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High order accuracy scheme for modeling the dynamics of predator and prey in heterogeneous environment

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Abstract. The *aim* of this work is to develop a compact finite-difference approach for modeling the dynamics of predator and prey based on reaction-diffusion-advection equations with variable coefficients. *Methods.* To discretize a spatially inhomogeneous problem with nonlinear terms of taxis and local interaction, the balance method is used. Species densities are determined on the main grid whereas fluxes are computed at the nodes of the staggered grid. Integration over time is carried out using the high-order Runge-Kutta method. *Results.* For the case of one-dimensional annular interval, the finite-difference scheme on the three-point stencil has been constructed that makes it possible to increase the order of accuracy compared to the standard second-order approximation scheme. The results of computational experiment are presented and comparison of schemes for stationary and non-stationary solutions is carried out. We conduct the calculation of accuracy order basing on the Aitken process for sequences of spatial grids. The calculated values of the effective order accuracy for the proposed scheme were greater than the standard two: for the diffusion problem, values of at least four were obtained. Decrease was obtained when directional migration was taken into account. This conclusion was also confirmed for non-stationary oscillatory regimes. *Conclusion.* The results demonstrate the effectiveness of the derived scheme for dynamics of predator and prey system in a heterogeneous environment.

Keywords: compact schemes, heterogeneous environment, predator and prey systems.

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Introduction

Compact schemes allow increasing the order of difference approximations and providing the desired accuracy with minimal computational costs [1,2]. Their development and application in acoustics, hydrodynamics and aerodynamics are described in a number of articles, see reviews [3–7]. For linear problems, the order of approximation is established by substituting the exact solution into difference analogues of the equations and direct expansion in a Taylor series [8]. In the case of nonlinear problems, computational procedures on condensing grids of the Richardson, Runge, Aitken type are used [9].

There are approaches based on difference approximations in space and time, as well as variants of the method of lines in which the difference approximation is carried out over spatial variables, and Runge-Kutta-type methods are used over time. High orders of time integrators [10] allow one to focus only on approximations over spatial coordinates.

In the study of population dynamics models based on reaction-diffusion-advection equations, it is necessary to calculate and analyze stationary solutions, as well as oscillatory regimes for systems describing the interaction of predators and prey [11–14]. The use of high-order schemes for problems in mathematical biology is quite rare. In [3], a compact high-order difference scheme is implemented to solve a one-dimensional reaction-advection-diffusion problem. In [4], an approximation of the three-dimensional convection-diffusion equation is proposed for the case of a non-uniform grid. In [5] finite-difference approximations in time and space coordinates were used for the Kolmogorov–Petrovskii–Piskunov–Fisher equation. To solve reaction-diffusion equations with variable coefficients and a nonlinear source term, a compact fourth-order finite-difference scheme was developed in [6]. In [7], a chemotaxis model for a system with cross-diffusion and a logistic source was considered.

In this paper, the method of lines is used to solve the nonlinear equations of the predator-prey system, similar to the scheme with staggered grids developed in [15, 16]. Species densities are determined on the main grid, and their fluxes are calculated at the nodes of the staggered grid. The discretization of the problem for the ring range is carried out on a three-point stencil. For time integration, the high-order Runge-Kutta method is used.

1. Mathematical model of predator and prey in a heterogeneous environment

The reaction-diffusion-advection equations are used to describe the spatiotemporal interactions between predator and prey [11,13]. In the case of a one-dimensional habitat, the mathematical model can be written as a system of equations for the densities of prey $u(x,t)$ and predator $v(x,t)$ [15, 16]

$$\dot{u} = -q_1' + F_1, \quad q_1 = -k_1 u' + u\varphi_1', \tag{1}$$

$$\dot{v} = -q_2' + F_2, \quad q_2 = -k_2 v' + v\varphi_2', \tag{2}$$

where the dot denotes differentiation with respect to time t, and the prime denotes the derivative with respect to x. The terms F_i ($i = 1,\, 2$) describe the local interaction of species based on the Holling functional response of the second kind, the hyperbolic growth model for prey, and the linear law of predator decline [17]

$$F_1(u,v) = u\left[u\left(1 - \frac{u}{p}\right) - \frac{v}{1+Cu}\right], \quad F_2(u,v) = v\left[-\lambda + \frac{Bu}{1+Cu}\right]. \tag{3}$$

Here $p = p(x)$ is the resource, λ is the mortality rate, B is the predator's growth as a result of contact with the prey, and C allows us to take into account the predator's inertia in searching for, absorbing, and processing the prey.

