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Analytical and Modeling Approaches to Studying the Integral Equation Appearing after a Power-3 Closure

S. R. Gadzhiev[1*], E. G. Galkin[2], and A. A. Nikitin[1***]**

[1]*Department of Computational Mathematics and Cybernetics, Moscow State University, Moscow, 119991 Russia*

[2]*National Research University Higher School of Economics, Moscow, 101978 Russia*

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Abstract—A study is performed of the nonlinear integral equation that arises in the biological model of Dieckmann and Law. A brief outline of the model is given, and the meaning and need to introduce spatial moments are described. The nonlinear equation (for the state of equilibrium) is derived from the system of dynamics of spatial moments after power-3 closure. The obtained equation is transformed to the form appropriate for applying an iterative numerical approach based on a Neumann series. A numerical way of solving the derived integral equation is developed, and an example of using the numerical approach and numerical modeling is provided. It is shown there exists a nontrivial solution to the considered nonlinear integral equation at a strictly positive parameter of natural mortality. This considerably differs the derived integral equation from its linear analog widely used in earlier works.

Keywords: mathematical modeling, integro-differential equations, mathematical biology.

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1. INTRODUCTION

The integral equation studied in this work appeared in those of U. Dieckmann and R. Law [1, 2]. Let us briefly describe the main points of this model. (See the more detailed description adapted to the mathematical problem in the authors' papers [3, 4].) We consider a single-species population on real axis R. Biological individuals can be born and die of competition with other individuals, or of environmental hazards.

Environmental impact is provided by some biological parameters: $d \geqslant 0$ is the homogeneous natural mortality, $d' \geqslant 0$ is the intensity of action of competing individuals, $b \geqslant 0$ is the intensity of birth of new individuals. Interaction among individuals is characterized by two radially symmetric functions, $m(\xi)$ and $w(\xi)$, $\xi \in R$, $m(\xi)$ describes the distribution of the shift of a new individual with respect to its parent at birth, and $w(\xi)$ describes a function that allows us to calculate the contribution from competition to the mortality of a specific individual.

The distribution of individuals in this model can be strongly structurized, so statistics are used to describe the spatial structure of the population that characterize, e.g., the joint distributions of pairs and trios of individuals.

Measures of factorial moments are used To describe the spatial structure of random point processes. The measure of the nth factorial moment $M^{(n)}$ describes the distribution of disordered sets of points, biological individuals in our model, in n sets that can intersect. This allows us to calculate the

*e-mail: gads06121994@yandex.ru.
**e-mail: radiation7@mail.ru.
***e-mail: nikitin@cs.msu.ru.

mathematical expectation of arbitrary function f, which is given for a disordered set of n points of random point process Φ:

$$E\left[\sum_{x_1\neq\ldots\neq x_n\in\Phi} f(x_1,\ldots,x_n)\right] = \int\limits_{R^n} f(x_1,\ldots,x_n)dM^{(n)}(x_1,\ldots,x_n).$$

In our model, we can consider the densities of factorial moments $C^{(n)}$, which allow us to describe the mathematical expectation of an arbitrary function in the form

$$E\left[\sum_{x_1\neq\ldots\neq x_n\in\Phi} f(x_1,\ldots,x_n)\right] = \int\limits_{R^n} f(x_1,\ldots,x_n)C^{(n)}(x_1,\ldots,x_n)dx_1\ldots dx_n.$$

Let us consider the detailed simplest structures used in this work.

- The simplest spatial structure is a singlet. The average density of the emergence of individuals of some species standing separately in the region of existence is simply the average density of the distribution of creatures of the considered species. The average density coincides with the first factorial moment and is denoted by N below. Here, N depends on the system of spatial coordinates in our model. It is a function of the density constant over the domain of integration.

- We also consider the density of pairs of individuals located at points x_1 and x_2 at vector distance ξ from each other. We consider only stationary point processes, and the spatial statistics in them are independent of specific coordinates of individuals. They dependen only on their position relative to each other. Here, the point process is isotropic; i.e., there is no special direction that affects the distribution of individuals in space. It is therefore logical to consider the average density of pairs of individuals averaged over the angular coordinates; i.e., the density of pairs of individuals situated at distance $r = |\xi|$ from each other. The density of pairs of individuals coincides with the second factorial moment is denoted below by $C(\xi)$. The average density over angular coordinates is widely used in the theory of random point processes and is called the function of pair correlation.

