

NONLOCAL REACTION-DIFFUSION EQUATIONS IN POPULATION DYNAMICS

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Various problems in population dynamics are described by nonlocal reaction-diffusion equations, where the conventional logistic term for the reproduction rate is replaced by some integral expressions. The properties of such equations, including the existence and stability of solutions, appear to be quite different in comparison with conventional reaction-diffusion equations. In this work, we discuss some nonlocal reaction-diffusion equations and their properties.

Keywords: nonlocal reaction-diffusion equations, pulses, waves.

1. INTRODUCTION

Reaction-diffusion equations and systems are widely used in ecology and population dynamics in order to study the evolution of biological populations under various conditions (see [14] and the references there in). One of the developments of the classical theory concerns the models with nonlocal consumption of resources, where some integral terms enter the equations. In this work, we discuss recent developments in this field. The reaction-diffusion equation:

$$\frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} + F(u) \quad (1)$$

describes the distribution of a population density $u(x; t)$ depending on the space variable x and on time t . The diffusion term in the right-hand side characterizes the random motion of the individuals in the population, and the second term corresponds to birth and death rates. It is often considered in the form:

$$F(u) = au^k(1-u) - \sigma u \quad (2)$$

where a and σ are some positive constants, $k = 1, 2$. If $k = 1$, then we obtain a conventional logistic term for the reproduction of the population, which is proportional to the population density u and to the available resources $1 - u$; the last term corresponds to the mortality of population, also proportional to population density. The case $k = 2$ corresponds to sexual reproduction, where the reproduction rate is proportional to the densities of males and females [15]. In the simplified model with a single equation, they are assumed to be equal to each other.

Consumption of resources in expression (2) is proportional to population density, so that the remaining available resources are conventionally written as $1 - u/K$, where K is a positive constant, carrying capacity. Setting $K = 1$ in the dimensionless variables, we write it in the form (2). In a more general setting, consumption of resources occurs not only at the spatial point x , where the individual is located, but in some area around its average location. In this case, the rate of resources consumption is given by the integral:

$$J(u) = \int_{-\infty}^{\infty} \phi(x - y)u(y, t)dy,$$

where the kernel $\phi(x - y)$ characterizes the efficiency of resources consumption depending on the distance between the average location x and the location of resources y . It is a non-negative bounded function. Let us note that, for the sake of simplicity, we consider here all real values of x . Alongwith the integral $J(u)$, which corresponds to non-local consumption of resources, we also consider the integral:

$$I(u) = \int_{-\infty}^{\infty} u(y, t)dy$$

which corresponds to the global consumption of resources proportional to the total population density and independent on the individual location. Instead of equation (1) we consider equation:

$$\frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} + au^k(1 - bJ(u)) - \sigma u \quad (3)$$

in the case of global consumption.

$$\frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} + au^k(1 - bI(u)) - \sigma u \quad (4)$$

Let us note that equation (3) becomes similar to the local equation (1) if the kernel $\phi(x)$ is replaced by the δ -function.

It appears that the properties of these questions, to be discussed in the next sections, are different in comparison with equation (1). Namely, we will study the

existence of pulses for global equations and the emergence of periodic patterns for non-local equations.

2. EXISTENCE OF PULSES

Local equation with bistable nonlinearity. Consider equation (1) with function $F(u)$ satisfying the following conditions:

$$F(u_i) = 0, i = 0, 1, 2; F'(u_i) < 0, i = 0, 2 \quad (5)$$

Here, $u_0 = 0 < u_1 < u_2$ and $F(u) \neq 0$ for $u \neq u_i$. Then, equation (1) has a positive stationary solution $w(x)$ decaying at infinity, that is, a solution to the problem:

$$Dw'' + F(w) = 0, w(\pm\infty) = 0, \quad (6)$$

if and only if $\int_{u_0}^{u_2} F(u) du > 0$. The proof of this assertion is elementary, and it is omitted. A positive solution of problem (6) is called a *pulse solution*.