In the expressions for the flows q_i (formulas (1)–(2)), the first term characterizes diffusion, and the second is responsible for directed migration (taxis) [13, 16]. The function φ_1 includes the taxis of the prey to the resource $p(x)$ nonuniformly distributed along the habitat, migration from individuals of its own species ($-\beta_{11}u$) and from the predator ($-\beta_{12}v$). The function φ_2 describes the taxis of the predator to the prey ($\beta_{21}u$) and the taxis ($-\beta_{22}v$) from the concentration of predators [16]:

$$\varphi_1 = \alpha p - \beta_{11}u - \beta_{12}v, \quad \varphi_2 = \beta_{21}u - \beta_{22}v. \tag{4}$$

The diffusion coefficients k_i and directional migration α, β_{ij} $(i, j = 1, 2)$ are non-negative values.

The system (1)–(4) is supplemented by periodicity conditions at $x = 0$ $(x = a)$:

$$\begin{aligned} u(0,t) = u(a,t), \quad q_1(0,t) = q_1(a,t), \\ v(0,t) = v(a,t), \quad q_2(0,t) = q_2(a,t). \end{aligned} \tag{5}$$

Initial conditions are given for the species densities

$$u(x,0) = u^0(x), \quad v(x,0) = v^0(x). \tag{6}$$

2. High-order accuracy difference scheme

In the works [15, 16] a finite difference scheme for solving population dynamics problems based on the finite difference method using staggered grids to calculate fluxes is described. To discretize the equations (1)–(6) along the spatial coordinate on the interval $[0, a]$, we introduce a uniform grid $x_r = rh$, $r = 0, \ldots, n$, $h = a/n$. At its nodes, the densities of species u, v and the local interaction terms F_i, $i = 1, 2$, are calculated. To determine fluxes, we use a staggered grid $x_{r-\frac{1}{2}} = rh - h/2$, $r = 1, \ldots, n$. Next we define the operators of the difference derivative and the calculation of the average

$$(dy)_r = \frac{y_{r+\frac{1}{2}} - y_{r-\frac{1}{2}}}{h}, \quad (\delta y)_r = \frac{y_{r+\frac{1}{2}} + y_{r-\frac{1}{2}}}{2}, \tag{7}$$

$$(dy)_{r-\frac{1}{2}} = \frac{y_r - y_{r-1}}{h}, \quad (\delta y)_{r-\frac{1}{2}} = \frac{y_r + y_{r-1}}{2}. \tag{8}$$

We apply the approach [1, 8] to approximate the equations (1)–(4), using the integro-interpolation method (balance method) [8] and Simpson's formula. We integrate (1) over the interval $[x_{r-\frac{1}{2}}, x_{r+\frac{1}{2}}]$, and replace the time derivative and F_1 with the half-sum of the values in the neighboring nodes of the main grid at the nodes of the staggered grid $x_{r-\frac{1}{2}}$. As a result, we have

$$0 = \int\limits_{x_{r-\frac{1}{2}}}^{x_{r+\frac{1}{2}}} (-q_1' - \dot{u} + F_1)dx \approx -q_1(x_{r+\frac{1}{2}}) + q_1(x_{r-\frac{1}{2}}) + (x_{r+\frac{1}{2}} - x_{r-\frac{1}{2}})\left[-\Psi\dot{u} + \Psi F_1\right]_r, \tag{9}$$

where the grid operator Ψ is defined by the following formula:

$$\Psi y_r = \frac{1}{12}\left(y_{r-1} + 10y_r + y_{r+1}\right).$$

Then from (9) we get

$$\Psi\dot{u}_r = -dq_{1,r} + \Psi F_{1,r}, \quad F_{1,r} = F_1(u_r, v_r), \quad r = 1, \ldots, n. \tag{10}$$

