EKOLOGIJA. 2005. Nr. 3. P. 1–4

Analytical dependence of population density on the characteristic of mobility in dissipative ecological systems

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In mathematical ecology, there exists a wide class of systems belonging to the so-called dissipative type. Investigation of such systems allows determining the basic dynamical peculiarities of population expansion. The most interesting properties appear in the case of nonlinear dissipative systems, which may exhibit bifurcations and irregular solitonic type waves. In the case when the impact of the Malthusian function is negligible and the mobility characteristic is of a special kind, it is possible to trace the dependence of population density and particularly of its irregular waves on the characteristic of mobility in an analytical aspect.

Key words: dissipative ecological systems, population dynamics, reaction–diffusion model

INTRODUCTION

The idea of using diffusion to study population dynamics was introduced by J. G. Skellam in the early 1950s (Skellam, 1951). General discussions and references on reaction–diffusion equations in biological aspects may be found in Britton, 1986; Cantrell, Cosner, 1991; Diekmann, Temme, 1976; Fife, 1979; Ludwig et al., 1979; Murray, 1997, 1993; Okubo, 1980. The simplest example of the nonlinear reaction diffusion equation is the one-dimensional diffusion logistic equation

$$\frac{\partial N}{\partial t} = \frac{\partial}{\partial x}[D(N)\frac{\partial N}{\partial x}] + F(N), \qquad (1)$$

where $F(N)$ is the Malthusian function and $D(N)$ is the characteristic of mobility.

In this paper, we restrict the consideration to the problem of the existence of solutions of a nonlinear reaction diffusion model for a single-species population moving in one space dimension. A single-species population dynamics with dispersal in a spatially heterogeneous environment is modelled by a nonlinear reaction–diffusion equation with a nonlinear term of mobility. Each nonlinear kinetics describes the relation between the growth rate and the density of a steady-state population distribution. Our main concern is investigation of the possible appearance of the area and time restrictions and the phenomenon of travelling waves. The existence of non-linear kinetics realized by the mobility terms in an explicit form is established. It is shown that the freedom of such kinetics in some cases is restricted by the influence of the nonlinear behaviour of mobility.

POWER DEPENDENCE OF THE MOBILITY CHARACTERISTIC

For simplicity we will consider a one-dimensional area. In the case when the mobility characteristic is a power function from population density and the Malthusian function is not large,

$$D(N) = aN^{v}, \qquad F(N) << 1, \qquad (2)$$

the type (1) system allows a complete analytical solution. Indeed, employing the method of similarity we will introduce a new variable, $\xi = x/(at)^{1/(2+v)}$.

The solution of equation (1) under conditions (2) has the form

$$N = (at)^{-\frac{1}{2+v}}[\frac{v}{2(2+v)}(\xi_0^2 - \xi^2)]^{\frac{1}{v}}, \qquad (3)$$

where ξ_0 is the integration constant. The behaviour of this solution essentially depends on the sign of the power v.

For $v > 0$, solution (3) gives the distribution of population density $N(x, t)$, peculiar to an area with the bounders $x = \pm x_0$ defined by the equality $\xi = \pm \xi_0$; beyond these boundaries $N(x, t) = 0$. Hence it follows that with time the population boundaries expand according to the law

$$x_0 = \text{const} \cdot t^{\frac{1}{2+v}}. \qquad (4)$$

Note here that the power v in the mobility characteristic $D(N) = aN^{v}$ is a free parameter of the model unknown in advance. The dependence $x_0(t)$ allows us to determine the power v. This remark is useful for applications.

The integration constant ξ_0 is determined by the condition of normalization of the whole number of the individuals:

$$\int_{-x_0}^{x_0} N(x)dx = \int_{-\xi_0}^{\xi_0} f(\xi)d\xi = 1, \qquad (5)$$

hence $$\xi_0^{2+v} = \frac{(2+v)^{1+v}\,2^{1-v}}{v\pi^{v/2}}\,\frac{\Gamma^v(1/2+1/v)}{\Gamma^v(1/v)}, \qquad (6)$$

where Ã(x) is the Euler gamma-function.

The irregular wave solution describes the motion of population with a constant velocity. Such solution is a special case of the travelling wave. For the travelling wave, *i.e.* in the case when $N = N(x + Vt)$, we obtain that equation (1) turns into

$$V\frac{\partial N}{\partial x} = a\frac{\partial}{\partial x}\left(N^v\frac{\partial N}{\partial x}\right), \qquad (7)$$

whence, after a double integration, we obtain the following solution:

$$N = N_0\left|x+Vt\right|^{\frac{1}{v}}, \qquad (8)$$

where $|x|$ is the distance from the boundary of the inhabited area.

For $v < 0$, the solution (3) can be expressed as

$$N = (at)^{-\frac{1}{2-v}}\left[\frac{v}{2(2-v)}(\xi_0^2+\xi^2)\right]^{-\frac{1}{v}}, \quad v \to |v|, \qquad (9)$$

where $v \to |v|$ means the positive value of v.