Equations with non-local and global consumption. Existence of pulses can be easily studied for equation (4) with $k = 2$ [14]. Consider the problem:

$$w'' + w(1 - bI(w)) - \sigma w = 0, w(\pm\infty) = 0 \quad (7)$$

$$(D = a = 1). \text{ Set } c = 1 - bI(w).$$

The problem:

$$w'' + cw^2 + \sigma w = 0, w(\pm\infty) = 0 \quad (8)$$

can be solved explicitly. Denote this solution by $w_c(x)$, where subscript c shows its dependence on coefficient c in (8). Then, we obtain the equation with respect to c :

$$c = (1 - bI(w_c)).$$

From its solution, there follows that there exists such $b_0 > 0$ that problem (7) has two solutions for $0 < b < b_0$, a single solution for $b = b_0$, and no solutions for $b > b_0$.

Stability of pulses. A positive stationary solution of equation (1) decaying at infinity is unstable. Indeed, let $w(x)$ be a positive solution of problem (6). Linearizing equation about this solution, we get the eigenvalue problem:

$$Dv'' + F'(w(x))v = \lambda v; v(\pm\infty) = 0.$$

The principal eigenvalue, that is, the eigenvalue with the maximal real part of this problem is real, simple, and the corresponding eigenfunction is positive [16]. Since $v(x) = w'(x)$ is an eigenfunction corresponding to the zero eigenvalue, and $w'(x)$ is not positive ($w(x)$ is not monotone), then $\lambda = 0$ is not the principal eigenvalue. Therefore, the principal eigenvalue is positive, and the solution $w(x)$ is unstable.

Equation (7), with global bistable nonlinearity, has two pulse solutions if constant b is less than some critical value. Numerical simulations show that one of these two solutions is stable. This result is important for biological applications, since it provides the persistence of solutions interpreted as biological species [10,11]. Stability of pulses in this model is not proved analytically.

Systems of equations. The result on the existence of pulses for the above formulated scalar equation, in terms of the sign of integral $\int_{-\infty}^{\infty} F(w) dx$, can be reformulated in terms of the sign of the wave speed. Let us recall that the travelling solution of equation (1) is a solution $u(x; t) = w(x - ct)$, where c is the wave speed. It satisfies the problem:

$$Dw'' + cw' + F(w) = 0, w(-\infty) = u_2; w(\infty) = u_0. \quad (9)$$

Integrating this equation over the whole axis, we conclude that the sign of the wave speed coincides with the sign of integral $\int_{-\infty}^{\infty} F(w) dx$. Therefore, the pulse solution exists if and only if the wave speed is positive.

In the case of reaction-diffusion systems, the question about the existence of pulses becomes much more important, and the existence condition cannot be reduced to the sign of the integral of non-linearity. However, it appears that the second formulation has the same result, that is, that the pulse exists if and only if the wave speed is positive, it remains valid for some classes of reaction-diffusion systems [12,13]. Existence of pulses for the reaction-diffusion system of two equations in the case of global consumption is proved in [15].

Bifurcations of pulses for the scalar equation. Integral $I(u) = \int_{-\infty}^{\infty} u(x,t) dx$ is well defined only for functions $u(x;t)$, integrable on the whole axis. Therefore, in order to study the emergence of pulses in the case of global consumption, we will consider a similar equation:

$$\frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} + au^2(1 - I_0(u)) - \sigma u, I_0(u) = \int_0^L u(y,t) dy \quad (10)$$

($b = 1$) on a bounded interval $0 < x < L$ with the no-flux boundary conditions: $x = 0,$

$$L : \partial u / \partial x = 0$$

We look for homogeneous in space stationary solutions of equation (10). If $b < a/(4L)$, then this problem has three constant solutions, $w = 0$, and two solutions of the equation:

$$aw(1 - I_0(w)) = \sigma. \quad (11)$$

We denote them by w_1 and w_2 assuming that $w_1 < w_2$.

