number  $n_j = n_j(0)$  and classes of particles at node  $j$  are, all the particles of class  $c$  will soon leave the node due to (1), and after some time  $t_j^{(c)}$  the node will be forever free of particles of this class.

It only remains to describe how long a particle stays at node  $j$  upon its arrival. We suppose that a probability distribution  $F_j^{(c)}$  of a positive random variable – called ‘resource’ henceforth – with expectation  $m_j^{(c)}$  is ascribed to each pair  $j, c$ . This distribution characterizes the ‘tendency’ of a particle of class  $c$  arriving at node  $j$  to stay there for a more or less long time. We suppose that to each such arrival there corresponds a realization of a random variable  $\tau_j^{(c)}$  distributed according to  $F_j^{(c)}$ , and that all these variables (for all arrival epochs, all particles, and all nodes) are independent. If the value of expectation  $m_j^{(c)}$  is large, a particle of class  $c$  would ‘prefer’ typically to remain longer at node  $j$ , for the ‘conditions’ there are, say, rather favorable for particles of this class. However, the presence of other particles at the same node influences the sojourn time of any particle at this node. We specify this as follows.

A particle stays at the node  $j$  as long as its current ‘remaining resource’  $\rho_j^{(c)}(t)$  is positive. This ‘resource’ is given by the abovementioned random variable just upon

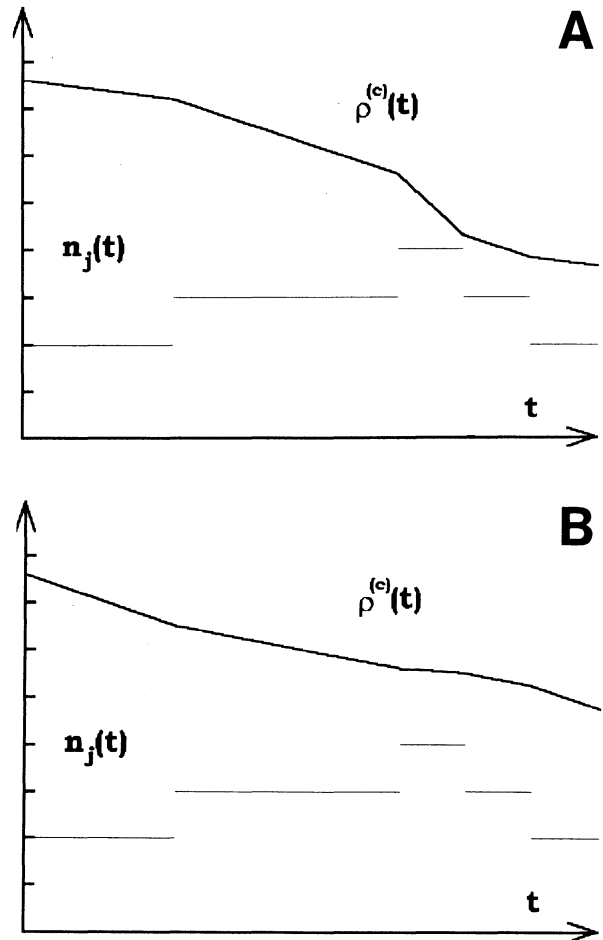


Fig. 1. A, B. Decay of ‘resource’ when  $v_j(n)$  is decreasing with  $n$ .

the arrival of the particle at this node (at time  $t_0$ ), and is spent with the rate proportional to some given function  $v_j(n_j)$  of the current total number  $n_j = n_j(t)$  of particles at the node:

$$(5) \quad \frac{d}{dt} \rho_j^{(c)}(t) = -v_j(n_j(t)), \quad t \geq t_0, \quad \rho_j^{(c)}(t_0) \text{ realization of } \tau_j^{(c)}$$

(Of course, all the variables here should be marked in fact by the index of our fixed particle, but we do not want to overload the notation.) As soon as one has  $\rho_j^{(c)}(t) = 0$ , the particle immediately leaves the current node  $j$  and changes for another one according to the probabilities from the routing matrix  $\Lambda^{(c)}$ . Note that since  $\{n_j(t) \mid t \geq t_0\}$  is a stochastic process the slope of  $\rho_j^{(c)}(t)$  in (5) is a random variable. Fig. 1 shows two typical decay curves of the ‘resource’  $\rho_j^{(c)}(t)$  depending on  $v_j$ . It must be pointed out that our notion of a ‘resource’ is not necessarily meant in a strongly physical sense. Rather, the ‘resource’ to be consumed by a particle is a general variable which depends in a complicated way on several biological and ecological quantities such as nutrient availability, population density, age structure of species etc.

