

Directed Movement of Predators and the Emergence of Density-Dependence in Predator–Prey Models

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We consider a bitrophic spatially distributed community consisting of prey and actively moving predators. The model is based on the assumption that the spatial and temporal variations of the predators' velocity are determined by the prey gradient. Locally, the populations follow the simple Lotka–Volterra interaction. We also assume predator reproduction and mortality to be negligible in comparison with the time scale of migration. The model demonstrates heterogeneous oscillating distributions of both species, which occur because of the active movements of predators. One consequence of this heterogeneity is increased viability of the prey population, compared to the equivalent homogeneous model, and increased consumption. Further numerical analysis shows that, on the spatially aggregated scale, the average predator density adversely affects the individual consumption, leading to a nonlinear predator-dependent trophic function, completely different from the Lotka–Volterra rule assumed at the local scale. © 2001 Academic Press

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INTRODUCTION

Because of heterogeneities in the environment, the spatial factor can play a crucial role in population dynamics. Here, we use partial differential equations (PDE) of the reaction–diffusion–advection type to describe local population interactions coupled with migration processes caused by the heterogeneity of the environment and of the populations themselves. This approach combines the advantages of numerical simulation and of pure analytical methods. In theoretical biology, it was pioneered independently by Kolmogorov *et al.* (1937) and Fisher (1937) and is now quite developed (see the books of Edelstein-Keshet (1988), Murray (1993), Czárán (1998), or Turchin (1998) for examples, details, and further references). Such models exhibit solutions that are heterogeneous in time as well as in space (see, e.g., the recent paper of Savill and Hogeweg, 1999). Such dynamics are known in the general theory of dynamical systems, the simplest example being the self-oscillation, but more complicated regimes exist also (e.g., Marsden and McCracken, 1976). The classical chemotaxis model introduced by Keller and Segel (1971) demonstrates the emergence of endogenous patterns, including travelling waves. The appearance of advection-driven heterogeneity in relation to single and multispecies ecological interactions was studied by Levin (1977), Levin and Segel, (1976), Okubo (1980), Mimura and Murray (1978), Mimura and Kawasaki (1980), Mimura and Yamaguti (1982), and many other authors. These studies form a theoretical basis for modelling complex spatio-temporal dynamics observed in real systems (e.g., Badaev *et al.* 1998).

Both random and directed movements should be considered for actively dispersing species. In the framework of the reaction–diffusion–advection approach, the advective velocity of migrants is usually expressed as the weighted sum of gradients of various biotic or abiotic factors (Czárán, 1998; Turchin, 1998; Berezovskaya and Karev, 1999; Berezovskaya *et al.*, 1999). Our approach will differ from previous work by the main assumption concerning the velocity of migrants. We will assume that not the velocity itself, but the acceleration (which is the variation of velocity both in magnitude and in direction) is influenced by the spatial distribution of external stimuli such as the density of food or the presence of natural enemies (Turchin, 1998). Assuming this, we follow the basic principle of some individual-based models where acceleration of moving animals is determined by an environmental gradient (see, e.g., Flierl *et al.*, 1999; Kareiva, 1982; Turchin, 1998).

In our model, the migrating population is characterized at each point in space by a certain density of

organisms and their velocity, considering that individuals accelerate in response to the heterogeneity of the resource (or of any other environmental factor). If the resource distribution is homogeneous, consumers move at constant velocity.

Several field studies measuring characteristics of individual movement confirm the basic hypothesis about the dependence of acceleration on a stimulus gradient. For example, acceleration vectors of individuals in fish schools (Parrish and Turchin, 1997) and in swarms of flying insects (Okubo and Chiang, 1974; Okubo *et al.*, 1977) are directed towards the centroid of such dynamically stable formations. The acceleration increases with distance from this point, being maximal on the edges (where the density gradient is maximal) and equal to zero at the centroid position (where the density gradient is zero). In both cases, the active movement of fish and midges is controlled by their own density and it was clearly demonstrated that at the centre of the school or swarm, individual motion loses its directional component and becomes random. Other experimental results were described by Kareiva (1982). Observing the movements of flea-beetles, he found that they modify their movements (i.e., accelerate) in response to patch quality. Flierl *et al.* (1999) observed that individual fish in schools adjust their probability of changing direction (i.e., variation of velocity) according to the difference between ambient and preferred temperatures.

We will demonstrate that a reaction–diffusion–advection predator–prey model based on the assumption of predator acceleration being proportional to prey gradient allows us to obtain stable spatially heterogeneous solutions only due to predator searching and feeding activities (Govorukhin *et al.*, 2000). The model will be studied analytically and the heterogeneous solutions will be obtained numerically.

Then, we will apply the model to the study of the spatially aggregated trophic function in a spatially distributed predator–prey system. (We prefer the term “trophic function” (Svirezhev and Logofet, 1983) to the common expression “functional response,” but these terms are strictly synonymous.) Assuming that, locally (i.e., at each point and each instant), predators attack prey following the familiar Lotka–Volterra interaction term, we intend to investigate how the heterogeneities induced by the behavioural mechanisms affect the functional relationships between the population abundances when they are considered on the macroscopic scale (i.e., averaging population densities over space and time). In particular, we will demonstrate that approximate ratio-dependence (Arditi and Ginzburg, 1989) can appear at the macroscopic scale.

THE MODEL

We consider a two-species system consisting of an actively migrating predator and a passive prey (acting as the migration stimulus). Spatial dispersal of the prey is pure diffusion. The dynamics of predators is characterized by a scalar field of population density $P(\mathbf{x}, t)$ and a vector field of velocity $\mathbf{v}(\mathbf{x}, t)$, where \mathbf{x} are the spatial coordinates and t is the time. In the general 3D case $\mathbf{x} = (x_1, x_2, x_3)$ and $\mathbf{v} = (v_1, v_2, v_3)$. Let $N(\mathbf{x}, t)$ be the scalar field of prey density. Our main assumption is that the prey density gradient determines the variation of the predator velocity (the acceleration),

$$\frac{d\mathbf{v}}{dt} = \kappa \nabla N, \quad (1)$$

where the coefficient of active migration κ is, in general, a function of $N, P, \mathbf{x}, t, \mathbf{v}$. However, we will assume here that it is a constant positive parameter. $\frac{d}{dt} = \frac{\partial}{\partial t} + \mathbf{v} \cdot \nabla$ is the total derivative. The quadratic term $\mathbf{v} \cdot \nabla \mathbf{v}$ in (1) describes the transport of the velocity itself by moving organisms.

To take into account the resistance of the environment, one could add a friction term $-\gamma \mathbf{v}$ on the right hand side of Eq. (1). In conventional prey–taxis models, it is usually assumed that $\mathbf{v} = \tilde{\kappa} \nabla N$ (Czárán, 1998; Turchin, 1998; Berezovskaya and Karev, 1999). This actually means that the velocity of predators is immediately adapted to the instantaneous prey density gradient. Therefore, conventional taxis models cannot account for movement inertia. In the special case in which both κ and γ tend to infinity with their ratio $\tilde{\kappa}$ remaining constant, the formula $\mathbf{v} = \tilde{\kappa} \nabla N$ can be obtained from the general equation $\frac{d\mathbf{v}}{dt} = \kappa \nabla N - \gamma \mathbf{v}$ as its main asymptotic. Here, we will neglect the friction term, assuming it to be small with respect to movement forces. Notice that since the friction term does not depend on spatial derivatives, this simplification is not crucial for further analysis: its presence would not lead to qualitative changes in the results.

We further assume that interactions like intraspecific competition for space or schooling effects equalize the velocities of neighbouring predators; i.e., there is a diffusion of the velocity. We obtain therefore the following equation for the velocity,

$$\frac{d\mathbf{v}}{dt} = \kappa \nabla N + \delta_v \Delta \mathbf{v}, \quad (2)$$

where δ_v is the nonnegative diffusion constant of the velocity, with the Laplacian of a vector field $\Delta = \text{grad div} - \text{curl curl}$.