Consider next the eigenvalue problem for the equation linearized about a constant solution u :

$$Du'' + 2au_*(1 - I_0(u_*))uu - \sigma u - au_*^2 I_0(u) = \lambda u, u'(0) = u'(L) = 0 \quad (12)$$

Taking into account (11), we can write it as:

$$Du'' + \sigma u - au_*^2 I_0(u) = \lambda u, u'(0) = u'(L) = 0 \quad (13)$$

We will search its solutions in the form:

$$u(x) = \cos(nx/L); n = 0, 1, 2,$$

Then we get:

$$\lambda_0 = \sigma - au_*^2 L, \quad \lambda_n = -D(n\pi/L)^2 + \sigma, \quad n = 1, 2, \dots$$

Hence, the presence of the integral term influences only the eigenvalue 0. From (11) we get:

$$\lambda_0 = au_*(1 - 2Lu_*).$$

If equation (11) has two solutions, then $\lambda_0 > 0$ for $u_* = w_1$ and $\lambda_0 < 0$ for $u_* = w_2$.

Thus, the problem linearized about solution w_2 has negative eigenvalue λ_0 . Eigenvalue 1 can be negative or positive. If it is negative, this solution is stable, otherwise it is unstable and another solution bifurcates from it. We can consider D as bifurcation parameter with the critical value

$$D^* = L^2/\pi^2. \text{ If } D < D^*,$$

then a nonhomogeneous stable solution emerges. Since the eigenfunction $\cos(\pi x/L)$ corresponding to the eigenvalue 1 has its extrema at the boundary, then the emerging solution also has its maximum at the boundary of the interval. If we consider a double interval, then this solution corresponds to the pulse solution.

Bifurcations of pulses for systems of equations. Consider the system of equations:

$$\frac{\partial u}{\partial t} = D_1 \frac{\partial^2 u}{\partial x^2} + a_1 u^2 (1 - b_{11} I_0(u) - b_{12} I_0(v)) - \sigma_1 u, \quad (14)$$

$$\frac{\partial u}{\partial t} = D_1 \frac{\partial^2 u}{\partial x^2} + a_2 v^2 (1 - b_{21} I_0(u) - b_{22} I_0(v)) - \sigma_2 u, \quad (15)$$

where:

$$I_0(u) = \int_0^L u(y, t) dy, \quad I_0(v) = \int_0^L v(y, t) dy,$$

on a bounded interval $0 < x < L$ with the no-flux boundary conditions: $x = 0, L : \partial u / \partial x = 0, \partial v / \partial x = 0$.

Stationary solutions to this problem satisfy the following algebraic equations:

$$a_1 u_* (1 - b_{11} I_0(u_*) - b_{12} I_0(v_*)) = \sigma_2, a_1 u_* (1 - b_{21} I_0(u_*) - b_{22} I_0(v_*)) = \sigma_2. \quad (16)$$

Linearizing system (14), (15) about a stationary solution, we obtain the eigenvalue problem:

$$D_1 u'' + \sigma_1 u - a_1 u_*^2 (b_{11} I_0(u) + b_{12} I_0(v)) = \lambda u, \quad (17)$$

$$D_2 v'' + \sigma_2 v - a_2 v_*^2 (b_{21} I_0(u) + b_{22} I_0(v)) = \lambda v, \quad (18)$$

and we look for its solution in the form:

$$u(x) = p \cos(n\pi x / L), v(x) = q \cos(n\pi x / L), n = 0, 1, 2, \dots$$

The eigenvalues of problem (17), (18) can be found as eigenvalues of the matrices:

$$A(0) = \begin{pmatrix} \sigma_1 - a_1 u_*^2 b_{11} L, & -a_1 u_*^2 b_{12} L \\ -a_2 v_*^2 b_{21} L, & \sigma_2 - a_2 v_*^2 b_{22} L \end{pmatrix},$$

and:

$$A(n) = \begin{pmatrix} \sigma_1 - D_1 (n\pi / L)^2, & 0 \\ 0, & \sigma_2 - D_2 (n\pi / L)^2 \end{pmatrix}, \quad n = 1, 2, \dots$$

If the eigenvalues of the matrix $A(0)$ have negative real parts, then the bifurcation of pulses are determined by matrix $A(1)$, that is, if at least one of its eigenvalues is positive.