In queueing theory a node as described above is considered to be a special case of the so-called *symmetric queue*. In queueing terminology, a *total service effort* is offered at the queue  $j$  at the rate  $n_j v_j(n_j)$ , when there are  $n_j$  customers at the queue, and all the customers at the queue obtain an equal part of this effort (the so-called *egalitarian processor sharing rule*). A network consisting of symmetric queues possesses the following remarkable property: under a natural assumption it has an equilibrium distribution, and what is more, this distribution does not depend on the laws  $F_j^{(c)}$  except for the value of their expectations  $m_j^{(c)}$ .

Before passing to the explicit expressions for the equilibrium distribution, we make one more remark on the nature of the process describing our stochastic network  $N$ . A convenient choice for such a process is

$$X(t) = (X_1(t), X_2(t), \dots, X_J(t))$$

with

$$X_j = X_j(t) = (n_j; Y_j^{(1)}, Y_j^{(2)}, \dots, Y_j^{(m)})$$

where  $Y_j^{(l)} = Y_j^{(l)}(t) = (C_j^{(l)}, t_j^{(l)}, s_j^{(l)})$  describes the  $l$ -th particle at node  $j$  (which are numbered according to their arrival times; when the  $l$ -th particle leaves the node, the  $(l+k)$ -th one becomes the  $(l+k-1)$ -st,  $k > 0$ ). Here

- $c_j^{(l)}$  is the class of the  $l$ -th particle,
- $t_j^{(l)}$  is its total 'resource' upon the arrival (these random variables have been 'obtained' as independent realizations of a random variable  $\tau_j^{(c)}$  distributed according to  $F_j^{(c)}$ , and
- $s_j^{(l)}$  is the amount of the 'resource' spent so far by the particle.

The process  $X(t)$  has an important property which is that of a *Markov process*. The future evolution of the process given the present thus does not depend on its past history. This allows not only using the well-developed theory of such processes, but is also a desirable and important property for simulation studies.

Put now

$$b_j^{(c)} = q_j^{(c)} m_j^{(c)}, \quad j \in \mathcal{J}, \quad c \in \mathcal{C}, \quad b_j = \sum_{c \in \mathcal{C}} b_j^{(c)}.$$

The value  $b_j^{(c)}$  can be interpreted as the average amount of the 'resource' carried to node  $j$  by particles of class  $c$ , and  $b_j$  is just the total amount of the 'resource' coming to the node. Set further

$$(6) \quad u_j(n) = n! \prod_{r=1}^n v_j(r), \quad j = 1, \dots, J, \quad n \geq 1, \quad u_j(0) = 1.$$

The following assertion (see POLLETT 1986) summarizes the most important equilibrium properties of the network  $N$ .

**Proposition.** *An equilibrium distribution exists for  $X(t)$  if and only if*

$$(7) \quad B_j^{-1} = \sum_{n=0}^{\infty} \frac{b_j^n}{u_j(n)} < \infty, \quad j = 1, \dots, J.$$

*In this case the counts  $n_j$  of particles of all classes at different nodes  $j$  are independent under the equilibrium distribution, and the probability that there are  $n$  particles at node  $j$  is*

$$(8) \quad P(n_j = n) = B_j^{-1} \frac{b_j^n}{u_j(n)}, \quad n = 0, 1, 2, \dots$$

*Further, the other components of the process  $X(t)$  have the following properties under the equilibrium distribution.*