The variation of population density at each point is supposed to be determined by the processes of reproduction, predation, mortality, diffusion, and deterministic migration in the case of predators. The latter is described by an advective term, expressing the contribution of directed movement in the net balance of predators in an elementary volume.

The full model for predator–prey dynamics with active migration is

$$\frac{\partial N}{\partial t} = f(N) N - g(N, P) P + \delta_N \Delta N, \quad (3)$$

$$\frac{\partial P}{\partial t} = e g(N, P) P - q(P) P - \text{div}(P \mathbf{v}) + \delta_P \Delta P, \quad (4)$$

$$\frac{d\mathbf{v}}{dt} = \kappa \nabla N + \delta_v \Delta \mathbf{v}, \quad (5)$$

where δ_N and δ_P are the nonnegative diffusion constants of prey and predator populations, the Laplacian of scalar fields in (3) and (4) is $\Delta = \text{div grad}$, $f(N)$ is the prey reproduction rate, and $g(N, P)$ is the predator trophic function. Being multiplied by the predation efficiency constant $e > 0$, the trophic function appears in (4) as the predator reproduction rate. Function $q(P)$ is the predator death rate (possibly density-dependent).

For simplicity, we further assume that the quadratic term $\mathbf{v} \cdot \nabla \mathbf{v}$ in the total derivative of the velocity $\frac{d\mathbf{v}}{dt}$ is small in comparison with the local derivative $\frac{\partial \mathbf{v}}{\partial t}$. This approximation turns out to be valid as long as either the velocity or its gradient are sufficiently small. Particularly, this condition is satisfied in a neighbourhood of the homogeneous equilibrium of system (3)–(5).

Neglecting $\mathbf{v} \cdot \nabla \mathbf{v}$, Eq. (5) becomes:

$$\frac{\partial \mathbf{v}}{\partial t} = \kappa \nabla N + \delta_v \Delta \mathbf{v}. \quad (6)$$

Since our objective here is to investigate specifically the influence of active migration on the spatial distribution of predators, we will assume in the rest of this paper that the functions of birth and death in the predator balance equation (4) are identically zero. In other words, we assume that, on the time scale being considered, predator reproduction and mortality are slow processes that can be neglected in front of migrations and prey consumption

and reproduction. The balance equation for the predator population is then

$$\frac{\partial P}{\partial t} = \delta_P \Delta P - \operatorname{div}(P\mathbf{v}). \quad (7)$$

Regarding the prey, we will assume logistic reproduction and the familiar Lotka–Volterra trophic function for predation mortality. That is, we assume that, locally, predators encounter prey according to the simple law of mass action

$$\frac{\partial N}{\partial t} = rN \left(1 - \frac{N}{K}\right) - aPN + \delta_N \Delta N. \quad (8)$$

Let us suppose the community habitat to be bounded with some characteristic lengths L_1, L_2, L_3 and closed in the sense that both diffusive and advective fluxes through the habitat boundary are zero. We consider the $L_1 \times L_2 \times L_3$ parallelepipedic box Ω as a simple example of a closed habitat. The closure of the habitat implies the boundary conditions

$$\mathbf{v} \cdot \mathbf{n} = \frac{\partial P}{\partial \mathbf{n}} = \frac{\partial N}{\partial \mathbf{n}} = \frac{\partial \mathbf{v}_\tau}{\partial \mathbf{n}} = 0, \quad (9)$$

where \mathbf{n} is the unit normal vector and \mathbf{v}_τ is the tangent velocity on the faces of Ω . The boundary condition for \mathbf{v}_τ means the absence of velocity diffusion through the boundary.

Thus, the model is reduced to the set of Eqs. (8), (7), (6) with boundary conditions (9).

Note that the model is invariant to rotation–reflection–translation. This implies the existence of special solutions being homogeneous in one, two, or all three spatial directions. Below, solutions homogeneous in one direction will be referred to as two dimensional (2D), solutions homogeneous in two directions as one dimensional (1D), and fully homogeneous solutions as point ones (or 0D). Note also that 2D or 1D solutions appear as limits of the general one if either one or two of the domain lengths are small with respect to another one (for instance $L_3/L_1 \rightarrow 0$ or $L_2/L_1 \rightarrow 0$ and $L_3/L_1 \rightarrow 0$).

According to Eq. (7) and the boundary conditions (9), the average density of predators is a constant parameter,

$$\langle P \rangle = \frac{1}{\operatorname{Vol}(\Omega)} \int_{\Omega} P \, d\mathbf{x} = \bar{P} = \text{const}, \quad (10)$$

where $\operatorname{Vol}(\Omega)$ is the volume of box Ω .

Without loss of generality, the units of space, time, prey, and predator densities can be chosen in such way that $r = 1, K = 1, a = 1$, the longest characteristic domain length (say, L_1) is scaled to $L_1 = \pi$, and predators are scaled to be measured by their deviation from \bar{P} : $p = P - \bar{P}$. Hence $\langle p \rangle \equiv 0$.

With these new units, the model (Eqs. (8), (7), (6)) becomes the normalized system

$$\frac{\partial N}{\partial t} = N(1 - N - p - \bar{P}) + \delta_N \Delta N; \quad (11)$$

$$\frac{\partial p}{\partial t} + \operatorname{div}(p\mathbf{v}) + \bar{P} \operatorname{div}(\mathbf{v}) = \delta_P \Delta p; \quad (12)$$

$$\frac{\partial \mathbf{v}}{\partial t} = \kappa \nabla N + \delta_v \Delta \mathbf{v}. \quad (13)$$

The normalized habitat has the form

$$\Omega = \{\mathbf{x}: 0 < x_i < L_i, i = 1, 2, 3\}, \quad (14)$$

with the spatial sizes

$$L_i = \pi \alpha_i, \quad i = 1, 2, 3; \quad \alpha_1 = 1, \alpha_3 \leq \alpha_2 \leq 1. \quad (15)$$

In the rest of this paper, we will study the solutions of Eqs. (11)–(13) satisfying the boundary conditions (9) on the faces of the normalized box (14), (15).

Note that Eqs. (11)–(13) have the homogeneous equilibrium

$$\begin{aligned} N &\equiv \bar{N} = 1 - \bar{P}, \\ p &\equiv 0, \\ \mathbf{v} &\equiv 0, \end{aligned} \quad (16)$$

provided that $0 < \bar{P} < 1$. Note that the average predator density $\langle P \rangle$ is always equal to the parameter \bar{P} but that the average prey density $\langle N \rangle$ is equal to \bar{N} only in the fully homogeneous case (16).

Besides the equilibrium (16), the system (11)–(13) has also the trivial equilibrium

$$N \equiv 0, \quad p \equiv 0, \quad \mathbf{v} \equiv 0. \quad (17)$$

On first sight, this may seem strange since it permits the predator population \bar{P} to live without prey, but it is due to the fact that predator reproduction and mortality are ignored in Eq. (12) as slow processes with respect to predation and migration.