3. ESSENTIAL SPECTRUM AND PROPERNESS

We now study the spectral properties of the integro-differential operators in a more general setting. Consider the system of integro-differential equations:

$$Bw = w'' + cw' + F(w, \Phi * w).$$

We are interested in the solutions $w = (w_1, \dots, w_n)^T$ of system (21) with some specific limits $w^\pm = (w_1^\pm, \dots, w_n^\pm)^T$ at $\pm\infty$. We are looking for solutions w_i of (21) under the form $w_i = u_i + \psi_i$, where $\psi_i \in C^\infty(\mathbb{R})$ are chosen so that $\psi_i(x) = w_i^\pm$ for $x \geq 1$ and $\psi_i(x) = w_i^-$ for $x \leq -1$. Thus, equation (21) becomes:

$$(u + \psi)'' + c(u + \psi)' + F(u + \psi, \Phi * (u + \psi)) = 0, \quad (22)$$

where $\psi = (\psi_1, \dots, \psi_n)^T$.

Denote by A the operator in the left-hand side of (22), $A: E \rightarrow E^0$,

$$Au = (u + \psi)'' + c(u + \psi)' + F(u + \psi, \Phi * (u + \psi)). \quad (23)$$

Linearization of A about a function $\tilde{u} = (\tilde{u}_1, \dots, \tilde{u}_n) \in E$ is the operator:

$$Lu = u'' + cu' + \frac{\partial F}{\partial u}(\tilde{u} + \psi, \Phi * (\tilde{u} + \psi))u + \frac{\partial F}{\partial U}(\tilde{u} + \psi, \Phi * (\tilde{u} + \psi))(\Phi * u), \quad (24)$$

where $\frac{\partial F}{\partial u} = \left(\frac{\partial F_i}{\partial u_j} \right)$ and $\frac{\partial F}{\partial U} = \left(\frac{\partial F_i}{\partial U_j} \right)$ are the matrices of derivatives of F, \dots, F_n

with respect to variables u_1, \dots, u_n and U_1, \dots, U_n , respectively.

For the linearized operator L , we introduce the limiting operators L^\pm , that is the operators obtained from L by replacing the coefficients of $u, u', u'', \Phi * u$ with their limits as $x \rightarrow \pm\infty$. Since for $\tilde{w} = \tilde{u} + \psi$, there exist the limits $\lim_{x \rightarrow \pm\infty} \tilde{w}(x) = w^\pm$, it follows that $\Phi * (\tilde{u} + \psi) \rightarrow w^\pm$, so that the limiting operators associated to L are:

$$L^\pm u = u'' + cu' + \frac{\partial F}{\partial u}(w^\pm, w^\pm)u + \frac{\partial F}{\partial U}(w^\pm, w^\pm)(\Phi * u). \quad (25)$$

Similar to elliptic problems in unbounded domains [8,9], the limiting operators determine the Fredholm property and properness of the integro-differential operators.

We study operator A acting from E_μ into E_μ^0 . In order to introduce a topological degree in a future section, we prove the properness of A in the more general case when coefficient c and function F depend also on a parameter $\tau \in [0, 1]$. Let $A^\tau: E_\mu \rightarrow E_\mu^0$, $\tau \in [0, 1]$, be the operator defined as:

$$A^\tau u = (u + \psi)'' + c(\tau)(u + \psi)' + F^\tau(u + \psi, \Phi^*(u + \psi)). \quad (268)$$

