Available online at www.sciencedirect.com
SCIENCE DIRECT®

Mathematical Biosciences 186 (2003) 79–91

Mathematical Biosciences

www.elsevier.com/locate/mbs

An exactly solvable model of population dynamics with density-dependent migrations and the Allee effect

Sergei Petrovskii [a,b,*], Bai-Lian Li [b]

[a] *Shirshov Institute of Oceanology, Russian Academy of Science, Nakhimovsky Prospekt 36, Moscow 117218, Russia*
[b] *Ecological Complexity and Modeling Laboratory, Department of Botany and Plant Sciences, University of California, Riverside, CA 92521-0124, USA*

Received 1 October 2002; received in revised form 7 April 2003; accepted 2 July 2003

Abstract

We consider a single-species model of population dynamics allowing for migrations and the Allee effect. Two types of migration are taken into account: one caused by environmental factors (e.g., a passive transport with the wind or water current) and the other associated with biological mechanisms. While the first type is apparently density-independent, the speed of migration in the second one can depend on the population density. Mathematically, this model consists of a non-linear partial differential equation of advection–diffusion-reaction type. Using an appropriate change of variables, we obtain an exact solution of the equation describing propagation of travelling population fronts. We show that, depending on parameter values and thus on the relative intensity of density-dependent and density-independent factors, the direction of the propagation can be different thus describing either species invasion or species retreat.

Keywords: Advection; Migration; Allee effect; Diffusion-reaction equation; Exact solution; Biological invasion

---

1. Introduction

Spatial aspects of population dynamics, particularly the processes and mechanisms underlying species dispersion and the patterns of spread during biological invasions have been a focus of intense research during the last decade [1–6]. Invasion of exotic species often results in dramatic

---

[*] Corresponding author. Address: Shirshov Institute of Oceanology, Russian Academy of Science, Nakhimovsky Prospekt 36, Moscow 117218, Russia. Fax: +7-095 124 5983.
E-mail address: spetrovs@sio.rssi.ru (S. Petrovskii).

0025-5564/$ - see front matter © 2003 Published by Elsevier Inc.
doi:10.1016/S0025-5564(03)00098-1

changes in native community and, consequently, in a major threat to biodiversity. Therefore, a highly practical and theoretically important question is what environmental and biological factors can affect the rate of invasion either speeding up or slowing down the spreading of invasive species. This issue is usually treated in terms of diffusion-reaction models [7–9] or their modifications [5,10] which are essentially based on the assumption that the motion of individuals of given population is random and isotropic, i.e., without any preferred direction.

There is, however, another type of dynamics when the individuals exhibit a correlated motion towards certain direction. The origin of this motion can be different, and there are at least two apparently different mechanisms resulting in the species transport. We will call ‘advection’ the correlated motion caused by purely environmental factors such as wind in case of seeds or pollen spreading or water current in case of plankton communities, and we will call ‘migration’ the transport caused by biological interactions. Evidently, species transport due to the advection is density-independent. As for migration, however, there are certain indications that the speed of the individual motion can increase with the population density [1]. Note that, since a focus of this paper is on the factors that can affect the rate of species invasion, we are not much interested in the periodical return migrations which are typical for many bird and fish species. A point of interest is the migration occurring on a smaller spatial scale when individuals or groups of individuals of given species move from the regions with high population density towards the regions where given species is either absent or exists at low population density [11]. Although these small-scale migrations are often interpreted in terms of random motion, cf. ‘stratified diffusion’ [1,12], this phenomenon exhibits apparent spatial anisotropy. Interestingly, this mechanism of species dispersion usually comes to operation when the population density becomes sufficiently high [2].

The goal of this paper is to study the interplay between diffusion and advection/migration regarding species invasion, spatiotemporal dynamics of the population being described by a non-linear partial differential equation of advection–diffusion-reaction type. An issue of particular interest is under what conditions such an interplay can block or reverse the species invasion.

Once the main processes underlying given phenomenon are identified and a mathematical model is developed, it becomes a major problem to assess its properties for different parameter values. Numerical simulations usually provide only meagre information on that account and analytical solutions are rare, especially when the model is non-linear. Some examples of ad hoc solutions to non-linear partial differential equations can be found in [13–15]. An approach first considered by Hopf [16] and later used by a few other authors [17–19] (for a more general framework see also [20]) is a suitable change of variables, which can linearize the equation under study. In our work, we apply this approach to a non-linear advection–diffusion-reaction equation taking into account the effect of density-dependent migrations and the Allee effect on population growth [21,22] and obtain an exact solution describing propagation and interaction of travelling population fronts.