In this case the population density is distributed all over the area, and for large distances N diminishes obeying the power law: $N \sim x^{-2}$. This solution is valid only if $v < 2$; if $v \geq 2$, the normalization integral (5) which now is taken on the whole real axis becomes diverged, implying an instantaneous distribution of the population at an infinite distance. The integration constant ξ_0 in expression (9)

$$\xi_0^{2-v} = \frac{2(2-v)\pi^{\frac{v}{2}}}{v}\,\frac{\Gamma^v(1/v-1/2)}{\Gamma^v(1/v)}. \qquad (10)$$

For $v < 0$, the equation for an irregular wave (8) has no solutions turning into zero at a finite distance, *i.e.* the population is distributed at any given moment throughout the whole space. Thus, such solution should be rejected.

Finally, for $v \to 0$, $\xi_0 \to 2/\sqrt{v}$, and the solution determined by expression (3) gives an ordinary Gaussian distribution.

INHOMOGENEOUS GENERALIZATION OF POWER DEPENDENCE

In the case when the mobility characteristic $D = D(x, t, N)$, we deal with the presence of inhomogeneous mobility in an ecosystem. In the general case, the problem of the evolution of the density of a population with an inhomogeneous mobility characteristic can be solved only numerically. Nevertheless, in some cases an exact analytical solution can be found. Let us consider an inhomogeneous generalization of the evolution of the population $N(x, t)$ in the form

$$\frac{\partial N}{\partial t} = x^{-\rho}\frac{\partial}{\partial x}\left[x^{\mu}N^{v}\frac{\partial N}{\partial x}\right] + F(N). \qquad (11)$$

This equation offers a rather wide detailing of equation (1) in the case of the power dependence $D(N)$; the properties of its solutions essentially depend on the value of the constituent parameters μ, v, ρ. The introduction of an explicit dependence of the mobility characteristic on the coordinate x, on the one hand, is determined by the consideration of nonhomogeneity and, on the other hand, by investigation of the process of evolution in a cylindrical or spherical system of coordinates, where the operator *div* explicitly depends on the coordinate r.

We will single out the following three groups of the solution of equation (11): a) the rapid ($v < 0$), b) slow ($v > 0$), and c) normal ($v = 0$) evolution, and consider the solutions of the equation of evolution (1) separately for each group.

Let $\mu = \rho$ in the case of rapid evolution ($v < 0$). We will search for the solution of the population density function in the form

$$N(x,t) = x^{\frac{2}{v}} f(t). \qquad (12)$$

The substitution of (12) into the initial equation (11) and integration give the following expression of the solution $N(x, t)$:

$$N(x,t) = x^{\frac{2}{v}}\left[\frac{x^2}{N_0^v} - \frac{4+2v(1+\rho)}{v}t\right]^{-\frac{1}{v}}, \qquad (13)$$

where $N_0 = N(x, 0)$ is the initial value of $N(x, t)$. For $v = -2/(1 + \rho)$ we have a stationary solution $N(x, t) = N_0(x)$.

Note an important circumstance: the expression in brackets in the solution (13) must be non-negative. This means that the evolution of population density, although not limited in space, proceeds in a finite time period $0 \leq t \leq t_{max}$:

$$t_{max} = \frac{v}{4+2v(1+\rho)}\,\frac{x^2}{N_0^v}. \qquad (14)$$

In any point of space, the population density diminishes from its initial value $N_0(x)$ to zero.

Now, let us consider the case of slow evolution ($v > 0$). We will seek the solution for the population density function in the form

$$N(x,t) = t^{-\frac{k}{2}} f(s), \quad s = xt^{-\frac{1}{2v}}. \qquad (15)$$

Thus, the solution of the initial equation (11) can be expressed as

$$N(x,t) = N_0 t^{-\frac{k}{2}} (s_m^2 - s^2)^{\frac{1}{v}}, \qquad s = xt^{-\frac{1}{2r}} \tag{16}$$

for $0 < s < s_m$, or in the dimensionless form

$$N(x,t) = N_0 \left[1 - \left(\frac{s}{s_m} \right)^2 \right]^{\frac{1}{v}}. \tag{17}$$

At a fixed value of the spatial variable x, from expressions (16) or (17) it follows that solution $N(x, t)$ exists only for $t > t_{min}$. Thus, we observe a "delayed" response of the population evolution.

In the case of slow evolution, the presented solution is not the only possible one. Indeed, let us consider the obtained solution (13) for $v > 0$. This solution is valid for the interval $0 \le t \le t_{max}$, where t_{max} is determined by the expression (17); however, in this case, for $t \to t_{max}$ the solution gains an unlimited increment.