Using the second difference derivative

$$\Lambda y_r = \frac{y_{r+1} - 2y_r + y_{r-1}}{h^2}, \quad r = 1, \ldots, n, \tag{11}$$

equation (10) is rewritten as follows:

$$\left(1+\frac{h^2}{12}\Lambda\right)\dot{u}_r = -dq_{1,r} + \left(1+\frac{h^2}{12}\Lambda\right)F_{1,r}, \tag{12}$$

and $F_{1,r}$ is calculated using the formula:

$$F_{1,r} = u_r\left[u_r\left(1-\frac{u_r}{P_r}\right) - \frac{v_r}{1+Cu_r}\right], \quad P_r = \left[\frac{1}{h}\int\limits_{x_{r-\frac{1}{2}}}^{x_{r+\frac{1}{2}}}\frac{dx}{p(x)}\right]^{-1}. \tag{13}$$

As a result of integrating the second equation (1) over the segment $[x_{r-1}\ x_r]$ for the flow q_i we obtain

$$q_{1,r-\frac{1}{2}} = (-k_1 du + \delta u d\varphi_1)_{r-\frac{1}{2}}. \tag{14}$$

Taking into account (4), (7) and (8) we have

$$q_{1,r-\frac{1}{2}} = [-k_1 du + \alpha dp\delta u - \beta_{11} du\delta u - \beta_{12} dv\delta u]_{r-\frac{1}{2}}. \tag{15}$$

Similarly, equations for the predator density v are derived from (2)

$$\left(1+\frac{h^2}{12}\Lambda\right)\dot{v}_r = -dq_{2,r} + \left(1+\frac{h^2}{12}\Lambda\right)F_{2,r}, \quad F_{2,r} = v_r\left[-\lambda_r + \frac{Bu_r}{1+Cu_r}\right], \tag{16}$$

and the expression for the flow q_2 at the nodes of the staggered grid is given by the formula

$$q_{2,r-\frac{1}{2}} = [-k_2 dv + \beta_{21} dv\delta u - \beta_{22} dv\delta v]_{r-\frac{1}{2}}. \tag{17}$$

As a result of discretization with respect to the spatial variable, we obtain a system of equations with unknowns $u_r(t)$, $v_r(t)$, $r = 1,\dots,n$, corresponding to the distribution densities of the population u, v at the nodes x_r. The system (12), (13), (16), $r = 1,\dots,n$ and (15), (17), $r = 1,\dots,n$ can be written in vector form

$$\dot{U} = -M^{-1}D_1 + G_1, \quad \dot{V} = -M^{-1}D_2 + G_2, \tag{18}$$

here

$$U = (u_1, ..., u_n), \quad V = (v_1, ..., v_n),$$

$$D_i = [dq_{i,1}, ..., dq_{i,n}], \quad G_i = [F_{i,1}, ..., F_{i,n}], \quad i = 1, 2,$$

and due to the conditions of periodicity $u_0 \equiv u_n$, $u_{n+1} \equiv u_1$, $v_0 \equiv v_n$, $v_{n+1} \equiv v_1$, $q_{i,n+\frac{1}{2}} \equiv q_{i,\frac{1}{2}}$. The matrix M of size n^2 has the form

$$M = \frac{1}{12}\begin{bmatrix} 10 & 1 & \cdots & 0 & 1 \\ 1 & 10 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & 10 & 1 \\ 1 & 0 & \cdots & 1 & 10 \end{bmatrix}. \tag{19}$$