The paper is organized as follows. In Section 2 we describe the model that will be used to study the interplay between diffusion and advection/migration. In Section 3 we describe the method to obtain exact solutions of non-linear partial differential equations and apply it to the equation without migrations. In Section 4 the interplay between diffusion and advection/migration is analyzed based on an exact solution of non-linear advection–diffusion-reaction equation. The last section gives a discussion of our results.

2. Main equations

Following the approach widely used in theoretical population dynamics, we assume that a population can be described by the population density U. In a general case, U depends on the position $\mathbf{R} = (X, Y, Z)$ in space and time T. There are two basically different mechanisms making U to change with time: the one associated with local processes such as birth, death and predation, and the other associated with the redistribution of the population in space due to the motion of its individuals. Correspondingly, in a rather general case the dynamics of a given population can be described by the following equation:

$$\frac{\partial U(\mathbf{R},T)}{\partial T} = -\operatorname{div}\mathbf{J} + f(U)U, \tag{1}$$

where $\mathbf{J}$ is the population density flux and the second term allows for the local processes, $f(U)$ being per capita growth rate. In the case $f(U) \equiv 0$, Eq. (1) has the form of the conservation law; it means that the total number of the individuals does not change with time unless the processes of birth and death are taken into account.

The form of the flux $\mathbf{J}$ essentially depends on the properties of the motion. In the case that the motion of the individuals can be regarded as random, the flux is usually assumed to be given by the following equation:

$$\mathbf{J} = -D\nabla U(\mathbf{R},T), \tag{2}$$

where D is diffusivity [23–25]. In this case Eq. (1) takes the form of the diffusion-reaction equation which is of common use in theoretical studies, cf. [2,25,26] and references therein.

However, the motion of individuals cannot always be regarded as random. Another widely observed dynamics is advection/migration when the individuals exhibit a correlated motion toward a certain direction. Assuming for the sake of simplicity that at given position all the individuals move with the same speed $\mathbf{A}$, we immediately obtain that $\mathbf{J} = \mathbf{A}U(\mathbf{R},T)$. In a more general case, when the correlated motion is combined with the random motion, the population density flux is given by the following equation:

$$\mathbf{J} = \mathbf{A}U(\mathbf{R},T) - D\nabla U(\mathbf{R},T). \tag{3}$$

For the rest of this paper we restrict our consideration to the one-dimensional case. The spatiotemporal dynamics of a given population allowing for migrations and diffusion is then described the following equation:

$$\frac{\partial U(X,T)}{\partial T} + \frac{\partial(AU)}{\partial X} = D\frac{\partial^2 U}{\partial X^2} + f(U)U, \tag{4}$$

where A is positive in the case that advection/migration is going in the direction of axis x and negative otherwise.

It is well-known that, for a wide class of initial conditions, Eq. (4) describes the propagation of travelling population fronts [27,28]. Concerning the dynamics of real ecological communities, that may correspond either to species invasion (when the front moves towards the region where a given species is absent) or to species retreat (when the front moves towards the region where a given species is at its carrying capacity). Interestingly, each type of underlying individual motion (random or correlated) can result in a similar phenomena, i.e., either in species invasion or species retreat. For the correlated motion, these two options are obvious; whether the species is actually invading or retreating depends on the sign of the speed of migration A. For the random motion, invasion of a species due to propagation of population fronts was first studied in [29,30], for an account of recent advances see [2]. A possibility of species retreat resulting from increasing Allee effect was considered in [4], for a more general discussion see also [27].

In theoretical studies, these two types of motion (random or correlated) are usually considered separately (but see [11]). In a real ecological community, however, the individuals are likely involved into a combination of these two types of motion. The following question may arise here: what can be the interplay between these two types of motion regarding species invasion? In particular, can advection (e.g., due to the impact of wind) block the species spreading in the case when the invasion would otherwise take place due to random motion?

To address this issue, we study analytically the properties of an exact solution of the advection–diffusion-reaction equation (4) describing propagation of travelling fronts. For the sake of analytical tractability, two additional assumptions are to be made. First, we assume that the growth rate is damped by the Allee effect [21,22]. Following [4], we choose the square polynomial to parameterize the per capita growth rate:

$$f(U) = \alpha(U - U_0)(K - U), \tag{5}$$

where K is the species carrying capacity, U_0 is the 'measure' of the Allee effect [4] and α is a coefficient. We mainly restrict our attention to the case $0 < U_0 < K$ which corresponds to the 'strong' Allee effect [7,31] when the growth rate becomes negative for sufficiently small population density.

Second, for the speed of migration, we assume that it is given by the following equation:

$$A = A_0 + A_1 U, \tag{6}$$

where A_0 and A_1 are parameters, A_0 is the speed of advection (e.g., due to the impact of wind or water current) and $A_1 U$ is the speed of migration due to biological mechanisms. For convenience, we will call parameter A_1 the per capita migration speed.