- In addition to pairs, we can consider spatial structures consisting of three individuals. We may also consider shifts ξ and ξ' of individuals 2 and 3 with respect to the first one from the trio. The density of trios of individuals coincides with the third factorial moment and is denoted below by $T(\xi,\xi')$. In an isotropic environment, such triangular configurations are described by three radii (r, r', and $r'' = |\xi' - \xi|$) reflecting three sides of the triangle constructed on the trio.

Using mathematical and ecological considerations, we obtain equations for the dynamics of spatial moments. The equations for the dynamics of moments are

$$\frac{\partial}{\partial t}N = bN - dN - d'\int\limits_{R} C(\xi)w(\xi)d\xi,$$

$$\frac{\partial}{\partial t}C(\xi) = bm(\xi)N + b\int\limits_{R} m(\xi')C(\xi+\xi')d\xi' - dC(\xi) - d'w(\xi)C(\xi) - d'\int\limits_{R} w(\xi')T(\xi,\xi')d\xi'.$$

The key point of the ecological results is to find the equilibrium position of the system, or the so-called stationary state. In the stationary state the system satisfies the system of stationary equations

$$\begin{cases} 0 = (b-d)N - d'\int\limits_{R} C(\xi)w(\xi)d\xi, \\ 0 = bm(\xi)N + b\int\limits_{R} m(\xi')C(\xi+\xi')d\xi' - dC(\xi) - d'w(\xi)C(\xi) - d'\int\limits_{R} w(\xi')T(\xi,\xi')d\xi'. \end{cases}$$

2. PROBLEM OF THE CLOSURE OF SPATIAL MOMENTS

Note from the system described above that the dynamics of the first moment depends on the second one, and the dynamics of the second moment depends on the third one. We can show that such tendency is also observed in higher spatial moments; i.e., $\frac{\partial}{\partial t}C^{(m)}$ depends on $C^{(m+1)}$. To resolve the arising hierarchy of dependences, we use the closure of spatial moments. The closure of a moment is a function of low-order moments approximately describing its value:

$$C^{(m+1)} \approx F\big(C^{(1)}, \dots, C^{(m)}\big).$$

As was shown in [5], such approximations must satisfy several requirements. In this work, we consider the closure of the third moment. Let us write the requirements imposed on such closures from [5]. The function can be a closure of the third moment if the following conditions are met:

1. $\lim\limits_{|\xi|\to\infty} T(\xi,\xi') = C(\xi')N$;
2. $\lim\limits_{|\xi'|\to\infty} T(\xi,\xi') = C(\xi)N$;
3. $\lim\limits_{\substack{|\xi|,|\xi'|\to\infty \\ |\xi-\xi'|=\text{const}}} T(\xi,\xi') = C(\xi-\xi')N$;
4. if $C(\xi) = N^3$, then $T(\xi,\xi') = N^3$.

In the above [5], Murrell and Dieckmann proposed several appropriate closures. As was shown in [6], some of these closures reduce the problem to solving a linear integral equation, while others reduce it to studying a nonlinear one.

These equations were thoroughly studied in [4, 6–8], where it was also shown that the linear equation (under additional conditions on the integral kernels) has nontrivial solutions only at the value of homogeneous mortality parameter $d = 0$. However, the nonlinear integral equation also allows nontrivial solutions for $d > 0$. After investigating different closures, we believe comparing them to results from IBM computer modeling using individual examples is a problem of great relevance.

In this work, we use the power-3 closure defined by the function

$$T(\xi,\xi') \approx \frac{C(\xi)C(\xi')C(\xi'-\xi)}{N^3}.$$

3. NUMERICAL EQUATIONS

We substitute the power-3 closure into the equation of the second moment:

$$0 = bm(\xi)N + b\int\limits_{\mathbb{R}} m(\xi')C(\xi+\xi')d\xi' - dC(\xi) - d'w(\xi)C(\xi)$$
$$- d'\int\limits_{\mathbb{R}} w(\xi')\frac{C(\xi)C(\xi')C(\xi'-\xi)}{N^3}d\xi'.$$