LINEAR ANALYSIS OF PERTURBED EQUILIBRIA

In order to assess the nontrivial spatial phenomena of the model, we will first study the disruption of the homogeneous equilibria. In this section we will analyse the instabilities of the two equilibria (16) and (17) using linear approximations. In both cases, we will consider small perturbations of the homogeneous equilibrium, i.e., search for nonzero solutions of the linearized system. These perturbations have the form

$$(N - \bar{N}, p, \mathbf{v}) = \text{Re}[(\hat{N}(\mathbf{s}), \hat{p}(\mathbf{s}), \hat{\mathbf{v}}(\mathbf{s})) e^{i\lambda(\mathbf{s}) + i\mathbf{s}\mathbf{x}}], \quad (18)$$

where \mathbf{s} is a so-called wavevector that, being fixed, determines the periods of perturbations (18) on each coordinate x_i . The appropriately chosen wavevector should satisfy the boundary conditions (9). The unknown complex values $\hat{N}(\mathbf{s}), \hat{p}(\mathbf{s}), \hat{\mathbf{v}}(\mathbf{s}), \lambda(\mathbf{s})$ have to be determined as follows. Substitute N, p, \mathbf{v} into the set (11)–(13), eliminate all terms being second order or higher in $\hat{N}, \hat{p}, \hat{\mathbf{v}}$, and then solve the resulting algebraic equations for the spectral value λ . Note that this linearization procedure keeps the reflection–rotation–translation invariance of the original set (11)–(13). This means in particular that λ depends on $|\mathbf{s}|$ only.

Remember that the solution must satisfy the boundary conditions (9) on the faces of the given box Ω . However, the general perturbation (18) is simply $2\pi/s_i$ -periodic in x_i and does not satisfy (9). At the same time, we can combine all perturbations (18) with equal λ in such a way that the resulting combination satisfies (9) on the faces of each half-period box. This is possible due to the symmetry of the problem. Furthermore, the half-period box is completely defined by the wavevector \mathbf{s} . Therefore, the appropriate choice of \mathbf{s} allows us to satisfy (9) on the faces of an arbitrary fixed box Ω . For the box defined by (14), (15) the set S of admissible values of \mathbf{s} has the form:

$$S = \{\mathbf{s}: s_i = m_i/\alpha_i, m_i = 0, \pm 1, \dots, i = 1, 2, 3\}. \quad (19)$$

In particular, if $\mathbf{s} = (m_1, 0, 0)$ then the perturbation satisfying the boundary conditions (9) has the 1D form:

$$(N - \bar{N}, p, v) = (N_k \cos kx, p_k \cos kx, v_k \sin kx) e^{\lambda_k t}, \quad (20)$$

$$k = 0, 1, 2, \dots$$

Here, the velocity $\mathbf{v} = (v, 0, 0)$ is parallel to the longest edge of the box (14), (15), $x = x_1$ is the Cartesian coordinate along this edge, $v_0 = p_0 = 0$, and $k = |m_1|$.

For general perturbations (18), (19), let us write

$$k = |\mathbf{s}|, \mathbf{s} \in S; \lambda(\mathbf{s}) = \lambda(|\mathbf{s}|) = \lambda_k \quad (21)$$

and consider the set S and consequently the set of perturbations (18) in the order of the magnitude of k .

If no growing perturbation exists ($\text{Re } \lambda_k \leq 0$ for all k), then the equilibrium is stable (with respect to small disturbances). If $\text{Re } \lambda_k > 0$ at least for one k , it is unstable. The case $\text{Re } \lambda_k = 0$ (for some k) corresponds to the neutral situation. The solutions (18) corresponding to these three cases are called stable, unstable, and neutral, respectively. The neutral mode only exists for critical parameter values. It is known that the appearance of neutral modes implies the appearance of bifurcations of the equilibrium when the varying parameters cross their critical values. In the case of a zero eigenvalue ($\lambda_k = 0$), the neutral mode is said to be monotonous; the corresponding bifurcation indicates disappearance of the equilibrium or branching of a new equilibrium. In the case of a pure imaginary eigenvalue $\lambda_k = \pm i\omega$, the neutral mode is called oscillatory and the corresponding bifurcation is (in the general case) the onset of self-oscillations of small amplitude (the so-called Poincaré–Andronov–Hopf (PAH) bifurcation; see, e.g., Marsden and McCracken, 1976; Amann, 1990).

Let us first consider the zero equilibrium (17). If $\bar{N} < 0$, this equilibrium is stable; if $\bar{N} > 0$, it is unstable. This loss of stability is monotonous: in the critical case $\bar{N} = 0$, the eigenvalue $\lambda_0 = 0$, and the neutral mode is spatially homogeneous ($k = 0$). Thus, the positive homogeneous equilibrium (16) branches from the zero equilibrium. This destabilization and bifurcation of the zero equilibrium are trivial in the sense that they do not generate spatial heterogeneity and one can obtain the same result using only the homogeneous solutions of the point model:

$$\frac{dN}{dt} = f(N) N - g(N, P) P; \quad (22)$$

$$\frac{dP}{dt} = eg(N, P) P - q(P) P.$$

Let us now examine the nonzero equilibrium (16). The results of the linear analysis are presented in Fig. 1. Suppose all parameters except \bar{P} to be fixed and let \bar{P} grow from 0 to 1. Two cases can occur: either the equilibrium is stable for all $\bar{P} \in (0, 1)$ or there is an oscillatory domain (\bar{P}_1, \bar{P}_2) , such that the equilibrium is unstable when \bar{P} belongs to this interval and is stable for $\bar{P} \in (0, \bar{P}_1) \cup (\bar{P}_2, 1)$. There exists $\kappa_* > 0$ dependent on the diffusion

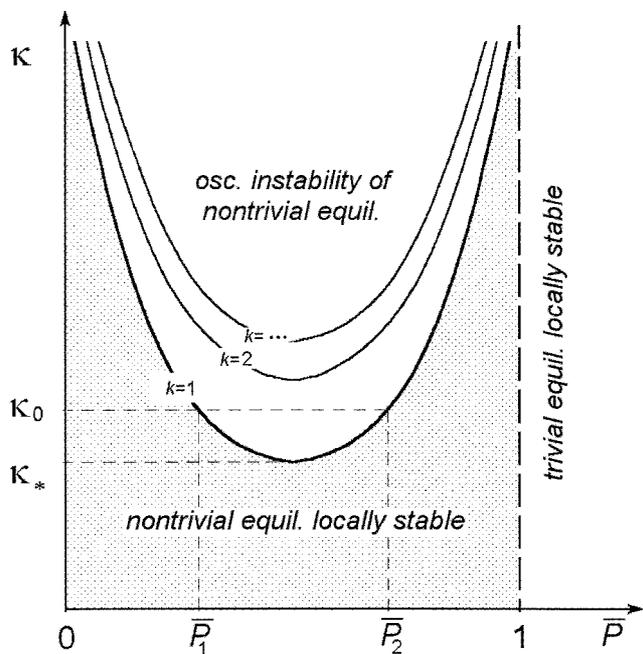


FIG. 1. Local stability conditions of the homogeneous equilibria in the space of parameters \bar{P} and κ . For a given $\kappa_0 > \kappa_*$, there exists an interval $[\bar{P}_1, \bar{P}_2]$ of \bar{P} values corresponding to instability of the nontrivial homogeneous solution. Thin solid curves denote the appearance of successive oscillatory modes with increasing spatial frequencies. The critical value κ_* depends on the diffusion coefficients. See text for more details.

rates only such that the oscillatory interval (\bar{P}_1, \bar{P}_2) is empty when $\kappa < \kappa_*$ and nonempty when $\kappa > \kappa_*$. The critical value κ_* increases with each diffusion rate $(\delta_N, \delta_P, \delta_V)$. If all diffusion rates tend to zero, then κ_* tends to zero but remains positive as long as at least two diffusion rates are nonzero. \bar{P}_1 and \bar{P}_2 depend on κ and on the diffusion rates.

In the first case ($\kappa < \kappa_*$), predators are unable to react fast enough to overcome the scarcity of the prey. In the second case ($\kappa > \kappa_*$), a neutral oscillatory mode exists at the critical values $\bar{P} = \bar{P}_1$ and $\bar{P} = \bar{P}_2$. Note that the homogeneous mode ($k=0$) decays with time for any $\bar{P} \in (0, 1)$. Therefore, the PAH bifurcation at $\bar{P} = \bar{P}_1$ really generates a heterogeneity and we can interpret the onset of self-oscillations as due to the active migrations of predators caused by prey scarcity.