The constructed finite-dimensional model can be written as

$$\dot{W} = \Phi(W), \quad W(0) = W_0, \tag{20}$$

here $W = (U, V)$ — vector of values of variables at grid nodes. The initial data for system (20) follow from (6):

$$W_0 = (U_0, V_0) = (u_1^0, ..., u_n^0, v_1^0, ..., v_n^0). \tag{21}$$

To integrate the (20) system over time, the high-order Punge–Kutta method is used (the ode89 time integrator from MATLAB). The second-order spatial discretization is obtained from (18) by replacing M with the identity matrix:

$$\dot{U} = -D_1 + G_1, \quad \dot{V} = -D_2 + G_2. \tag{22}$$

3. Results of computational experiments

To evaluate the accuracy of approximations (18) and (22), calculations of the stationary and oscillatory modes of the (1)–(6) system were performed for fixed values of the following parameters: $k_1 = 0.02$, $k_2 = 0.01$, $B = 4$, $\beta_{12} = \beta_{11} = \beta_{22} = 0$. The number of nodes in the area n, the mortality parameter λ, the value C, the migration coefficients α and β_{21} varied. The resource distribution was specified on the interval [0, 1] as

$$p(x) = 1 - 0.2\sin 2\pi x + 0.2\sin 4\pi x. \tag{23}$$

The experiment was carried out on grids n_i, $n_{i+1} = 2n_i$, $n_{i+2} = 4n_i$, and W_i is the numerical solution on grid n_i. The effective order of accuracy η based on the Aitken process ($h_i = 1/n_i$) was calculated by the formula

$$\eta_i = \log_2 \frac{S_i}{S_{i+1}}, \quad S_i = \|W_i - W_{i-1}\|,$$

where S_i are the norms of the difference between the numerical solutions of W on grids n_i and n_{i-1}.

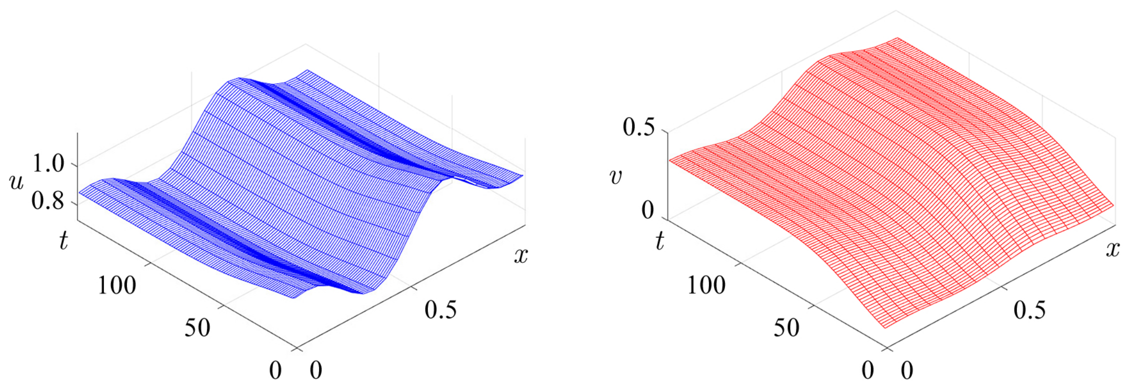

Fig 1. Spatial-temporal distribution of prey u (left) and predator v (right) for $\alpha = 0.005$, $\beta_{21} = 0.01$, $\lambda = 1.1$, $C = 2.5$, $n = 20$