From (4)–(6), we obtain

$$\frac{\partial U(X,T)}{\partial T} + (A_0 + 2A_1 U)\frac{\partial U}{\partial X} = D\frac{\partial^2 U}{\partial X^2} + \alpha U(U - U_0)(K - U). \tag{7}$$

The dimensionless variables

$$u = \frac{U}{K}, \quad t = T\alpha K^2, \quad x = X\sqrt{\frac{\alpha K^2}{D}}, \tag{8}$$

are substituted to transform Eq. (7) as follows:

$$u_t + (a_0 + a_1 u)u_x = u_{xx} - \beta u + (1 + \beta)u^2 - u^3, \tag{9}$$

where $\beta = U_0/K$, $a_0 = A_0 K^{-1}(\alpha D)^{-1/2}$, $a_1 = 2A_1(\alpha D)^{-1/2}$ are dimensionless parameters, and subscripts x and t stand for the partial derivatives with respect to dimensionless space and time, respectively. Eq. (9) will be studied in the unbounded domain with the following conditions at infinity: the species is absent for $x \to -\infty$ and the species is at its carrying capacity for $x \to +\infty$.

3. No-migration case

Although the main goal of this paper is to study the interplay between the advection/migration and the diffusive spread of the population (which will be done in the next section), for the sake of clarity we begin with the case when the individuals perform only random motion. In this case $a_0 = a_1 = 0$ and Eq. (9) reduces to

$$u_t = u_{xx} - \beta u + (1 + \beta)u^2 - u^3. \tag{10}$$

It was shown in [17,19,32] using different methods that Eq. (10) has an exact solution in the following form:

$$u(x,t) = \frac{\beta \exp(\lambda_1 \xi_1) + \exp(\lambda_2 \xi_2)}{1 + \exp(\lambda_1 \xi_1) + \exp(\lambda_2 \xi_2)}, \tag{11}$$

where $\xi_i = x - n_i t + \phi_i$, $n_i = \sqrt{2}(1 + \beta) - 3\lambda_i$, $i = 1, 2$,

$$\lambda_1 = \frac{\beta}{\sqrt{2}}, \quad \lambda_2 = \frac{1}{\sqrt{2}} \tag{12}$$

and $\phi_{1,2}$ are arbitrary constants. Since $u(x,t)$ must be non-negative for any x and t, solution (11) is valid only for $\beta \geqslant 0$. The spatial distribution of the population as given by (11) for different time is shown in Fig. 1. It must be mentioned here that, although solution (11) formally corresponds to a

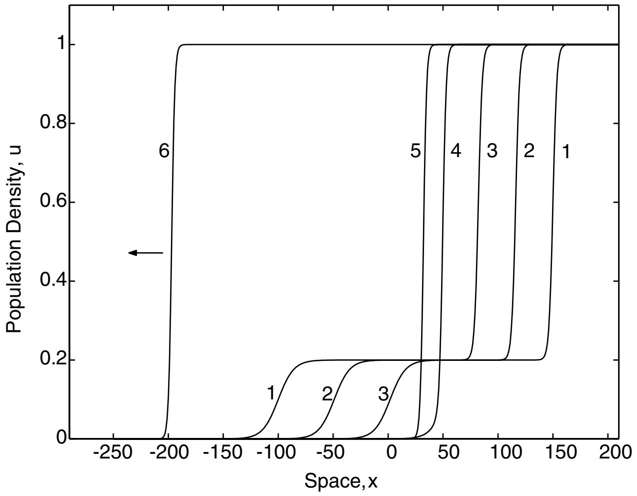

Fig. 1. Population density vs space at different moments as given by the exact solution (11) of diffusion-reaction equation (10); curve 1 for $t = 0$, curve 2 for $t = 40$, curve 3 for $t = 80$, curve 4 for $t = 120$, curve 5 for $t = 160$, curve 6 for $t = 700$. Parameters are $\beta = 0.2$, $\phi_1 = 100$, $\phi_2 = -100$. For small time, the solution describes the propagation of two 'partial' population fronts connecting the homogeneous stable steady states $u \equiv 0$ and $u \equiv 1$ to the unstable state $u \equiv \beta$, cf. upper and lower parts of curves 1–3. For large time, the solution describes propagation of a single population front, cf. curves 4–6, the arrow indicating the direction of further propagation. While the 'partial' fronts always propagate towards each other (see [17,19] for details), the direction of propagation of the population front connecting the states $u \equiv 0$ and $u \equiv 1$ (curves 4–6) depends on parameter β, cf. conditions (15).

specific initial condition (which is immediately obtained from (11) setting $t = 0$, cf. curve 1 in Fig. 1), convergence of initial conditions from a wide class to solution (11) was shown in [19].