The neutral oscillatory mode corresponds to the minimal value of k ($k=1$). Therefore it has the 1D form (20). Remember that the nonlinear equations (11)–(13) allow 1D solutions. Therefore, according to the general theory (e.g., Amann, 1990; Marsden and McCracken, 1976), the PAH bifurcation at $\bar{P} = \bar{P}_1$ generates 1D nonlinear oscillations close to the neutral oscillatory mode as long as the bifurcation parameter \bar{P} remains close to its critical

value \bar{P}_1 . It appears that these oscillations are stable at least for a small supercriticality (see numerical simulation results below). Thus the disruption of the nonzero homogeneous equilibrium (16) is manifested by a 1D heterogeneous wave oscillation of species densities along the longest edge of habitat Ω . Note that this is not true for large supercriticality. Moreover, even for small supercriticality, the above 1D heterogeneous regime can coexist with other attractors, and the dynamics on these attractors can be essentially multidimensional.

If \bar{P} exceeds some value $\bar{P}_2 < 1$, the equilibrium (16) becomes stable again. This critical value depends on κ and on diffusion rates. When $\bar{P} = 1$, the equilibrium (16) coincides with the zero equilibrium. For $\bar{P} > 1$, the nontrivial equilibrium loses its biological meaning: it becomes negative (and unstable). As was mentioned earlier, the trivial equilibrium is stable in this case. The oscillatory interval $[\bar{P}_1, \bar{P}_2]$ widens with increasing κ : \bar{P}_1 decreases to 0 and \bar{P}_2 increases to 1. However, some stability intervals $(0, \bar{P}_1)$ and $(\bar{P}_2, 1)$ remain nonempty for any arbitrary large value of the parameter κ . The higher modes ($k > 1$) appear with further increase of κ , for each fixed \bar{P} in the oscillatory domain (see Fig. 1). These modes do not generate new instabilities because the equilibrium is already unstable. However, it should be noted that the number of excited modes (and therefore the number of effective degrees of freedom) grows with κ .

NUMERICAL STUDY OF NONLINEAR PHENOMENA

The results of the previous section are valid locally only. In order to study the phenomena occurring for strong perturbations of the equilibria, numerical simulations were performed with the Galerkin and grid methods (see below). They exhibit gradual oscillatory destabilization of the nonzero equilibrium (16) for a sufficiently large value of κ ($\kappa > \kappa_*$). Since the model is invariant to rotation–reflection–translation, its solutions obviously depend on the initial distribution. There exist simultaneously various regimes: symmetric and nonsymmetric heterogeneous dynamics can be observed with different initial conditions.

Taking values $\kappa > \kappa_*$, and starting (with heterogeneous initial conditions) in the domain of local stability, we studied the bifurcations caused by the increase of parameter \bar{P} . If κ is sufficiently high, various types of spatially heterogeneous oscillations (travelling waves) appear when $\bar{P} > \bar{P}_1$. As \bar{P} increases, this heterogeneous regime can take different forms. Particularly, it

continues to bifurcate for $\bar{P} > \bar{P}_2$ and even for $\bar{P} > 1$. Thus, heterogeneous regimes exist although the nontrivial equilibrium is locally stable ($\bar{P}_2 < \bar{P} < 1$) and even when the trivial equilibrium is locally stable ($\bar{P} > 1$). In this case, the heterogeneous dynamics attracts the trajectories even with a rather small initial heterogeneity either in the predators or in the prey. The heterogeneous regime persists until some value $\bar{P} \gg 1$ after which the trivial equilibrium becomes globally attractive. At low κ , the homogeneous equilibria appear to be global attractors.

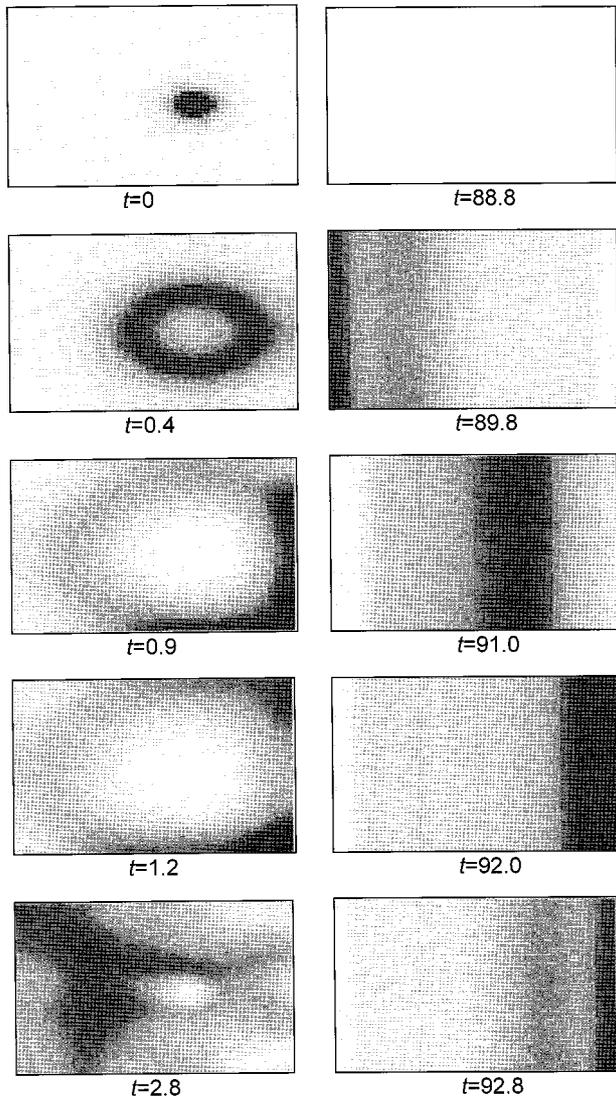


FIG. 2. One-dimensional travelling waves of predator density that can be obtained in both 1D and 2D formulations of the model. A darker shade of grey indicates higher population density. The first five snapshots (left column) illustrate the transient behaviour in the first instants, starting from a nonsymmetrical initial condition, and the last five snapshots (right column) illustrate the stabilized regime. $\bar{P} = 0.43$, $\kappa = 0.048$, $\delta_N = 0.001$, $\delta_P = 0.028$, $\delta_v = 0.000001$.

The transition scenario was found to become more complex with increasing migration activity κ . The most complex scenario observed in the numerical simulations was the following: nontrivial equilibrium \rightarrow periodic regime \rightarrow doubly periodic regime \rightarrow quasi-periodic regime \rightarrow chaotic regime \rightarrow quasi-periodic regime \rightarrow periodic regime \rightarrow trivial equilibrium. As κ decreases, the transition scenarios become simpler, down to the most primitive: nontrivial equilibrium \rightarrow trivial equilibrium. Examples of such dynamics corresponding to two qualitatively different periodic solutions are given in Figs 2–4. In these numerical simulations, the initial velocities of predators were taken as zero.

The results presented in Figs. 2 and 3 illustrate the conclusions of the analytical investigation of the previous section. For some given, high enough, value of the migration activity κ , a lower supercritical value of \bar{P} ($= 0.43$) generates a 1D heterogeneous solution (Fig. 2) even for a 2D initial disturbance. For a higher value of \bar{P} ($= 0.64$), a 2D heterogeneous solution is observed (Fig. 3).