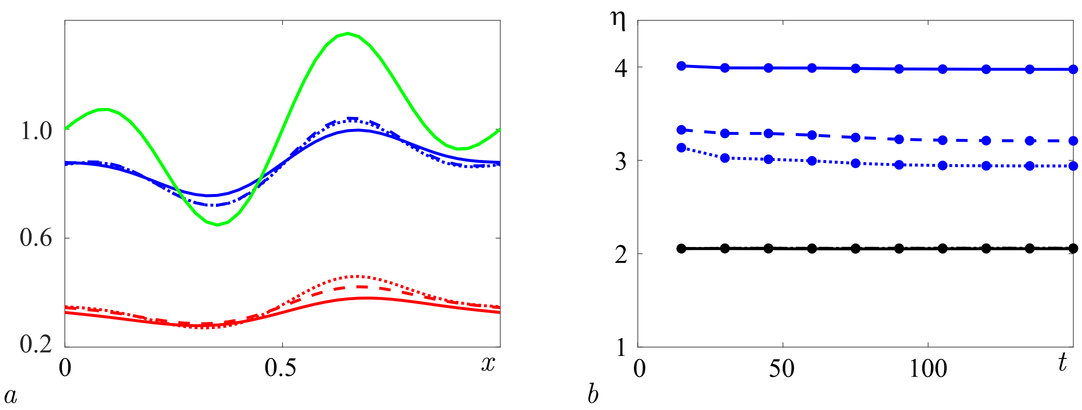

Fig 2. a — Stationary distributions of prey $u(x)$ (blue curves), predator $v(x)$ (red), resource $p(x)$ (green); b — order of accuracy values at various times for $PC2$ (black), $PC4$ (blue): $\alpha = 0.001$, $\beta_{21} = 0.005$ (solid curves), $\alpha = 0.005$, $\beta_{21} = 0.005$ (dashed line) and $\alpha = 0.005$, $\beta_{21} = 0.01$ (dots); $\lambda = 1.1$, $C = 2.5$ (color online)

Table 1. Efficient order of standard scheme ($PC2$) and high order scheme ($PC4$); $\lambda = 1.1$, $C = 2.5$, $n_1 = 10$, $n_2 = 20$, $n_3 = 40$ (Aitken process)

α	β_{21}	$PC2$	$PC4$
0.001	0.005	2.054	3.9745
0.005	0.005	2.0588	3.209
0.005	0.01	2.0589	2.9398

The Table and Figs. 1, 2 present the results of calculations for establishing stationary solutions with coexisting predator and prey at $\lambda = 1.1$, $C = 2.5$ for a number of values of the migration parameters α and β_{21}. Fig. 1 shows the change in spatial distributions over time at $\alpha = 0.005$, $\beta_{21} = 0.01$. For three sets of migration parameters α and β_{21}, Fig. 2 shows stationary distributions (a) and calculated values of the effective order of accuracy at different moments in time (b). Depending on the values of the parameters, different distributions of predator and prey are realized. In the Table, column $PC2$ corresponds to the calculation of order η using the standard scheme of the second order of accuracy, and $PC4$ — calculations using the scheme of the increased order of accuracy. At $\alpha = 0.001$, $\beta_{21} = 0.005$ the value of η is almost equal to four. With an increase in migration parameters, the value of η decreases.

With a decrease in the mortality rate ($\lambda = 0.95$), the stationary solution of the coexisting

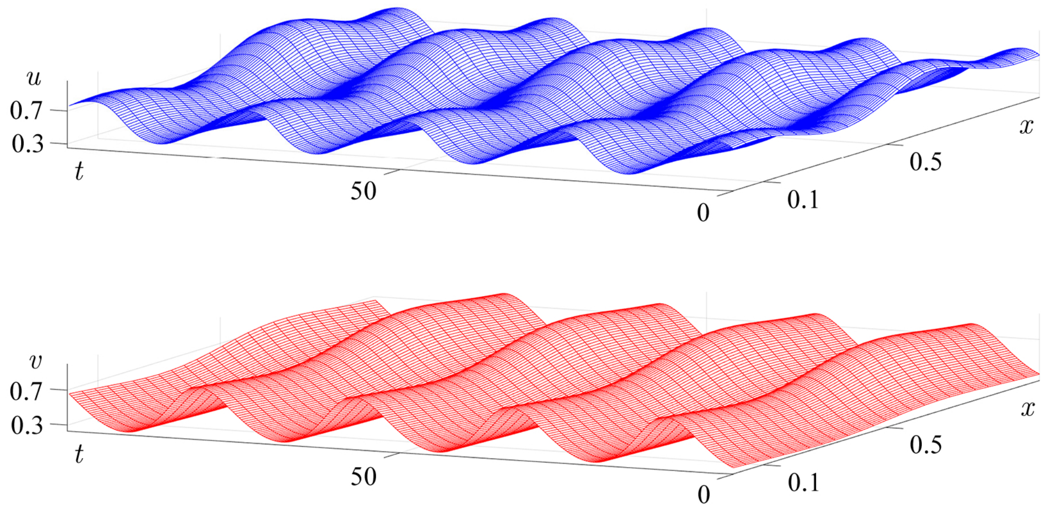

Fig 3. Spatial-temporal distribution of u (top) and v (bottom) for $C = 2.5$, $\alpha = 0.01$, $\beta_{21} = 0$, $\lambda = 0.95$, $n = 24$