We explicitly express the first moment from the first equation:

$$N = \frac{d'}{b-d}\int\limits_{\mathbb{R}} C(\xi')w(\xi')d\xi'.$$

We now substitute the expression for the first moment into the equation:

$$0 = \frac{bd'}{b-d}m(\xi)\int\limits_{\mathbb{R}} C(\xi')w(\xi')d\xi' + b\int\limits_{\mathbb{R}} m(\xi')C(\xi+\xi')d\xi' - dC(\xi) - d'w(\xi)C(\xi)$$

$$- d' \int_{\mathbb{R}} w(\xi') \frac{C(\xi)C(\xi')C(\xi'-\xi)}{N^3} d\xi'.$$

Let us obtain similar terms and transpose the ones with the linear second moment to the left-hand side:

$$(d + d'w(\xi))C(\xi) = \frac{bd'}{b-d} m(\xi) \int_{\mathbb{R}} C(\xi')w(\xi')d\xi' + b \int_{\mathbb{R}} m(\xi')C(\xi+\xi')d\xi'$$
$$- d' \int_{\mathbb{R}} w(\xi') \frac{C(\xi)C(\xi')C(\xi'-\xi)}{N^3} d\xi'.$$

This equation and the one for the first order lies at the heart of the numerical approach. We use Neumann series in our calculations and transform the equation to the form best suited to the numerical approach.

To minimize the bulkiness of the below manipulations, we introduce the denotations

$$\widetilde{m} = bm, \quad \widetilde{w} = d'w,$$

$$\langle C, w \rangle = \int_{\mathbb{R}} C(\xi')w(\xi')d\xi',$$

$$[m * C] = \int_{\mathbb{R}} m(\xi')C(\xi+\xi')d\xi'.$$

We rewrite the equation using these denotations. Instead of such functions depending on ξ as $C(\xi)$ and $w(\xi)$, we write C and w, respectively,

$$(d + \widetilde{w})\, C = [\widetilde{m} * C] + \frac{\widetilde{m}}{b-d}\langle \widetilde{w}, C\rangle - \frac{C}{N^3}\left[\widetilde{w}C * C\right].$$

Numerically, we must use the normalizing second moment asymptotically tending to 0. We replace the second moment in the equation with the normalized one:

$$\overline{C} = \frac{C}{N^2}, \quad C = N^2\overline{C},$$

$$(d+\widetilde{w})N^2\overline{C} = N^2\left[\widetilde{m} * \overline{C}\right] + \frac{\widetilde{m}N^2}{b-d}\langle \widetilde{w}, \overline{C}\rangle - N^3\overline{C}\left[\widetilde{w}\overline{C} * \overline{C}\right].$$

We reduce the equation by N^2:

$$(d+\widetilde{w})\overline{C} = \left[\widetilde{m} * \overline{C}\right] + \frac{\widetilde{m}}{b-d}\langle \widetilde{w}, \overline{C}\rangle - N\overline{C}\left[\widetilde{w}\overline{C} * \overline{C}\right]$$

and omit N in the right-hand side. To do so, we use a formula explicitly expressing N via C. We replace C with $\bar{C}$ and express N:

$$N = \frac{\langle \widetilde{w}, C\rangle}{b-d} = \frac{N^2\langle \widetilde{w}, \overline{C}\rangle}{b-d},$$

$$N = \frac{b-d}{\langle \widetilde{w}, \overline{C}\rangle},$$

$$(d+\widetilde{w})\overline{C} = \left[\widetilde{m} * \overline{C}\right] + \frac{\widetilde{m}}{b-d}\langle \widetilde{w}, \overline{C}\rangle - \frac{(b-d)\overline{C}}{\langle \widetilde{w}, \overline{C}\rangle}\left[\widetilde{w}\overline{C} * \overline{C}\right].$$

For convenience and brevity of further transformations, we introduce new denotation Y:

$$Y = \langle \widetilde{w}, \overline{C}\rangle = \langle \widetilde{w}, (Q+1)\rangle,$$

$$(d+\widetilde{w})\overline{C} = \left[\widetilde{m} * \overline{C}\right] + \frac{\widetilde{m}}{b-d}Y - \frac{(b-d)\overline{C}}{Y}\left[\widetilde{w}\overline{C} * \overline{C}\right].$$

Normalized second moment $\overline{C}$ converges to 1 as ξ tends to infinity. To make the moment converge to 0, we perform the substitution

$$Q = \overline{C} - 1, \quad \overline{C} = Q + 1,$$

$$(d+\widetilde{w})(Q+1) = [\widetilde{m} * (Q+1)] + \frac{\widetilde{m}}{b-d}Y - \frac{(b-d)(Q+1)}{Y}\left[\widetilde{w}(Q+1) * (Q+1)\right].$$