To study the 1D solutions, we used the Galerkin method. We rewrote the model (11)–(13) in the 1D form,

$$\frac{\partial N}{\partial t} = N(1 - N - p - \bar{P}) + \delta_N \frac{\partial^2 N}{\partial x^2}, \quad (23)$$

$$\frac{\partial p}{\partial t} = -\bar{P} \frac{\partial v}{\partial x} - \frac{\partial(pv)}{\partial x} + \delta_P \frac{\partial^2 p}{\partial x^2}, \quad (24)$$

$$\frac{\partial v}{\partial t} = \kappa \frac{\partial N}{\partial x} + \delta_v \frac{\partial^2 v}{\partial x^2}, \quad (25)$$

and we searched for an approximate solution of the form:

$$\begin{aligned} N &= N_0(t) + \sum_{k=1}^q N_k(t) \cos kx, \\ p &= \sum_{k=1}^q p_k(t) \cos kx, \\ v &= \sum_{k=1}^q v_k(t) \sin kx. \end{aligned} \quad (26)$$

It is obvious that the approximate solution (26) satisfies the boundary conditions (9) on the box (14), (15). We substituted the expressions (26) into Eqs. (23)–(25) and, after projection, we obtained a system of $3q + 1$ ordinary differential equations for the unknown coefficients N_k , p_k , v_k .

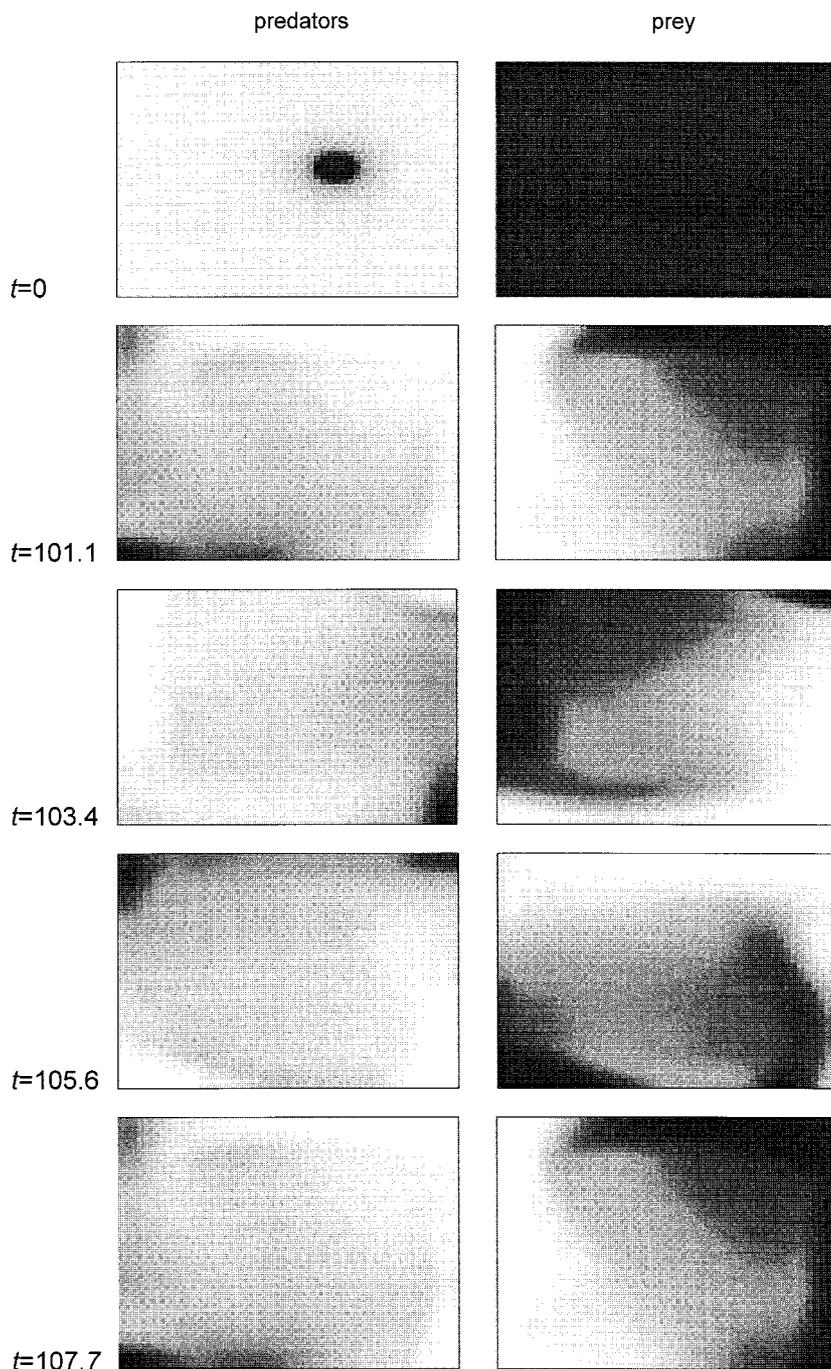


FIG. 3. Two-dimensional stable self-oscillations obtained in a bounded two-dimensional domain, starting from a nonsymmetrical predator distribution and a homogeneous prey distribution. $\bar{P} = 0.64$, other parameters as in Fig. 2.

To study numerically the 2D solutions of (11)–(13), we considered a closed rectangular habitat. The $m \times n$ grid approximation was applied to reduce the problem to a system of $m \times n$ ordinary differential equations. Here we used a grid with $m = n = 50$ and $\alpha_2 = 1$ (equal sides of the

2D habitat). The spatial derivatives in Eqs. (11)–(13) were approximated by using central differences with a precision of the second order. The resulting ODE system was integrated numerically with a Runge–Kutta method with variable time step.

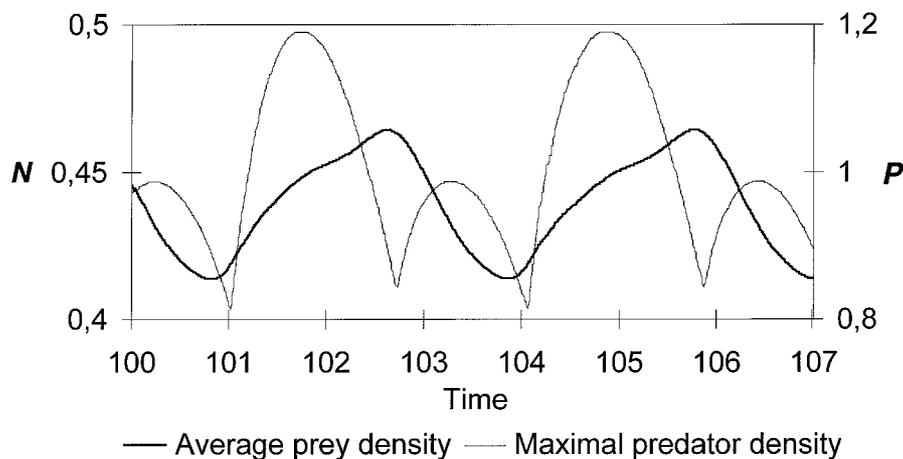


FIG. 4. Cyclic temporal dynamics of average prey density and maximal predator density for the oscillations of Fig. 3. Since the average density of predators is constant, the maximum density is an indicator of their spatial heterogeneity.

We now describe some numerical simulations of averaged characteristics of the 1D dynamics. Here, we consider the spatio-temporal averaging defined by the formula:

$$\langle\langle f \rangle\rangle = \lim_{T \rightarrow \infty} \frac{1}{T} \int_0^T \langle f \rangle dt.$$

As was said above, in the 1D case, we used the Galerkin approximation ($q = 10$) with parameter values

$\kappa = 8, \delta_N = 0.1, \delta_P = 0.1, \delta_v = 0.01$, and we varied only the parameter \bar{P} by small increments. For each value of \bar{P} , starting from a heterogeneous initial condition (that has been achieved upon stabilization of the nonequilibrium regime obtained for the previous value of the parameter \bar{P}), the calculation of the solution and the averaging procedure are carried out till the stabilization of the dynamics.