Since $\lambda_1 < \lambda_2$, it is readily seen that, in the large-time limit (when the transients die out, cf. curves 4–6 in Fig. 1 and see [17,19] for details) or for suitable values of ϕ_1, ϕ_2, solution (11) reduces to

$$u(x,t) \simeq \frac{\exp(\lambda_2\xi_2)}{1+\exp(\lambda_2\xi_2)}, \tag{13}$$

thus describing a travelling population front propagating with the speed n_2 given by the following equation:

$$n_2 = \sqrt{2}(1+\beta) - \frac{3}{\sqrt{2}} = \frac{2\beta-1}{\sqrt{2}}. \tag{14}$$

The direction of the propagation can be either positive or negative:

$$\text{(a)}\quad n_2 < 0 \quad \text{for } \beta < \frac{1}{2} \quad \text{and} \quad \text{(b)}\quad n_2 > 0 \quad \text{for } \beta > \frac{1}{2}. \tag{15}$$

Thus, under condition (15a) the front propagates to the region where the species is absent, which corresponds to species invasion, cf. Fig. 1; under condition (15b) the front propagates to the region where the species is at its carrying capacity, which corresponds to species retreat. Conditions (15) are in full agreement with more general mathematical considerations [27].

The fact that (11) is an exact solution of Eq. (10) can be checked immediately by substituting it into (10). To arrive at solution (11) from Eq. (10), various approaches are available. In the original paper [17], solution (11) was obtained by using a formal perturbation scheme. Later, it was shown in [32] that (11) can be obtained by expanding the solution into Dirichlet series. In this paper, however, we will use another approach [16,19] which is much less laborious, leads to essentially the same result, and has been successfully applied to a few other non-linear problems as well, cf. [16,18,33,34] and also see [35] for less straightforward examples.

Since we are going to apply to the general Eq. (9) the same method that was used in [19] to obtain the exact solution (11) of Eq. (10), it is convenient to give a brief description here. Let us introduce a new variable $w(x,t)$ defined by the following equation:

$$u(x,t) = \mu\frac{w_x}{w+\sigma}, \tag{16}$$

where $\mu \neq 0$ is a coefficient (the case $\mu = 0$ would correspond to the trivial solution $u(x,t) \equiv 0$) and σ is a constant. In so far as we are, for biological reasons, primarily interested in bounded solutions of Eq. (10), σ is included into the denominator of (16) in order to avoid singularities. If we assume that function w is semi-bounded, i.e., there exists a certain $\bar{w}$ that either (i) $w(x,t) \leqslant \bar{w}$ or (ii) $w(x,t) \geqslant \bar{w}$ for $\forall x$, t, then constant σ can have an arbitrary value under the constraint $\sigma < -\bar{w}$ or $\sigma > -\bar{w}$ corresponding to the cases (i) and (ii), respectively.

Substitution of (16) to (10) leads to the following equation:

$$\begin{aligned}&[(2-\mu^2)w_x^3](w+\sigma)^{-3} + w_x[w_t - 3w_{xx} + (1+\beta)\mu w_x](w+\sigma)^{-2} + [w_{xxx} - \beta w_x - w_{xt}]\\&\quad \times (w+\sigma)^{-1} = 0,\end{aligned} \tag{17}$$

which, as constant σ is (nearly) arbitrary and different powers of $(w+\sigma)$ are linearly independent, is equivalent to the following system:

$$w_{xt} = w_{xxx} - \beta w_x, \tag{18}$$

$$w_t = 3w_{xx} - (1+\beta)\mu w_x, \tag{19}$$

$$\mu = \pm\sqrt{2}. \tag{20}$$

Without loss of generality, we choose plus in Eq. (20) (minus would correspond to the change $x \to -x$). Taking the partial derivative of Eq. (19) with respect to x in order to eliminate w_{xt} from Eq. (18), then from the system (18)–(20) we arrive at

$$w_{xxx} - \frac{1+\beta}{\sqrt{2}} w_{xx} + \frac{\beta}{2} w_x = 0, \tag{21}$$

$$w_t = 3w_{xx} - \sqrt{2}(1+\beta) w_x. \tag{22}$$

The solution of linear equation (21) has the following form:

$$w(x,t) = f_0(t) + f_1(t)\mathrm{e}^{\lambda_1 x} + f_2(t)\mathrm{e}^{\lambda_2 x}, \tag{23}$$

where $\lambda_{1,2}$ are the roots of the square polynomial:

$$\lambda^2 - \frac{1+\beta}{\sqrt{2}}\lambda + \frac{\beta}{2} = 0 \tag{24}$$

and thus $\lambda_{1,2}$ are given by (12).