We expand the parentheses in the right-hand side: $[\widetilde{w}(Q+1) * (Q+1)]$:

$$[(Q+1) * \widetilde{w}(Q+1)] = [Q * \widetilde{w}Q] + [1 * \widetilde{w}Q] + [Q * \widetilde{w}] + [1 * \widetilde{w}] = [Q * \widetilde{w}Q] + \langle \widetilde{w}, Q\rangle + [Q * \widetilde{w}]\langle \widetilde{w}, 1\rangle$$
$$= [Q * \widetilde{w}Q] + [Q * \widetilde{w}] + Y.$$

We substitute the resulting formula into the equation:

$$(d+\widetilde{w})(Q+1) = [\widetilde{m} * (Q+1)] + \frac{\widetilde{m}}{b-d}Y - \frac{(b-d)(Q+1)}{Y}\left([Q * \widetilde{w}Q] + [Q * \widetilde{w}] + Y\right).$$

We expand parentheses

$$dQ + \widetilde{w}Q + d + \widetilde{w} = [\widetilde{m} * Q] + b + \frac{\widetilde{m}Y}{b-d} - bQ + dQ - b + d - \frac{(b-d)(Q+1)}{Y}\left([Q * \widetilde{w}Q] + [Q * \widetilde{w}]\right)$$

and collect the similar terms

$$\widetilde{w}Q + bQ = [\widetilde{m} * Q] - \widetilde{w} + \frac{\widetilde{m}Y}{b-d} - \frac{(b-d)(Q+1)}{Y}\left([Q * \widetilde{w}Q] + [Q * \widetilde{w}]\right),$$

$$Q = \frac{[\widetilde{m} * Q] - \widetilde{w} + \frac{\widetilde{m}Y}{b-d} - \frac{(b-d)(Q+1)}{Y}\left([Q * \widetilde{w}Q] + [Q * \widetilde{w}]\right)}{\widetilde{w} + b}.$$

It is this expression that we use in the numerical approach.

Let us outline the numerical procedure of Neumann series that we use: Consider the equation

$$Q = KQ + f,$$

where K is a nonlinear integral operator, f is a known function, and Q is a sought function.

It was proved earlier that if a series of the form

$$f + Kf + K^2 f + \dots + K^n f + \dots$$

converges, it does so to the solution to the above equation. If operator K is converging, the Neumann series converges as well.

The iteration of Neumann series consists of applying contracting operator to the function and thus computing an approximate solution to the equation. For more detailed information on this topic, see [4, 9].

4. MODELING IN A BOUNDED DOMAIN

Modeling acts in a bounded periodic domain and calculates a single event (birth or death) at a time. The original distribution of individuals is taken from the uniform distribution with a prescribed number, and the modeling further computes events in the main cycle until the given points of observations. The algorithm for modeling consists of three steps.

1. We calculate the sum of all flows of births and deaths B_{total} and D_{total} and find the time until the next event occurs that is distributed exponentially with parameter $B_{\text{total}} + D_{\text{total}}$.

2. We find which event occurs (birth or death) using the Bernoulli distribution. The probability of birth is $\frac{B_{\text{total}}}{B_{\text{total}}+D_{\text{total}}}$ and the probability of death is $\frac{D_{\text{total}}}{B_{\text{total}}+D_{\text{total}}}$.

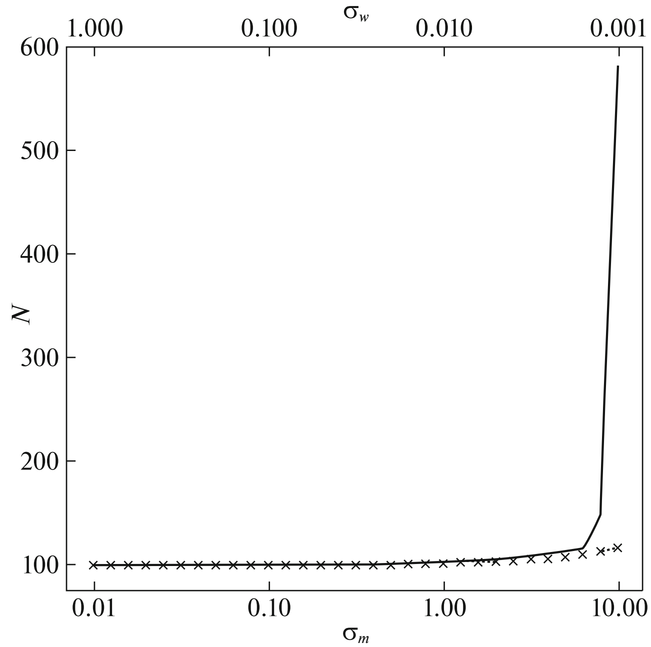

Fig. 1. Complete graph.