The average local consumption of prey $\langle\langle NP \rangle\rangle$ is represented in Fig. 5 while Fig. 6 shows the average prey density $\langle\langle N \rangle\rangle$. Note that if the trajectory tends to the

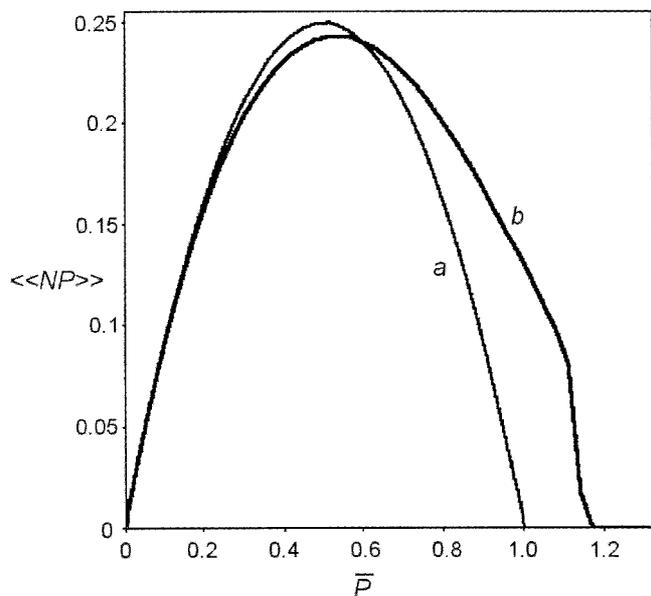


FIG. 5. Dependence of the average prey consumption $\langle\langle NP \rangle\rangle$ on parameter \bar{P} . (a) Point model (fully homogeneous). (b) Spatial model in the spatially heterogeneous regime.

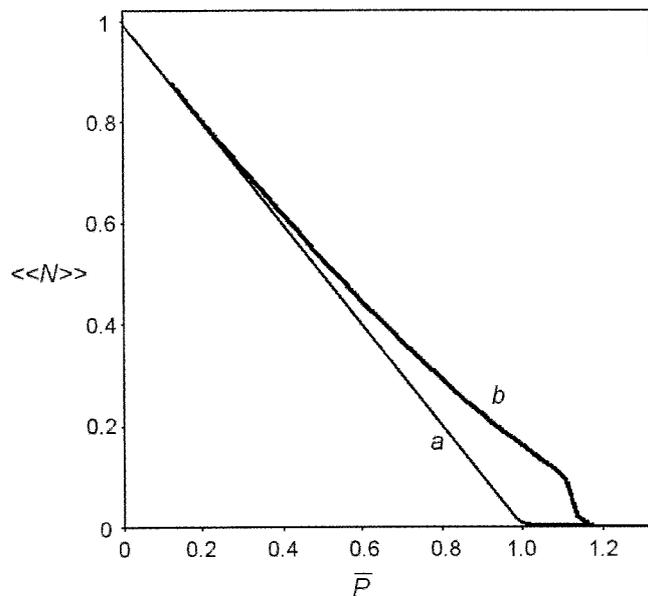


FIG. 6. Dependence of the average prey density $\langle\langle N \rangle\rangle$ on parameter \bar{P} . (a) Point model (fully homogeneous). (b) Spatial model in the spatially heterogeneous regime.

homogeneous equilibria, then either $\langle\langle NP \rangle\rangle = \langle NP \rangle = \bar{P}(1 - \bar{P})$ and $\langle\langle N \rangle\rangle = \langle N \rangle = 1 - \bar{P}$ when the nonzero equilibrium (16) attracts the trajectory, or $\langle\langle NP \rangle\rangle = \langle\langle N \rangle\rangle = 0$ when the zero equilibrium (17) attracts the trajectory.

On both graphs, the effect of predator active migration is shown by the comparison of curve **a** ($\kappa = 0$, i.e., no migration, stable homogeneous equilibria) and curve **b** ($\kappa = 8$). One can see that, with enough prey (\bar{P} close to zero) the curves **a** and **b** coincide. This coincidence reflects the fact that the homogeneous distribution of both predators and prey is the attractor. Increasing \bar{P} leads to an increase of the deviation of curve **b** from curve **a**. This deviation corresponds to the development of the spatial heterogeneity due to the onset of self-oscillations. For large \bar{P} , curves **a** and **b** merge again: predators do not migrate because of the absence of prey. Figure 6 shows that, if active migrations take place (curve **b**), the prey can survive at higher average predator densities \bar{P} , and the prey density is always higher than in the absence of migration (curve **a**). It is interesting that, in a condition of prey paucity ($\bar{P} \approx 1$), the predator searching activity leads to a higher consumption of prey (Fig. 5). Thus, model (11)–(13) displays a migration mechanism for overcoming prey insufficiency.

FROM SPATIAL HETEROGENEITY TO PREDATOR-DEPENDENT TROPHIC FUNCTION

The Lotka–Volterra trophic function $g(N) = aN$ used in (11) for the description of local interactions of species is based on an analogy with the law of mass action, i.e., on the assumption of random encounters between particles in a homogeneous environment. Although this is a reasonable assumption at the local scale (Haydon and Lloyd, 1999), it is known that it is not an accurate description of the average attack rate in large scale natural populations. First, the Lotka–Volterra model does not account for the saturation of predators with increasing prey density. The best known models that involve this effect are the Holling (1959) model $g(N) = aN/(1 + ahN)$ and the Ivlev (1955, 1961) model $g(N) = R(1 - e^{-sN})$. Second, interference between predators leads to predator-dependence in the trophic function (e.g., Hassell and Varley, 1969; Beddington, 1975; DeAngelis et al., 1975). One rather versatile model (Arditi and Akçakaya, 1990) is the combination of the models of Hassell and Varley (1969) and Holling (1959), $g(N, P) = (\alpha N/P^m)/(1 + \alpha hN/P^m)$, where $m \geq 0$ is the *mutual*

interference constant which quantifies the decrease of the searching efficiency with increasing predator density. If $m = 0$, this model reduces to Holling's.

A special case of predator-dependent trophic function was proposed by Arditi and Ginzburg (1989). They suggested that this function may often depend simply on the ratio of prey to predator abundances $g(N, P) = g(N/P)$. If $m = 1$, the above formula gives the ratio-dependent expression $g(N/P) = (\alpha N/P)/(1 + \alpha hN/P)$. Using verbal arguments, Arditi and Ginzburg (1989) suggested that ratio dependence could appear as a consequence of spatial heterogeneity and spatial behaviour of individuals. Actually, this concurs with earlier results in discrete time (Free et al., 1977) that had shown that imposed heterogeneity could lead to apparent interference when the searching efficiency was measured over the whole environment.

In this section, we apply model (11)–(13) to examine how the active migration behaviour and the ensuing spatial heterogeneity can influence the trophic interactions in the predator–prey system. Namely, we will examine how the average per capita predation mortality of the prey

$$Q = \lim_{T \rightarrow \infty} \frac{1}{T} \int_0^T \frac{\langle g(N, P) P \rangle}{\langle N \rangle} dt$$

$$\stackrel{\text{def}}{=} \left\langle \frac{\langle g(N, P) P \rangle}{\langle N \rangle} \right\rangle$$

depends on the average predator concentration $\langle P \rangle$. It is reasonable to investigate this function $Q = Q(\langle P \rangle)$ because the point analogue $Q = (g(N, P) P)/N$ presents very clear differences between the alternative models with Lotka–Volterra, Hassell–Varley–Holling, and ratio-dependent trophic functions (Fig. 7).