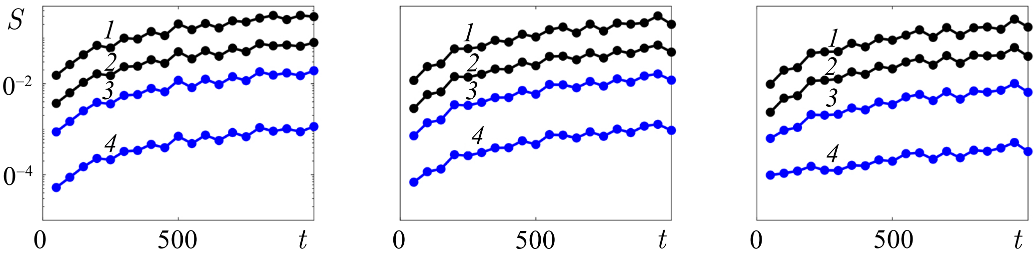

Fig 4. Graphs of changes S_i over time for $\alpha = 0.001$ (left), $\alpha = 0.005$ (center), $\alpha = 0.01$ (right): high-order accuracy scheme (blue color), second order accuracy scheme (black), $n_i = 24$ (curves *1* and *3*), $n_i = 48$ (*2* and *4*); $\beta_{21} = 0$, $\lambda = 0.95$, $C = 2.5$ (color online)

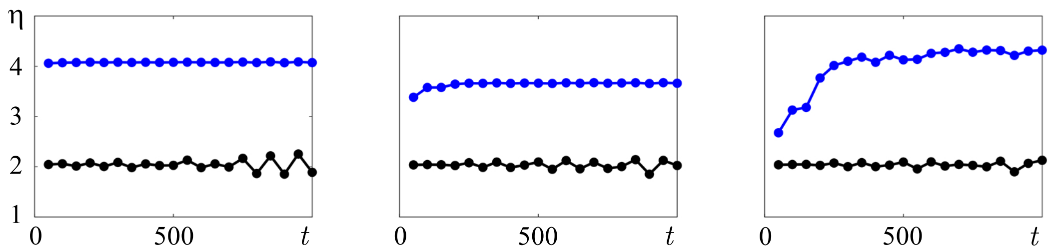

Fig 5. Graphs of changes η over time for $\alpha = 0.001$ (left), $\alpha = 0.005$ (center), $\alpha = 0.01$ (right): high-order accuracy scheme (blue color), second order accuracy scheme (black); $\beta_{21} = 0$, $\lambda = 0.95$, $C = 2.5$ (color online)

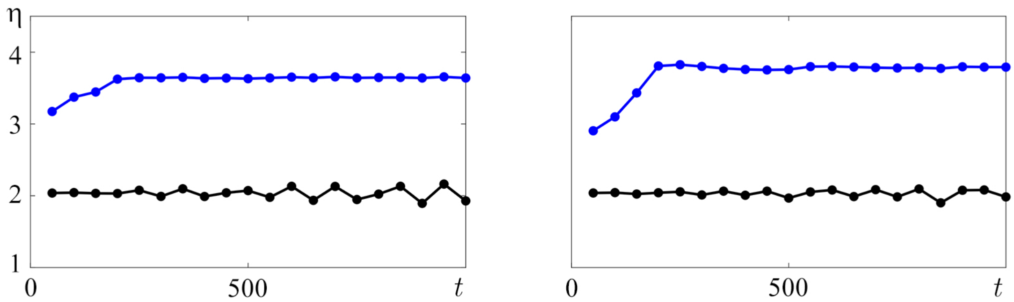

Fig 6. Change in time of the order accuracy η for $\beta_{21} = 0.005$ (left), $\beta_{21} = 0.01$ (right): high-order accuracy scheme (blue), second order accuracy scheme (black); $\alpha = 0.005$, $\lambda = 0.95$, $C = 2.5$ (color online)