(a) If a birth occurs, we randomly choose one individual with probability $\frac{1}{N}$. We then add a new individual with ooordinate $x_i + m(x)$, where x_i are the coordinates of the individual and $m(x)$ is a random value distributed normally with parameter σ_m.

(b) If a death occurs, we randomly choose one individual corresponding to their mortality d_i, which includes competitive and homogeneous mortality. The probability of death of ith individual is equal to $\frac{d_i}{D_{\text{total}}}$.

3. After determination of the type of event and of the specific individual, we add or remove the individual in the modeling and update the mortality of its neighbors.

The modeler contains functions for obtaining coordinates of all individuals and their total number, and for starting the main cycle given number of times or until the prescribed time instance. When the set of individuals is updated, the mortality of only those individuals is updated that are inside the radius of action of the born or dead individual. In addition, there exists a set of scripts and libraries on language R for calculating the necessary spatial statistics using the modeling results.

5. COMPARING MODELING RESULTS TO ONES OBTAINED NUMERICALLY

Modeling requires a great deal of computational resources, so it is logical to start them only for most interesting domains. We see in the graphs (Figs. 1 and 2) that the results change greatly upon moving along the secondary diagonal and can compare results from modeling to one obtained numerically on curve $\sigma_m \cdot \sigma_w = 0.01$. There are three ways of improving the statistical estimate of the first moment from the modeling results: averaging over independent simulation runs, averaging over sufficiently independent time points, and increasing the size of the modeling region. For this comparison, we use averaging over 150 independent time points chosen on the basis of the following heuristics: two time points are independent if more than half a population has been replaced because of birth and depth.

We used a periodic domain of sufficient size (50 standard deviations from the widest kernel) and chose a 95% confidence interval based on independent time points. Modeling and numerical calculations were done for parameters $b = 1$, $d = 0$, $d' = 0.01$, $\sigma_w \in [0.01, 1]$, and $\sigma_m = 0.01/\sigma_w$, and we took 31 points for σ_w. These points were uniformly distributed over the logarithmic axis from 0.01 to 1. As is seen in the graphs, the results from numerical calculations and modeling differ substantially at extremely low values of σ_w, but they are particularly close for $\sigma_w \geqslant 0.1$ and behave in a qualitatively similar manner.

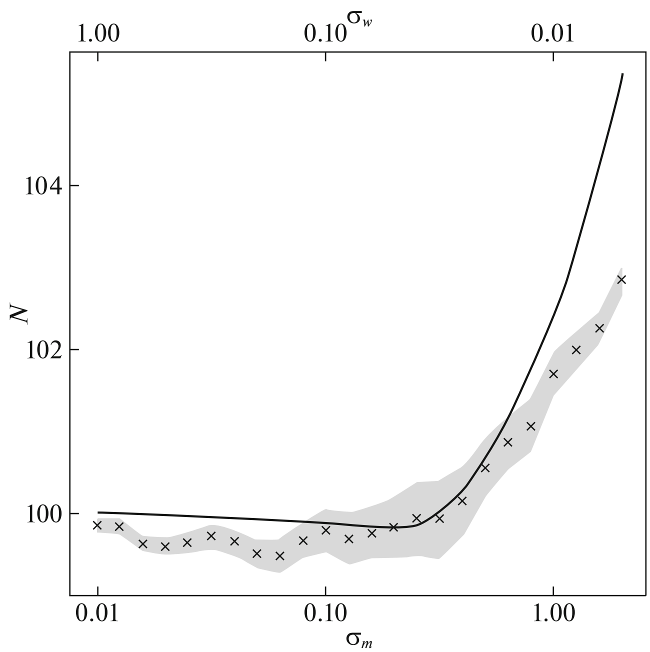

Fig. 2. Scaled graph.

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