In the normalized model (11)–(13), $g(N, P) = g(N) = N$ and $\langle P \rangle = \bar{P}$ (due to the conservation of total predator abundance). Therefore, if one of the homogeneous equilibria attracts the trajectory, then we simply have

$$Q = \left\langle \frac{\langle NP \rangle}{\langle N \rangle} \right\rangle = \left\langle \frac{\langle N \rangle \bar{P}}{\langle N \rangle} \right\rangle = \bar{P}.$$

We next study (by simulation) the changes of Q with variation of the parameter \bar{P} . Such curves, calculated for several values of κ , are shown in Figs. 8 (2D dynamics) and 9 (1D dynamics). One can see that, even though the local trophic interactions are modelled with the Lotka–Volterra trophic function, the aggregated rate Q is completely different if the migration activity κ is sufficiently

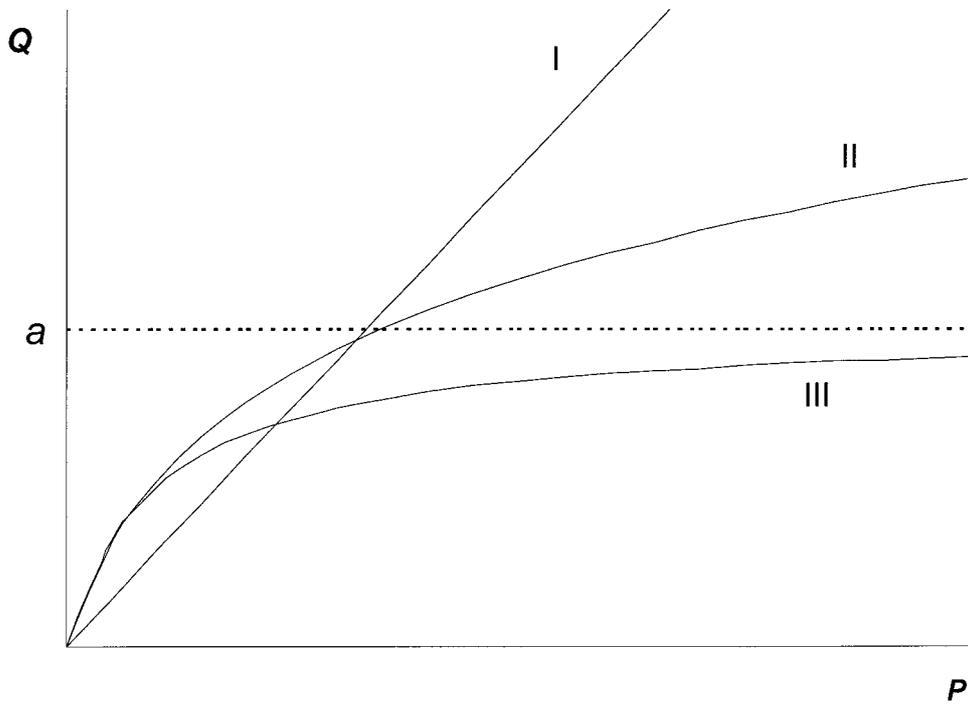


FIG. 7. Consumption mortality rate Q as a function of predator density P for the point model (corresponding to the fully homogeneous solution). (I) Lotka–Volterra model: $Q = aNP/N = aP$ is linear. (II) Hassell–Varley–Holling model: $Q = (\alpha/P^{m-1})/(1 + \alpha hN/P^m)$ ($m < 1$) is strongly nonlinear, growing to infinity. (III) Ratio-dependent model: $Q = \alpha/(1 + \alpha hN/P)$ increases monotonously and tends to an upper horizontal asymptote.

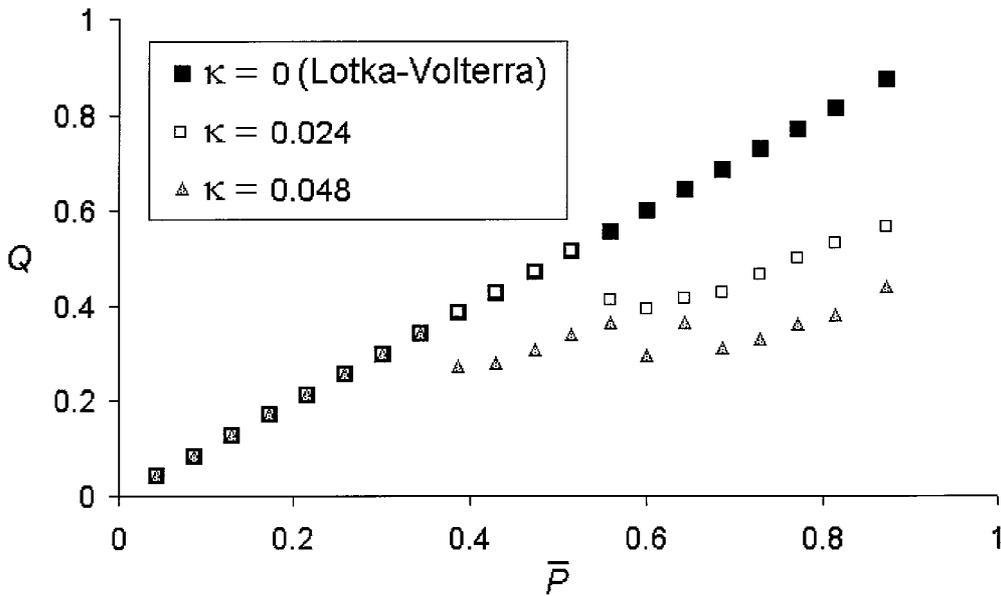


FIG. 8. Aggregated consumption mortality rate Q as a function of average predator abundance \bar{P} , in the 2D case. Diffusion coefficients are $\delta_N = 0.001$, $\delta_P = 0.028$, and $\delta_v = 0.000001$.

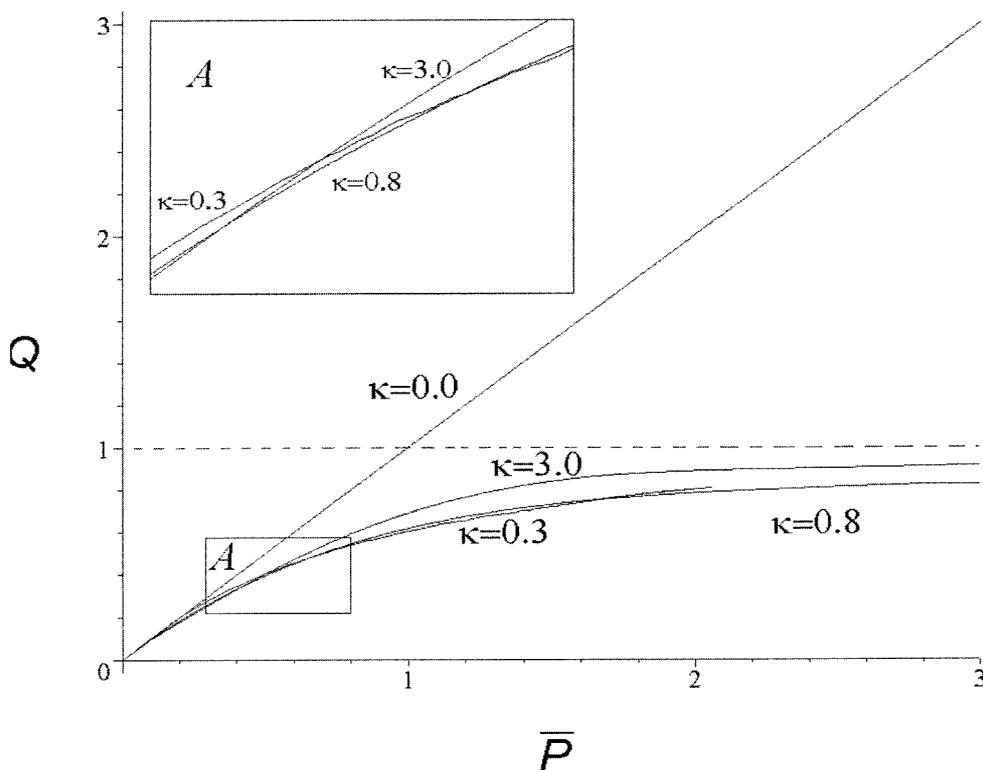


FIG. 9. Aggregated consumption mortality rate Q as a function of average predator abundance \bar{P} , in the 1D formulation of the model (23)–(25), for different values of the migration activity κ . Diffusion coefficients are $\delta_N = 0.03$, $\delta_P = 0.02$, and $\delta_v = 0.00001$. Note that the heterogeneous oscillatory regime (the cause of the upper asymptote) persists for values of $\bar{P} > 1$. (With the relatively low migration activity $\kappa = 0.3$, this regime disappears after $\bar{P} = 2$ and the prey is brought to extinction.)