1. *Given the total number  $n_j$  of particles of all classes at node  $j$ , the classes of particles are independent and the conditional probability that the  $l$ -th particle at the node is of class  $c$  is*

$$b_j^{(c)} / b_j.$$

2. *Given the numbers of particles at each node and the classes of each of them, the total amounts of their 'resources' upon arrival at the node are independent<sup>1)</sup> and, if the  $l$ -th particle at node  $j$ ,  $l=1, \dots, n_j$ , is of class  $c$ , the conditional probability that  $t_j(l)$  does not exceed  $x$  is given by*

$$\frac{1}{m_j^{(c)}} \int_0^x y dF_j^{(c)}(y).$$

3. *Given the numbers of particles at each node and the classes of each of them, the amounts of 'resources' already spent are independent and, if the  $l$ -th particle at node  $j$  is of class  $c$ , the conditional probability that  $s_j(l)$  does not exceed  $x$  is given by*

$$\frac{1}{m_j^{(c)}} \int_0^x (1 - F_j^{(c)}(y)) dy.$$

4. *Given the numbers of particles at each node and the classes of each of them together with their initial 'resources', the amounts of 'resources' already spent are independent and the variable  $s_j(l)$  is uniformly distributed on  $(0, \tau_j(l))$ .*

**Remark.** Of course, it is also important to know whether the Markov process  $X(t)$  is ergodic. That is the question whether the distribution of  $X(t)$  converges to the equi-

1) Although all these initial 'resources' are given by independent random vectors, the conditions that these particles are present at the node *now* could in general destroy the independence.

brium distribution as  $t \rightarrow \infty$  whatever the initial value  $X(0)$  is. The method employed in BOROVKOV (1986) can be extended to the networks of the type considered above to get similar ergodicity theorems. Sufficient conditions for ergodicity of  $X(t)$  could be formulated as follows.

- (a) The series (7) converges.  
 (b) The boundedness of initial 'resources', i.e. that  $F_j^{(c)}(x^*) = 1$  for all  $c \in C$  and  $j \in J$  and for some  $x^* < \infty$  (in fact this can be weakened to a less restrictive condition on the tails of these distribution, see Condition I in BOROVKOV (1986)).

(c) The initial 'resources' can assume arbitrarily small values with positive probabilities, that is  $F_j^{(c)}(x) > 0$  for all  $c \in C$  and  $j \in J$ , and for all  $x > 0$ .

(d) The interaction functions  $v_j(n)$  are bounded away from zero:  $v_j(n) > v_0 > 0$  for all  $j \in J$  and all  $n = 0, 1, 2, \dots$ .

An interesting discussion of the 'travel times' in such a network, that is the times spent by a particle when it makes a specified 'path' via the nodes of the network, including an expression for the expectation of a general travel time, can be found in a recent paper by KOOK & SERFOZO (1993).

## Discussion of the Model

In this section we discuss the use of the model presented in the preceding section for describing space-time population patterns of benthic fauna. The classes  $c \in C$  could be either different species or different size (or age) groups of individuals. The data are given in the form of counts of individuals in disjoint observation windows  $W_j$ ,  $j = 1, \dots, J$  at successive times  $t_1, t_2, t_3$ , etc. We identify these windows with the nodes of our stochastic network  $N$ . The form of the routing matrix  $\Lambda^{(c)}$  is defined by both configuration of the windows and their mutual positions and also by the presence of streams or other factors which influence the movement of the individuals from the population. Typically  $W_j$ ,  $j = 1, 2, \dots, J = K \times L$ , are rectangles, forming a  $K \times L$ -partition of the whole observation area which is also a rectangle. Then  $\lambda_{jk}^{(c)}$  are positive for all  $j, k \in J$  such that  $W_j$  and  $W_k$  have a common side, and zero otherwise. In the symmetric homogeneous case, when  $W_j$  are all equal squares and there are no interfering factors, we take all these entries equal to a common value  $\lambda^{(c)}$ . In what follows, this simplest case, when all the parameters are supposed to be independent of  $j$ , will be referred to as the case (S).

The arrival rates  $a_j^{(c)}$  describe (for the 'internal' windows  $W_j$ ) e.g. the influx of larvae from both neighbouring and distant sites. For the 'boundary' windows, these should also include the moving adult individuals from the neighbouring sites outside the observation area. A simple possible solution here is to suppose that the neighbouring 'external' sites have the same parameters as the observed boundary windows having common sides with them. This reduces just to changing somewhat the system of balance equations (3) which remains nevertheless linear. All the assertions of the proposition in the preceding section remain of course valid for the parameters defined by this modified balance equation. In the abovementioned symmetric case (S), the latter look as follows:

$$(9) \quad q^{(c)} = a^{(c)} + 4\lambda^{(c)}q^{(c)}$$

with  $q_j^{(c)} = q^{(c)}$  and  $a_j^{(c)} = a^{(c)}$  for all  $j \in J$ . Equation (9) refers to a 'typical' window  $W_j$ . It has 4 neighbouring sites, from which a leaving individual decides to go to this typical window with probability  $\lambda^{(c)}$ . The 'defect' of the row in the routing matrix, that is the probability for an individual to leave the network when it is leaving a typical site, is supposed to be positive:

$$\lambda_0^{(c)} = 1 - 4\lambda^{(c)} > 0.$$

Clearly (9) means that

$$q^{(c)} = \frac{a^{(c)}}{\lambda_0^{(c)}},$$

and the equilibrium distribution (8) now has the form

$$(10) \quad P(n_j = n) = B \frac{b^n}{u(n)}, \quad n = 0, 1, 2, \dots,$$

where

$$(11) \quad b = \sum_{c \in C} \frac{a^{(c)} m^{(c)}}{\lambda_0^{(c)}}, \quad u(n) = n! \prod_{r=1}^n v(r), \quad B^{-1} = \sum_{n=0}^{\infty} \frac{b^n}{u(n)}.$$

Now we shall discuss some possible forms of the equilibrium distribution (10) in case (S), corresponding to different 'interaction functions'  $v$ . If this function is constant, then there is no influence of individuals on each other. If  $v$  is decreasing as  $n$  grows, then the individuals stay readily longer at the site, when there are other 'companions'. If  $v$  is increasing with  $n$ , then the presence of other individuals forces one to leave the site sooner than it could happen otherwise (overpopulation). The simplest special cases are as follows.

(i) **No interaction.** This means that  $v(n) = w = \text{const}$ , so that the 'resource' of an individual is spent with a constant rate independently of how many other individuals visit this site, see (5). In this case

$$u(n) = w^n n!, \quad n = 0, 1, 2, \dots,$$

and hence the series in (11) is always convergent with

$$B^{-1} = e^{b/w}.$$

The equilibrium distribution (10) is *Poissonian*:

$$(12) \quad P(n_j = n) = e^{-b/w} \frac{(b/w)^n}{n!}, \quad n = 0, 1, 2, \dots$$

This case corresponds in fact to 'rare' populations (which is confirmed by empirical data), when the number of individuals is relatively small and there is no interaction between them.

(ii) **Aggregation.** This means that an individual 'prefers' to stay at the site for a longer time, if there are other individuals. The simplest choice of the 'interaction function' here is

$$v(n) = \frac{w}{n}, \quad n = 1, 2, \dots, \quad w = \text{const},$$

that is, the 'resource' is spent with a rate being inverse proportional to the number of individuals at the site. In this case

$$u(n) = w^n, \quad n = 0, 1, 2, \dots,$$

so that

$$B^{-1} = (1 - b/w)^{-1} \text{ if } b < w$$

(otherwise the series in (11) diverges), and then the equilibrium distribution is *geometric*:

$$(13) \quad P(n_j = n) = (1 - b/w)(b/w)^n, \quad n = 0, 1, 2, \dots$$

A slight generalization hereof is the choice

$$v(n) = \frac{w}{M + n - 1}, \quad n = 1, 2, \dots, \quad w = \text{const}, \quad M \in \mathbb{N}.$$

The equilibrium distribution is *negative binomial*:

$$(14) \quad P(n_j = n) = \binom{M + n - 1}{n} (1 - b/w)^M (b/w)^n, \quad n = 1, 2, \dots$$

(iii) **Repulsion.** Here  $v(n)$  increases with  $n$ . Let us put

$$v(n) = \frac{w}{M - n + 1}, \quad n = 1, 2, \dots, M; \quad v(n) = \infty, \quad n > M,$$

$M$  is a natural number (the upper boundary for the size of a 'colony' at a site: the latter cannot just bear more than  $M$  individuals). With this particular choice one has according to (11) that

$$u(n) = \frac{n!(M - n)!}{M!} w^n, \quad n = 0, 1, 2, \dots, M; \quad u(n) = \infty, \quad n > M,$$

and the series in (11) is always convergent, giving

$$B^{-1} = \sum_{n=0}^M \binom{M}{n} \left(\frac{b}{w}\right)^n = \left(\frac{b+w}{w}\right)^M.$$