To obtain functions $f_{0,1,2}$, we substitute Eq. (23) into (22). That leads to the following result:

$$f_0(t) = C_0, f_i(t) = C_i \mathrm{e}^{\gamma_i t} \quad \text{where } \gamma_i = 3\lambda_i^2 - \sqrt{2}(1+\beta)\lambda_i, \quad i = 1,2 \tag{25}$$

and $C_{0,1,2}$ are arbitrary constants. Note that the form of $w(x,t)$ defined by Eqs. (23)–(25) appears to be in agreement with our earlier assumption about semi-boundedness of w; thus our analysis has been consistent.

From (16), (23) and (25), we obtain

$$u(x,t) = \sqrt{2}\frac{C_1\lambda_1 \exp(\lambda_1 x + \gamma_1 t) + C_2\lambda_2 \exp(\lambda_2 x + \gamma_2 t)}{(C_0+\sigma) + C_1 \exp(\lambda_1 x + \gamma_1 t) + C_2 \exp(\lambda_2 x + \gamma_2 t)}. \tag{26}$$

Obviously, for $u(x,t)$ to be positive, it is necessary that $C_0+\sigma$, C_1 and C_2 have the same sign, i.e., either $C_0+\sigma > 0$, $C_{1,2} > 0$ or $C_0+\sigma < 0$, $C_{1,2} < 0$. Thus, introducing new constants as $\phi_i = (1/\lambda_i)\ln(C_i/[C_0+\sigma])$, $i = 1, 2$ and taking into account that $\sqrt{2}\lambda_{1,2} = u_{1,2}$ (where $u_1 = \beta$ and $u_2 = 1$ are the steady states of the spatially homogeneous system), from Eq. (26) we arrive at (11).

4. Interplay between diffusion and migration

Now we are going to apply the method described in the previous section to obtain an exact solution of the advection–diffusion-reaction equation (9). The exact solution will be then used to study the interplay between the advection/migration and the diffusive spreading of the population.

We begin by considering the cases of density-independent migration (advection) and density-dependent migration separately proceeding then to a general case.

4.1. Density-independent migration

In the case that the speed of the species migration does not depend on the population density, e.g., when drifting with the wind, the dynamics of the population are described by the following equation:

$$u_t + a_0 u_x = u_{xx} - \beta u + (1+\beta)u^2 - u^3, \tag{27}$$

where a_0 is the (dimensionless) speed of advection.

Considering travelling wave coordinates, $(x,t) \to (z,t)$ where $z = x - a_0 t$, so that $u = \tilde{u}(z,t)$, from Eq. (27) we obtain

$$\tilde{u}_t = \tilde{u}_{zz} - \beta\tilde{u} + (1+\beta)\tilde{u}^2 - \tilde{u}^3. \tag{28}$$

Eq. (28) coincides with (10) and thus the exact solution (11) gives also an exact solution of (28) with the obvious change $x \to z$. In particular, in the large-time limit when the solution describes a single travelling population front, it reads as follows:

$$u(x,t) = \tilde{u}(x - a_0 t, t) \simeq \frac{\exp\{\lambda_2[x - (n_2 + a_0)t + \phi_2]\}}{1 + \exp\{\lambda_2[x - (n_2 + a_0)t + \phi_2]\}}. \tag{29}$$

Here $n_2 + a_0$ is the speed of the front where n_2 is given by Eq. (14); $n_2 + a_0 < 0$ corresponds to the species invasion, $n_2 + a_0 > 0$ corresponds to the species retreat. Advection enhances the species invasion in case $a_0 < 0$ and enhance the species retreat otherwise. Thus, the species will invade in spite of the counteracting impact of advection (e.g., cross-wind or cross-current) in case $n_2 < -a_0$, i.e., for

$$\frac{2\beta - 1}{\sqrt{2}} < -a_0, \tag{30}$$

which is equivalent to

$$\beta < \frac{1}{2}\left(1 - \sqrt{2}a_0\right). \tag{31}$$

Relation (31) has an intuitively clear meaning: the weaker the Allee effect is for a given population, the higher is its capability to invade new areas. This conclusion is in a good agreement with the results of other authors, cf. [4,7]. In case we are restricted to the case of the 'strong' Allee effect, β is positive while a_0 can be arbitrary. It means that the species affected by a 'strong' Allee effect cannot invade in case the cross-wind is sufficiently strong, $a_0 < 2^{-1/2}$.

4.2. Density-dependent migration

In this section, we consider the case when the density-independent advection caused by environmental factors is absent and migration takes place due to biological mechanisms which are assumed to be density-dependent. Then $a_0 = 0$ and from (9) we arrive at the following equation:

$$u_t + a_1 u u_x = u_{xx} - \beta u + (1+\beta)u^2 - u^3. \tag{32}$$

Eq. (32) differs from (10) and the exact solution (11) is not immediately applicable. However, to obtain an exact solution of Eq. (32), we can try to make use of the approach described in Section 3.