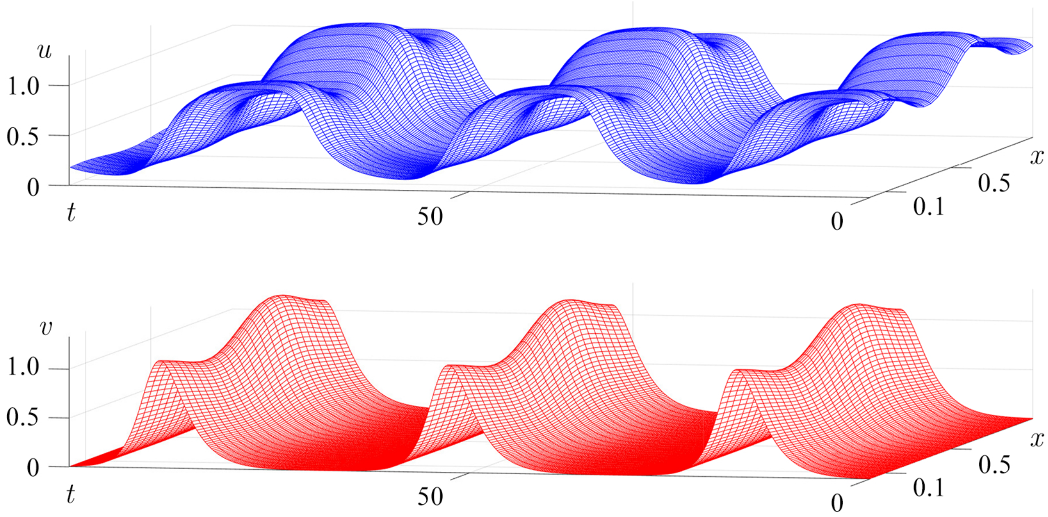

Fig 7. Spatial-temporal distribution of u (top) and v (bottom) for $C = 2$, $\alpha = 0.01$, $\beta_{21} = 0$, $\lambda = 0.95$, $n = 24$

predator and prey becomes unstable and periodic oscillations of the species arise (Fig. 3), that is, traveling waves of population densities are realized in the area. Fig. 4–7 shows the results of calculations of oscillatory modes and calculations of effective orders of accuracy on grids $n =$ 12, 24, 48 for $\lambda = 0.95$. Fig. 4, 5 shows calculations of the norm S and the order of accuracy η at different points in time for three values of α in the absence of taxis ($\beta_{21} = 0$). The difference norm for $n = 12, 24$ in the case of the proposed scheme is always less than the difference norm for the second-order accuracy scheme for $n = 24, 48$, and comparable results are obtained only when using grids $n = 48, 96$.

For the second-order scheme, on a large time interval [0...1000], the value of S increases, and oscillations of the calculated order of accuracy are visible. This is the result of the accumulated error when calculating the cycle on a coarse grid. For the high-order scheme, with an increase in the migration parameter α, some time is required to establish η. For the problem taking into account taxis ($\beta_{21} = 0.005, 0.01$), the results of calculating the order of accuracy are shown in Fig. 6. With a twofold increase in β_{21}, the order of accuracy changes insignificantly.

The influence of the parameter C on the nature of periodic oscillations is illustrated by Fig. 3 and 7. For close values of the predator inertia parameter $C = 2, 2.5$, oscillatory modes with different amplitudes and periods are realized. The scheme of a high order of accuracy allows for calculations of relaxation oscillations on fairly coarse grids ($n = 24$), when the predator is practically absent for significant periods of time (Fig. 7).

Conclusion

The paper proposes a simple to implement compact numerical scheme for solving a system of parabolic equations with nonlinear advective and source terms. The problem of the dynamics of predator and prey populations in a heterogeneous environment is considered. The results of calculating stationary distributions of species and oscillatory modes are presented. The calculated values of the effective order of accuracy showed the advantages of the proposed scheme compared to the classical second-order approximation in calculating stationary and non-stationary solutions. The scheme of a higher order of accuracy allows using smaller grids. This is important when calculating stationary distributions using the establishment method and when calculating non-stationary processes such as traveling waves. This is especially important when analyzing population dynamics problems with highly heterogeneous resource distributions in the environment and in the case of several spatial variables.

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