Operator L^τ linearized about a function $\tilde{u} \in E_\mu$ is:

$$L^\tau u = u'' + c(\tau)u' + \frac{\partial F^\tau}{\partial u}(\tilde{u} + \psi, \Phi^*(\tilde{u} + \psi))u + \frac{\partial F^\tau}{\partial U}(\tilde{u} + \psi, \Phi^*(\tilde{u} + \psi))(\Phi^*u), \quad (27)$$

The associated limiting operators are given by:

$$(L^\tau)^\pm u = u'' + c(\tau)u' + \frac{\partial F^\tau}{\partial u}(w^\pm, w^\pm)u + \frac{\partial F^\tau}{\partial U}(w^\pm, w^\pm)(\Phi^*u). \quad (28)$$

Assume that the following hypotheses are satisfied:

(H1) For any $\tau \in [0, 1]$, functions $F_i^\tau(u, U)$ and their derivatives with respect to u and U satisfy the Lipschitz condition: there exists $K > 0$, so that:

$$|F_i^\tau(u, U) - F_i^\tau(\hat{u}, \hat{U})| \leq K(|u - \hat{u}| + |U - \hat{U}|)$$

for any $(u, U), (\hat{u}, \hat{U}) \in \mathbb{R}^{2n}$.

Similarly for $\partial F_i^\tau / \partial u_j$ and $\partial F_i^\tau / \partial U_j$:

$$\left| \frac{\partial F_i^\tau}{\partial u_j}(u, U) - \frac{\partial F_i^\tau}{\partial u_j}(\hat{u}, \hat{U}) \right| \leq K(|u - \hat{u}| + |U - \hat{U}|)$$

$$\left| \frac{\partial F_i^\tau}{\partial U_j}(u, U) - \frac{\partial F_i^\tau}{\partial U_j}(\hat{u}, \hat{U}) \right| \leq K(|u - \hat{u}| + |U - \hat{U}|)$$

(H2) $c(\tau), F_i^\tau(u, U)$ and the derivatives of $F_i^\tau(u, U)$ are Lipschitz continuous in τ , i.e., there exists a constant $K > 0$ so that:

$$|c(\tau) - c(\tau_0)| \leq K|\tau - \tau_0|, |F_i^\tau(u, U) - F_i^{\tau_0}(u, U)| \leq K|\tau - \tau_0|,$$

$$\left| \frac{\partial F_i^\tau}{\partial u_j}(u, U) - \frac{\partial F_i^{\tau_0}}{\partial u_j}(u, U) \right| \leq K|\tau - \tau_0|,$$

$$\left| \frac{\partial F_i^\tau}{\partial U_j}(u, U) - \frac{\partial F_i^{\tau_0}}{\partial U_j}(u, U) \right| \leq K|\tau - \tau_0|.$$

$\forall \tau, \tau_0 \in [0, 1]$ and for all (u, U) from any bounded set in \mathbb{R}^{2n} .

(H3) (Condition NS) For any $\tau \in [0, 1]$, the limiting equations:

$$u'' + c(\tau)u' + \frac{\partial F^\tau}{\partial u}(w^\pm, w^\pm)u + \frac{\partial F^\tau}{\partial U}(w^\pm, w^\pm)(\Phi * u) = 0$$

do not have non-zero solutions in E .

Theorem 3.1. *Assume that functions $\varphi_{ij} : \mathbb{R} \rightarrow \mathbb{R}$ and $F_i : \mathbb{R}^{2n} \rightarrow \mathbb{R}$ ($1 \leq i, j \leq n$) satisfy the conditions from Section 1 and hypotheses (H1)-(H3). In addition, assume that $\varphi_{ij} \in C^\alpha(\mathbb{R})$. Then, operator $A^\tau : E_\mu \times [0, 1] \rightarrow E_\mu^0$ from (3.8) is proper on $E_\mu \times [0, 1]$ (with respect to both u and τ).*

The proof of this theorem, given in [4], allows the construction of the topological degree for the corresponding operator. Properness and the degree are used to study the existence and bifurcations of solutions including travelling wave solutions [3,5]. One of the key assumptions here is hypothesis (H3), and its stronger form, assuming that the essential spectrum of the operator lies in the left-half plane for the complex plane. If this condition is not satisfied, then the corresponding operator can lose the Fredholm property, and nonstandard bifurcations through the essential spectrum can lead to the emergence of periodic structures and waves. We consider some examples in the next section.