Introducing a new variable $p(x,t)$,

$$u(x,t) = v\frac{p_x}{p+\sigma}, \tag{33}$$

where v is a coefficient and σ is a (nearly) arbitrary constant included in order to avoid singularities, cf. Section 3. Having substituted Eq. (33) into (32), we arrive at the following system:

$$p_{xt} = p_{xxx} - \beta p_x, \tag{34}$$

$$p_t = (3 + a_1 v)p_{xx} - (1+\beta)v p_x, \tag{35}$$

$$v = \frac{1}{2}\left(a_1 \pm \sqrt{a_1^2 + 8}\right). \tag{36}$$

Choosing plus in Eq. (36) without any loss of generality (minus would correspond to the change $a_1 \to -a_1$, $x \to -x$) and excluding p_{xt} form Eq. (34), from (34)–(36) we obtain

$$(2 + a_1 v)p_{xxx} - (1+\beta)v p_{xx} + \beta p_x = 0, \tag{37}$$

$$p_t = (3 + a_1 v)p_{xx} - (1+\beta)v p_x. \tag{38}$$

The solution of the linear equation (37) has the following form:

$$p(x,t) = g_0(t) + g_1(t)e^{\omega_1 x} + g_2(t)e^{\omega_2 x}, \tag{39}$$

where

$$\omega_1 = \frac{\beta}{v}, \quad \omega_2 = \frac{1}{v}. \tag{40}$$

Having substituted (39) into (38), we obtain

$$g_0(t) = B_0, g_i(t) = B_i e^{\delta_i t} \quad \text{where } \delta_i = (3 + a_1 v)\omega_i^2 - (1+\beta)v\omega_i, \quad i = 1, 2 \tag{41}$$

and $B_{0,1,2}$ are arbitrary constants.

Considering Eq. (33) together with (39) and (41) and taking into account that coefficients $B_0 + \sigma$, B_1 and B_2 must have the same sign in order to provide positiveness of the solution, we arrive at the following exact solution of Eq. (32):

$$u(x,t) = \frac{\beta \exp(\omega_1 \psi_1) + \exp(\omega_2 \psi_2)}{1 + \exp(\omega_1 \psi_1) + \exp(\omega_2 \psi_2)}, \tag{42}$$

where $\psi_i = x - q_i t + \epsilon_i$, $q_i = (1+\beta)v - (3 + a_1 v)\omega_i$ and $i = 1$, 2, and $\epsilon_{1,2}$ are arbitrary constants.

Note that, apart from the above arguments leading to (42), the fact that (42) is an exact solution to Eq. (32) can be proved straightforwardly having substituted (42) into (32).

The structure of solution (42) is apparently similar to that of (11) and it has similar properties. Particularly, since $\omega_1 < \omega_2$, in the large-time limit solution (42) describes a single travelling population front:

$$u(x,t) \approx \frac{\exp(\omega_2 \psi_2)}{1+\exp(\omega_2 \psi_2)} \tag{43}$$

propagating with the speed q_2. The species spreads into the region with low population density in the case $q_2 < 0$, i.e., for

$$q_2 = (1+\beta)v - \frac{1+v^2}{v} < 0. \tag{44}$$

From inequality (44), we readily obtain the following condition of successful invasion:

$$\beta < \frac{1}{v^2}, \tag{45}$$

where $v = 0.5(a_1 + \sqrt{a_1^2 + 8})$ so that $v \to +0$ for $a_1 \to -\infty$ and $v \to +\infty$ for $a_1 \to +\infty$. In the case $a_1 = 0$ (no-migration), $v = \sqrt{2}$ and (45) coincides with (15a).

Unlike the density-independent case, cf. (31), the right-hand side of inequality (45) is always positive. Consequently, the interplay between the diffusive spread of the population and migration appears to be different. Even a strong density-dependent migration (corresponding to large positive a_1) going from the region with low population density towards the region with high population density cannot block the species invasion caused by the random dispersion of the individuals in case the Allee effect (quantified by parameter β) is sufficiently small.

4.3. General case

In a general case, migrations can take place due to both density-dependent and density-independent factors. The dynamics of a given population are then described by full equation (9) where now $a_0 \neq 0$ and $a_1 \neq 0$. The results of the two preceding sections immediately apply to this case leading to the following exact solution:

$$u(x,t) = \frac{\beta \exp\{\omega_1[x-(q_1+a_0)t+\epsilon_1]\} + \exp\{\omega_2[x-(q_2+a_0)t+\epsilon_2]\}}{1+\exp\{\omega_1[x-(q_1+a_0)t+\epsilon_1]\} + \exp\{\omega_2[x-(q_2+a_0)t+\epsilon_2]\}}, \tag{46}$$

where the notations are the same as in Eq. (42). Particularly, in the large-time limit, the solution (46) takes the following form describing propagation of a population front:

$$u(x,t) \approx \frac{\exp\{\omega_2[x-(q_2+a_0)t+\epsilon_2]\}}{1+\exp\{\omega_2[x-(q_2+a_0)t+\epsilon_2]\}}. \tag{47}$$