Therefore the equilibrium distribution (10) is *binomial*:

$$(15) \quad P(n_j = n) = \binom{M}{n} \left(\frac{b}{b+w}\right)^n \left(\frac{w}{b+w}\right)^{M-n}, \quad n = 0, 1, 2, \dots, M.$$

A more realistic model combines seemingly all these three types of behaviour. For small  $n$ , there is usually almost no interaction between individuals (case (i)). For moderate  $n$ , many species exhibit the typical aggregation-type behaviour (case (ii)): they 'notice' the presence of each other and try to 'keep together'. For large  $n$ , the nutrition problems could cause all the individuals to leave the site soon (case (iii)). So to fit the model, one should look for an interaction function  $v(n)$  having the following properties:

- (1)  $v(n)$  is almost constant for small  $n$ ,
- (2)  $v(n)$  decreases for moderate values of  $n$ , and
- (3)  $v(n)$  increases for large  $n$ .

**Remark.** Note that in fact any probability distribution  $\{p(n), n = 0, 1, 2, \dots\}$  on the set of non-negative integers with  $p(n) > 0, n > 0$ , can be represented in the form (3.2). Indeed, if we put

$$(16) \quad v(n) = \frac{bp(n-1)}{np(n)}, \quad n = 1, 2, \dots, \quad B = p(0),$$

then clearly  $u(n) = b^n p(0)/p(n), n = 1, 2, \dots$ , and hence the assertion follows directly from (10). Thus one can choose an appropriate interaction function using empirical data and substituting, say, some estimates  $\hat{p}(n)$  for  $p(n)$  into (16) to get an estimate  $\hat{v}(n)$  for  $v(n)$ .

A simple variant combining the first two properties (1) and (2) above is

$$(17) \quad v(n) = \begin{cases} w & \text{for } n \leq n_0, \\ w(n - n_0)^{-1/2} & \text{for } n > n_0 \end{cases}$$

for some 'change-point'  $n_0 > 0$ .

The equilibrium distribution (10) has now the form

$$(18) \quad P(n_j = n) = \begin{cases} \frac{B \left(\frac{b}{w}\right)^n}{n!} & \text{for } n \leq n_0, \\ \frac{B \left(\frac{b}{w}\right)^n \left((n - n_0)!\right)^{1/2}}{n!} & \text{for } n > n_0. \end{cases}$$

It is remarkable that already this simple construction allows to model an experimentally observed effect, namely a special 'functional' dependence between sample means and variances of counts of individuals. For small values of the expectation, this dependence proves to be almost linear; for moderate values the variance increases much faster, and then suddenly slows down and even decreases. An example related to the equilibrium distribution (18) with  $n_0 = 6$  shows that our model exhibits the same 'phase transition' property when the ratio  $r = b/w$  is varied. For small values of  $r$  this distribution is 'almost Poissonian' and thus its expectation and variance are close to each other; for larger  $r$  the form of the distribution is changing, and after this it becomes rather 'close' to another (non-Poissonian) parame-