Finally, in the case of normal evolution $v = 0$, the solution for the population density function can be expressed as

$$N(x,t) = Ct^{-\frac{k}{2}} e^{-\frac{kx^2}{4t^k}}, \tag{18}$$

where k is an arbitrary constant. For $k = 1$ we obtain a solution corresponding to a normal or Gaussian distribution. The solution (18) exists in the whole region of the determination of variables (x, t_0).

CONCLUSIONS AND DISCUSSION

A comparison of the results of Parts 1 and 2 allows concluding that the power nonlinearity and non-homogeneity exert an influence on the behaviour of the solution of a diffusive dissipative system.

In both cases the population density $N(x, t)$ essentially depends on the index of power dependence: for $v < 0$ the solution is determined on the entire numerical axis, while for $v > 0$ the solution is compact in the region $|x| < x_0$, the limits of the region expanding with time in accordance with the law $x_0 = ct^{\frac{1}{2+v}}$.

A traditional way of presenting the subject of the paper would be to take concrete results of population dynamics measurements and to apply to them the proposed theoretical results. However, the aim of the present paper is somewhat different: we want to show the great possibilities contained in the classical reaction–diffusion system. One of these possibilities is the nonlinear characteristic of mobility which, to our knowledge, has not been this far used for investigating ecological models. The usual way of treating the results obtained from observations is to "squeeze" them into the known mathematical reaction–diffusion model, which has proven correct in a number of cases. In our opinion, the procedure deserves a more "creative" approach involving consideration of the inherent possibilities of the reaction–diffusion model. This would allow not only to improve the qualitative correspondence between the model and the results, but also to account for the intrinsic qualitatively new phenomena. In the classical reaction–diffusion model, the border of a population area changes its position obeying the dependence $x_0 = \text{const} \cdot t^{1/2}$. In case we account for the possible power characteristic of mobility $D(N) = aN^v$, this dependence can take another form: $x_0 = \text{const} \cdot t^{1/(2+v)}$. The power index v modifies the population area expressed through the constant $\xi_0 : -\xi_0 \le \xi \le \xi_0$, *i.e.* throughout all the dynamics the population is distributed not in the whole area but only in its expanding, though always limited, part. In our opinion, this property could be useful while explaining the phenomenon of overcrowding.

The solutions themselves of the concentration and traveling excitation wave qualitatively differ form the respective case of the constant characteristic of mobility $D(N) = a = \text{const}$.

The reaction–diffusion model has a deep relation with the theory of active media. At present, this theory is based on the reaction–diffusion type evolution equation

$$\frac{\partial X}{\partial t} = F(X) + \frac{\partial}{\partial R_i} \left(D_{ij}(X) \frac{\partial X}{\partial R_j} \right), \tag{19}$$

where $X = X(R, t)$ is a set of macroscopic functions, which characterizes the investigated system, *e.g.*, substance concentration of the chemically active media, $F(X)$ is a nonlinear function determined by the structure of the process under study, $D_{i,j}$ are the coefficients of the space diffusion of the system elements.

Concrete examples of such equations were introduced rather long ago (see, for instance, Murray, 1977). It is important to note that various modifications of the Ginsburg–Landau equation also belong to type (19) equations. These modifications are widely used in the theory of equilibrium and non-equilibrium phase transitions.

To elucidate the effect of the nonlinear function of mobility $D(N)$ on population concentration, we have deliberately limited ourselves by a negligibly low effect of the Malthusian function. In case the total effect of mobility and Malthusian functions is accounted for, we see that due to the nonlinearity of the mobility $D(N)$ such effect is not a mere sum total of separate contributions, but presents a complicated nonlinear effect.

When applying the reaction–diffusion model for assessing population dynamics, the general peculiarities of the diffusion process should be accounted for. Their effect can essentially change the properties of the model (see, *e.g.*, Miskinis, 2002). For instance, even linear diffusion, because of various effects of nonlocality, may be more rapid or slower than the normal Gaussian diffusion, thus inducing considerable changes in the properties of the population dynamics model.

Received 29 June 2005

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POPULIACIJOS TANKIO ANALITINË PRIKLAUSOMYBË NUO MOBILUMO CHARAKTERISTIKOS DISIPACINËSE EKOLOGINËSE SISTEMOSE

S a n t r a u k a

Matematinëje ekologijoje yra gausi klasë sistemø, priklausanèiø vadinamajam disipaciniam tipui. Ðitokiø sistemø tyrimai ágalina nustatyti pagrindinius dinaminius populiacijø plitimo ypatumus. Ádomiausios savybës pasireiðkia netiesinëse disipacinëse sistemose, kurioms plintant gali pasireikðti bifurkacijos ir nereguliarios solitoninës bangos. Kai Maltuso funkcijos átaka neþymi ir mobilumas yra specifinio pobûdþio, galima analitiðkai nustatyti populiacijø tankio ir, pavyzdþiui, nereguliariø tankio bangø priklausomybæ nuo mobilumo charakteristikos.

Raktaþodþiai: disipacinës ekologinës sistemos, populiacijø dinamika, reakcijos–difuzijos modelis