The condition of successful invasion now takes the form $q_2 < -a_0$ which, after a little algebra, reads as follows:

$$\beta < r(v,a_0) = \frac{1}{v^2} - \frac{a_0}{v}. \tag{48}$$

It is readily seen that $r \geqslant 0$ for $v \leqslant 1/a_0$ and r is negative otherwise. Thus, since β is assumed to be non-negative, for any fixed β and v inequality (48) is violated in the case a_0 is positive and sufficiently large. In agreement with the results of Section 4.1, it means that the species invasion can always be blocked or reversed in case of sufficiently strong counteractive advection (such as cross-wind or cross-current) provided that the density-dependent migrations are either absent or enhance the species retreat (which corresponds to $a_1 \geqslant 0$ and $v \geqslant \sqrt{2}$). However, another property of relation (48) is that, for any fixed positive value of a_0, however large it can be, inequality (48) becomes true for sufficiently small v. Small v corresponds to large negative a_1, i.e., to the case when the density-dependent migrations takes place towards the region where the species is absent. It means that even strong counteractive advection cannot stave off the spread of a given population in the case of cooperative impact of biological factors enhancing the species invasion.

5. Concluding remarks

In this paper, we have considered a single-species model of spatiotemporal population dynamics taking into account advection and/or migrations, diffusion due to the random motion of the individuals, and the local growth of the population damped by a 'strong' Allee effect. The model consists of a non-linear partial differential equation of the advection–diffusion-reaction type. Using a suitable change of variables, we have found an exact solution of the equation describing the propagation of a population front. By means of studying the properties of the solution, the interplay between diffusion and different types of advection/migration (density-dependent and density-independent) has been thoroughly investigated. Exact relations between the parameters have been obtained, cf. (31), (45) and (48), which make it possible to forecast whether the interplay between various factors leads to species invasion or to species retreat. In particular, we have shown that species invasion caused solely by isotropic random motion of the individuals can be blocked by sufficiently strong counteracting advection. However, in the case that invasion caused by the random isotropic motion is supported by a correlated motion by the individuals towards the region with low population density, the species spread cannot be blocked by purely environmental factors (such as wind or water current) provided that per capita migration speed is sufficiently large. Surprisingly, our model predicts that density-dependent migration alone cannot block diffusive spreading in the case that the Allee effect is 'not too strong': however large v is (which corresponds to the species retreat with large per capita migration speed), there always exists a small positive β so that inequality (45) is true.

Since our conclusions are based on the properties of exact solutions (11), (42), (46), and thus restricted to the assumptions made beforehand in order to obtain the solutions, cf. Section 2, our study leaves a number of open questions. First, since the solutions are non-negative only for $\beta \geqslant 0$, our conclusions mainly apply to the case of 'strong' Allee effect. It would be interesting to know how the interplay between diffusion and advection/migration can be modified in the case of species with either a 'weak' Allee effect (i.e., for $-1 < \beta \leqslant 0$, cf. [4,7]) or without an Allee effect at all (for $\beta \leqslant -1$, cf. [4]). Second, to describe the density-dependent migrations, we assumed that the migration speed increases linearly with the population density. It is quite possible, however, that in real ecological communities this relation is more complicated. Third, Eqs. (7), or (9) in dimensionless variables, which we used to describe the spatiotemporal dynamics of a given population, actually implies that the individuals migrate and produce offspring at the same time. In reality, it seems more probable that the individuals are involved in different activities at different life-stages. These issues outline the direction of future research.

Acknowledgements

This work was partially supported by Russian Foundation for Basic Research under grants 01-04-048186 and 03-04-48018, by US National Science Foundation under grants DEB-00-80529 and DBI-98-20318, by the University of California Agricultural Experiment Station and by UCR Center for Conservation Biology. Discussion of the issue with Daniel Simberloff is appreciated.