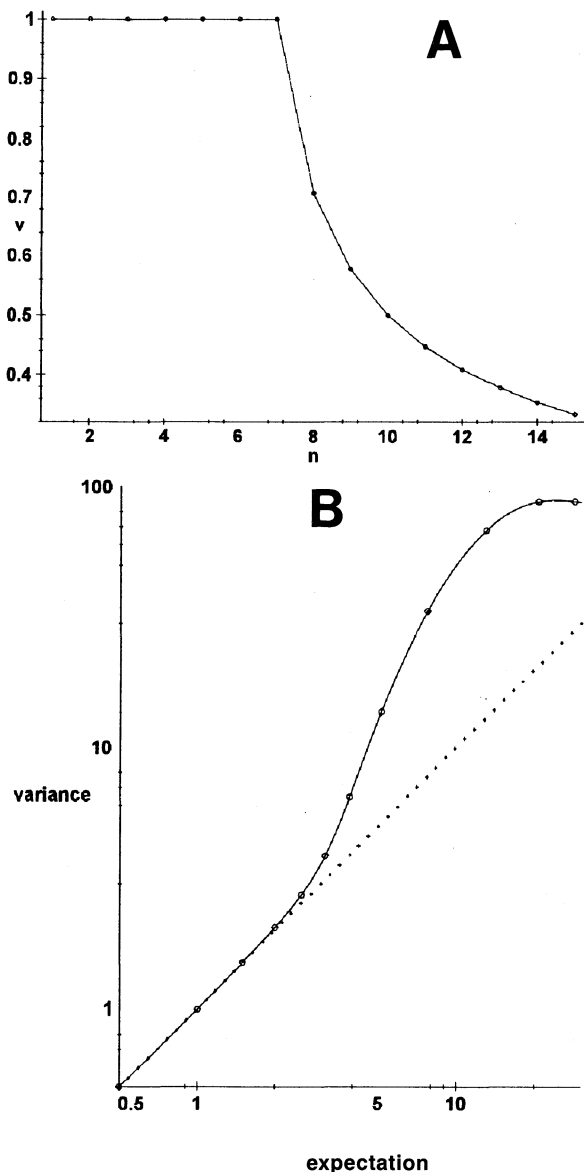


Fig. 2. A. Graph of  $v_j(n)$ . – B. Variance vs. expectation plot.

#### Acknowledgement

Financial support for this research has been provided by the Bundesminister für Forschung und Technologie within the project Ökosystemforschung Niedersächsisches Wattenmeer, Hauptphase B (ELAWAT), Teilprojekt B2: Untersuchungen zu Reaktionen raum-zeitlicher Muster von Organismengemeinschaften auf Umwelteinflüsse: Beiträge der Angewandten Statistik zur Versuchsplanung, Durchführung und Auswertung.

#### References

- BOROVKOV, A. A. (1986): Limit theorems for queueing networks. – *Theory Probab. Appl.*, 31: 413–427.
- EKSCHMITT, K. (1993): Über die räumliche Verteilung von Bodentieren. Zur ökologischen Interpretation der Aggregation und zur Probenstatistik. – Bremen (Diss. Univ. Bremen).

tric family. Fig. 2 shows the graphs of  $v$  and of the variance vs. the expectation for the preceding example, in logarithmic scales.

Thus we have seen that our model even in the simplest case (S) is rather flexible and has properties which had been observed earlier in experimental data. This might suggest that e.g. variance-to-expectation relationships as discussed above could be ‘emergent properties’ of those ecosystems which allow interactions between individuals roughly in the way described.

Analysing the general case is more difficult, but the model itself provides then convenient possibilities of taking into consideration various factors determining the evolution of a population. The sites with poor supply of nutrients should have relatively large corresponding interaction functions  $v_j(n)$ , and the sites with more favorable conditions will be marked by smaller values of  $v_j(n)$ . The presence of streams or obstacles etc. determines the routing matrices, reflecting possibilities for individuals to move in this or that direction. Age-dependent differences in mobility can – to some extent – be also modeled using different routing matrices  $\Lambda^{(c)}$  for different  $c$ , etc. However, since age or size classes are generally changing over time in ‘real’ populations, the model is only applicable if the system approaches its equilibrium in a time span which is essentially smaller than the time span necessary to change from one class  $c \in C$  to another.

As a final remark, we want to point out that although ecological modeling in the sense outlined above is of *theoretical* character in the first place, it is – in our opinion – also of practical importance since it potentially offers *different* alternatives of explanations for the same observed facts to the ecologist as long as the processes governing the system are not completely known or even impossible to investigate in complete detail. Being aware of such alternatives could be of help when future lines of research have to be formulated.

GANTMACHER, F. R. (1977): *The Theory of Matrices*, Vol. 2 – New York (Chelsea).

KOOK, K. H. & SERFOZO, R. F. (1993): Travel and sojourn times in stochastic networks. – *Ann. Appl. Probab.*, 3: 228–252.

PFEIFER, D. & BÄUMER, H.-P. & ALBRECHT, M. (1992): Spatial point processes and their applications to biology and ecology. – *Modeling Geo-Biosphere Processes*, 1: 145–161.

POLLET, P. K. (1986): Some Poisson approximations for departure processes in general queueing networks. – *Statistics*, 17: 393–405.

REISE, K. (1985): *Tidal Flat Ecology. An Experimental Approach to Species Interactions.* – *Ecol. Stud.*, 54. – New York, Heidelberg, Berlin (Springer).