high to provide stabilization of the heterogeneous oscillatory dynamics. The figures show that the higher the value of κ , the more pronounced is the deviation of Q from the straight line corresponding to the homogeneous steady state (the equilibrium of the Lotka–Volterra point model).

The one-dimensional case, which is computationally more stable and faster, provides more detailed and more precise results, obtained with much higher values of the parameter \bar{P} increasing with a smaller step (Fig. 9), that clearly exhibit saturation of the aggregated predation mortality Q with increasing total abundance of predators \bar{P} . This saturation is typical of ratio-dependence in the aggregated trophic function (compare with the curves of Fig. 7).

The behavioural explanation that can be given for this effect is the following. A heterogeneous spatial structure arises as a consequence of the high migrating activity of predators. This structure can be considered as an ensemble of two types of moving zones: some with high predator density and extremely low prey density, others with high prey density and a virtual absence of predators. Passive diffusion or displacement of the zones themselves bring

to the zones of the first type an amount of prey proportional to the prey population in the zones of the second type (which is almost equal to the total prey population). All such prey, entering zones of high predator density, are consumed almost immediately. Thus, the aggregated trophic function, which is by definition the total prey consumed divided by the total predator population, will be proportional to the ratio of the total prey and predator populations.

DISCUSSION

The analytical and numerical investigation of the proposed model has shown the following properties. With a high degree of active migrations, intrinsically heterogeneous dynamics (travelling waves) appear, induced by the migration phenomenon only. This provides coexistence of prey and predator populations under much more severe prey scarcity than in the equivalent homogeneous steady state (point model). For some parameter values, several attractors can exist simultaneously; i.e., starting from different initial conditions,

different dynamics can be reached. Any small heterogeneity in the initial distribution of either the prey or the predators causes the appearance of the travelling waves. Such dynamics can only appear if the active migration coefficient κ is higher than a critical value κ_* that depends on the diffusion coefficients.

The model is extremely simplified. We have ignored predator reproduction and friction in the velocity equation, and we deal with the simplest Lotka–Volterra functional response. Considering spatial behaviour, the predators' searching phase only is modelled, neglecting the handling phase. Only one factor (prey density gradient) is supposed to influence the variations of predator velocity and this influence is supposed to be simply linear. However, even with all these simplifications, the model exhibits nontrivial dynamical properties.

It is important to note that neglecting the friction term in the velocity equation (13) is not a crucial hypothesis for obtaining spatially heterogeneous solutions. In the case of nonzero friction, all qualitative conclusions remain unchanged: the critical value κ_* only increases with an increase of the friction parameter v . The same is true for fixing the spatially averaged density of predators ($F_p \equiv 0$) in model (11)–(13): being reasonable for slowly reproducing predators, this assumption gives the possibility to analyse various consequences of spatial heterogeneity and, particularly, in terms of the effect of predator density on the trophic function.

In his experimental studies of predation in various fish species, Ivlev (1955, 1961) noticed that individual consumption depended very much on spatial heterogeneity of available food. The higher the spatial heterogeneity of the same food amount, the higher the total consumption rate. Ivlev concluded that the spatial characteristics of food distribution were at least as important as the average food density.

In the presented model, spatial heterogeneity is not given a priori. Rather, it appears spontaneously as a result of reaction–diffusion–advection and the response of acceleration. The hypothesis of predator acceleration being proportional to prey density gradient is the most important assumption of the proposed model (Govorukhin *et al.*, 2000). We must emphasize that neither pure diffusive models nor conventional taxis models (i.e., with the assumption that predator velocity is proportional to prey density gradient) are able to demonstrate heterogeneous regimes on a short time scale, under the same hypotheses about local interactions and boundary conditions as we use here (Lotka–Volterra trophic function and reflecting boundaries). In such models for two interacting species, complex local dynamics (limit cycles) induced by nonlinear prey production and predator

trophic function in the corresponding point models is a key condition for the appearance of stationary or travelling spatial structures within the closed habitat (Okubo, 1980; Mimura and Kawasaki, 1980; Mimura and Yamaguti, 1982; Murray, 1993; Czárán, 1998; Petrovskii and Malchow, 1999; Berezovskaya and Karev, 1999; Malchow, 2000).

It has been shown that the spatial heterogeneity induced by the migration activity is the cause of strong predator-dependence in the aggregated trophic function, with the extreme ratio-dependent form. Thus, the present work illustrates the suggestion of Arditi and Ginzburg (1989) that ratio-dependence is a simple way of summarizing the effects induced by spatial heterogeneity, while the prey-dependent form (e.g., Lotka–Volterra) is more appropriate in homogeneous environments. This confirms earlier results in which the sources of spatial heterogeneities were very different. In an experimental study in which Cladocerans were forced to different spatial distributions, Arditi and Saïah (1992) showed that homogeneously distributed populations presented characteristic features of predator-independent trophic functions (e.g., Lotka–Volterra or Holling) while heterogeneity induced features characteristic of predator-dependent functions (ratio-dependent or not). In a theoretical study, Cosner *et al.* (1999) investigated the effects of various modes of spatial grouping, including nonuniformity of the landscape itself and presence of refuges. They found that ratio-dependence can arise if either the predators or the prey form clusters. Other types of trophic functions (e.g., the response of DeAngelis *et al.*, 1975) can also be obtained with other grouping scenarios (see also Cantrell and Cosner, 1991) or other migration scenarios (Michalski *et al.*, 1997). In another theoretical study, Poggiale *et al.* (1998) modelled a situation with a fixed prey refuge. Their results were very similar to those of the present model: prey migrating out of the refuge are consumed almost immediately and the per capita consumption rate is necessarily proportional to the ratio of prey and predator densities. In the present model, the refuge is not predetermined. The subdivision into two types of zones arises spontaneously, with zones of low predator density acting as refuges for the prey. Moreover, the structure is not spatially stationary: zones are in constant movement. The heterogeneous solutions obtained with our PDE model are similar to those demonstrated by other authors who used cellular automata or individual based models (see, e.g., spatial chaos and schooling behaviour in Comins *et al.*, 1992; Flierl *et al.*, 1999). The problems of spatial averaging (aggregation) and of correct translation of the dynamics of a distributed population with density dependent

disturbances from one spatial scale to a finer or coarser modelling scale were recently investigated by Pascual and Levin (1999).

In sum, whatever their nature and causes (environmentally forced or behaviourally induced), spatial and temporal heterogeneities make the aggregated trophic function deviate from its local counterpart and increases the viability of the prey population and of the whole community. Conversely, systems with simple organisms in a homogeneous environment have shown a better agreement with prey-dependent models $g(N)$ (e.g., Gause, 1935; Luckinbill, 1973; Bohannan and Lenski, 1997, 1999; Kaunzinger and Morin, 1998; Jost and Arditi, 2000).

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