4. BIFURCATION OF PERIODIC SOLUTIONS

Consider equation (3) with $k = 1$, $a = b = 1$, $\tau = 0$. It has a stationary solution $u = 1$.

Linearizing this equation about u , we obtain the eigenvalue problem:

$$Du'' - \int_{-\infty}^{\infty} \phi(x-y)u(y)dy = \lambda u \quad (29)$$

Applying the Fourier transform to this equation, we find the expression for the spectrum:

$$\lambda = -D\xi^2 - \tilde{\phi}(\xi). \quad (30)$$

Consider as example the kernel $\phi(x) = 1/(2N)$ for $|x| \leq N$ and $\phi(x) = 0$ otherwise. Then, $\tilde{\phi}(\xi) = \sin(\xi N)/(\xi N)$. Since this function becomes negative for some ξ , the eigenvalue λ can become positive. In this case, the homogeneous in space stationary solution $u = 1$ of equation (3) loses its stability, resulting in the emergence of a stationary periodic solution (Fig. 1).

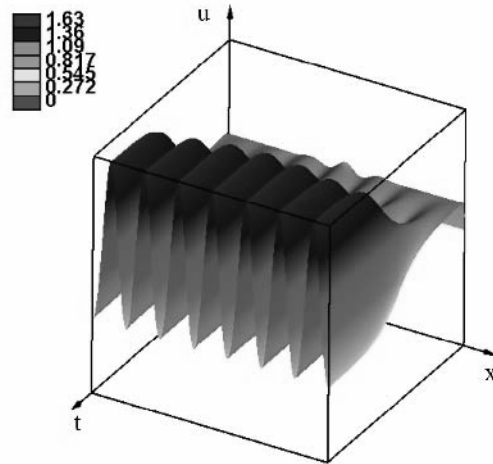


Fig. 1. Periodic solution $u(x; t)$ of equation (3). The values of parameters: $k = 1$, $a = b = 1$, $\sigma = 0$, $L = 1$; $D = 10^{-4}$, $N = 0.1$, $t = 350$.

Instead of usual travelling waves with fixed limits at infinity we observe periodic travelling waves where a periodic spatial structure is established behind the wave (Fig. 2).

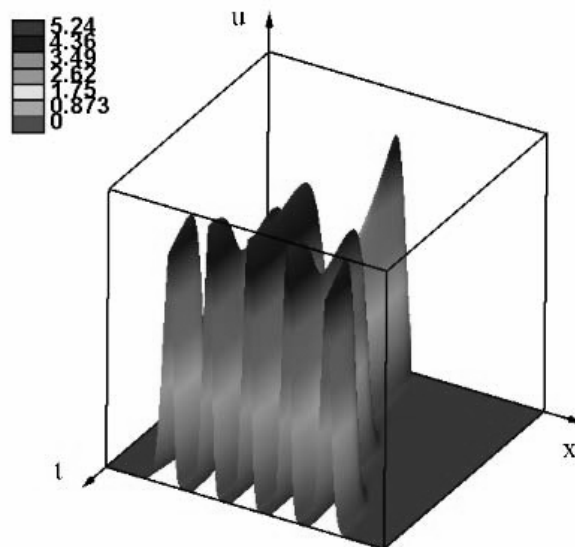


Fig. 2. Propagation of a periodic travelling wave solution of equation (3). The values of parameters: $k = 1$, $a = b = 1$, $\sigma = 0$, $L = 1$, $D = 10^{-5}$, $N = 0.1$, $t = 70$.

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