References

[1] R. Hengeveld, Dynamics of Biological Invasions, Chapman and Hall, London, 1989.
[2] N. Shigesada, K. Kawasaki, Biological Invasions: Theory and Practice, Oxford University, Oxford, 1997.
[3] A. Okubo, S. Levin, A theoretical framework for data analysis of wind dispersal of seeds and pollen, Ecology 70 (1989) 329.
[4] M.A. Lewis, P. Kareiva, Allee dynamics and the spread of invading organisms, Theor. Popul. Biol. 43 (1993) 141.
[5] M. Kot, M.A. Lewis, P. van der Driessche, Dispersal data and the spread of invading organisms, Ecology 77 (1996) 2027.
[6] J.A. Sherratt, M.A. Lewis, A.C. Fowler, Ecological chaos in the wake of invasion, Proc. Nat. Acad. Sci. USA 92 (1995) 2524.
[7] M.R. Owen, M.A. Lewis, How predation can slow, stop or reverse a prey invasion, Bull. Math. Biol. 63 (2001) 655.
[8] S.V. Petrovskii, N. Shigesada, Some exact solutions of a generalized Fisher equation related to the problem of biological invasion, Math. Biosci. 172 (2001) 73.
[9] S.V. Petrovskii, Localization of a nonlinear switching wave in an active medium with an isolated inhomogeneity, Tech. Phys. 42 (1997) 866.
[10] S.V. Petrovskii, On the plankton front waves accelerated by marine turbulence, J. Mar. Syst. 21 (1999) 179.
[11] F.S. Berezovskaya, R.G. Khlebopros, The role of migrations in forest insect dynamics, in: E.E. Shnol (Ed.), Studies in Mathematical Biology—in Memorial of Alexander D. Bazykin, Pushchino Scientific Center, Pushchino, 1996, pp. 61–69.
[12] N. Shigesada, K. Kawasaki, Y. Takeda, Modelling stratified diffusion in biological invasions, Am. Nat. 146 (1995) 229.
[13] M.J. Ablowitz, A. Zeppetella, Explicit solutions of Fisher's equations for a special wave speed, Bull. Math. Biol. 41 (1979) 835.
[14] A.S. Fokas, A symmetry approach to exactly solvable evolution equations, J. Math. Phys. 21 (1980) 1318.
[15] W.I. Newman, Some exact solutions to a nonlinear diffusion problem in population genetics and combustion, J. Theor. Biol. 85 (1980) 325.
[16] E. Hopf, The partial differential equation $u_t + uu_x = \mu u_{xx}$, Commun. Pure Appl. Math. 3 (1950) 201.
[17] T. Kawahara, M. Tanaka, Interactions of travelling fronts: an exact solution of a nonlinear diffusion equation, Phys. Lett. A 97 (1983) 311.
[18] N.A. Kudryashov, Singular manifold equations and exact solutions for some nonlinear partial differential equations, Phys. Lett. A 182 (1993) 356.
[19] M.V. Ognev, S.V. Petrovskii, V.M. Prostokishin, Dynamics of formation of a switching wave in a dissipative bistable medium, Tech. Phys. 40 (1995) 521.
[20] F. Calogero, J. Xiaoda, C-integrable nonlinear partial differential equations, J. Math. Phys. 32 (1991) 875.
[21] W.C. Allee, The Social Life of Animals, Norton, New York, 1938.
[22] B. Dennis, Allee effects: population growth, critical density, and the chance of extinction, Nat. Res. Model. 3 (1989) 481.
[23] J.G. Skellam, Random dispersal in theoretical populations, Biometrika 38 (1951) 196.
[24] A. Okubo, Diffusion and ecological problems: mathematical models, in: Biomathematics, vol. 10, Springer, Berlin, 1980.

[25] E.E. Holmes, M.A. Lewis, J.E. Banks, R.R. Veit, Partial differential equations in ecology: spatial interactions and population dynamics, Ecology 75 (1994) 17.
[26] J.D. Murray, Mathematical Biology, 2nd Ed., Springer, Berlin, 1993.
[27] A.I. Volpert, V.A. Volpert, V.A. Volpert, Travelling Wave Solutions of Parabolic Systems, Amer. Math. Society, Providence, 1994.
[28] F.S. Berezovskaya, G.P. Karev, Bifurcations of travelling waves in population taxis models, Phys.-Usp. 169 (1999) 1011.
[29] R. Fisher, The wave of advance of advantageous genes, Ann. Eugenic. 7 (1937) 355.
[30] A.N. Kolmogorov, I.G. Petrovsky, N.S. Piskunov, Investigation of the equation of diffusion combined with increasing of the substance and its application to a biology problem, Bull. Moscow State Univ. Ser. A: Math. Mech. 1 (6) (1937) 1.
[31] M.-E. Wang, M. Kot, Speeds of invasion in a model with strong or weak Allee effects, Math. Biosci. 171 (2001) 83.
[32] V.G. Danilov, P.Yu. Subochev, Exact single-phase and two-phase solutions for semilinear parabolic equations, Teor. Mat. Fiz. 89 (1991) 25.
[33] S.V. Petrovskii, Exact solutions of the forced Burgers equation, Tech. Phys. 44 (1999) 878.
[34] S.V. Petrovskii, H. Malchow, B.-L. Li, An exact solution of diffusive Lotka–Volterra equations, submitted to SIAM J. Appl. Math.
[35] A.C. Newell, Solitons in Mathematics and Physics, SIAM, Philadelphia, 1985.