Taylor & Francis
Taylor & Francis Group

Spatiotemporal dynamics of two generic predator–prey models

Marcus R. Garvie[a]* and C. Trenchea[b]

*[a]Department of Mathematics and Statistics, University of Guelph, Guelph, ON, Canada N1G 2W1;
[b]Department of Mathematics, University of Pittsburgh, Pittsburgh, PA 15260, USA*

We present the analysis of two reaction–diffusion systems modelling predator–prey interactions, where the predator displays the Holling type II functional response, and in the absence of predators, the prey growth is logistic. The local analysis is based on the application of qualitative theory for ordinary differential equations and dynamical systems, while the global well-posedness depends on invariant sets and differential inequalities. The key result is an L^∞-stability estimate, which depends on a polynomial growth condition for the kinetics. The existence of an *a priori* L^p-estimate, uniform in time, for all $p \geq 1$, implies L^∞-uniform bounds, given any nonnegative L^∞-initial data. The applicability of the L^∞-estimate to general reaction–diffusion systems is discussed, and how the continuous results can be mimicked in the discrete case, leading to stability estimates for a Galerkin finite-element method with piecewise linear continuous basis functions. In order to verify the biological wave phenomena of solutions, numerical results are presented in two-space dimensions, which have interesting ecological implications as they demonstrate that solutions can be 'trapped' in an invariant region of phase space.

Keywords: predator–prey interaction; Holling type II functional response; reaction–diffusion system; invariant region; global existence; classical solution; limit cycle; *a priori* estimate

AMS Subject Classification: 35K57; 35B45; 92D25; 35A05

1. Introduction

In this paper, we study a class of generic spatially extended predator–prey systems in ecology, modelled by a coupled pair of reaction–diffusion equations. Although the reaction–diffusion system is a relatively simple model for the invasion of prey species by predators in a spatial domain, the solutions exhibit a wide spectrum of ecologically relevant behaviour. Spatiotemporal dynamics includes spiral waves, target patterns, and chaos [16,17,21]. The study of such spatiotemporal dynamics is an intensive area of research and there are still many unanswered questions concerning these solution types [21,24,37].

*Corresponding author. Email: mgarvie@uoguelph.ca
Author Email: trenchea@pitt.edu

We focus on reaction–diffusion systems modelling predator–prey interactions with the following general form [20, p. 84; 24, p. 71; 35]

$$\frac{\partial u}{\partial t} = \delta_1 \Delta u + r\, u \left(1 - \frac{u}{w}\right) - p\, v\, h(ku) \quad \text{in} \quad \Omega_T := \Omega \times (0, T),$$

$$\frac{\partial v}{\partial t} = \delta_2 \Delta v + q\, v\, h(ku) - s\, v \quad \text{in} \quad \Omega_T,$$

$$u(\mathbf{x}, 0) = u_0(\mathbf{x}), \quad v(\mathbf{x}, 0) = v_0(\mathbf{x}), \quad \mathbf{x} \in \Omega \tag{1}$$

$$\frac{\partial u}{\partial \boldsymbol{\nu}} = \frac{\partial v}{\partial \boldsymbol{\nu}} = 0 \quad \text{on} \quad \partial \Omega \times (0, T),$$

where $u(\mathbf{x}, t)$ and $v(\mathbf{x}, t)$ are the population densities of prey and predators at time t and (vector) position $\mathbf{x}$. The parameters δ_1, δ_2, r, w, p, k, q, and s are strictly positive. u and v represent the prey and predator densities with positive diffusion coefficients δ_1 and δ_2, respectively. The 'functional response' $h(\cdot)$ is assumed to be a C^2 function satisfying:

(i) $h(0) = 0$,
(ii) $\lim_{x \to \infty} h(x) = 1$,
(iii) $h(\cdot)$ is strictly increasing on $[0, \infty)$.

The functional response represents the prey consumption rate per predator, as a fraction of the maximal consumption rate p. The constant k determines how fast the consumption rate saturates as the prey density increases. q and r denote maximal per-capita predator and prey birth rates, respectively. s is the per-capita predator death rate and w is the prey carrying capacity.

We assume the domain Ω is a bounded and open subset of $\mathbb{R}^d$, $d \leq 3$, with a boundary $\partial \Omega$ of class $C^{2+\nu}$, $\nu > 0$ (i.e. $\partial \Omega$ is a $d - 1$ dimensional $C^{2+\nu}$ manifold on which Ω lies locally on one side). $\boldsymbol{\nu}$ denotes the outward normal to $\partial \Omega$ and Δ denotes $\sum_{i=1}^{d} \partial^2 / \partial x_i^2$.

In the above model, the local growth of the prey is logistic and the predator shows the 'Holling type II functional response' [11]. Type II functional responses are the most frequently studied functional responses, and are well documented in empirical studies (see [9,15,39] for reviews).

Our results apply to general boundary conditions, but for ease of exposition we focus on the homogeneous Neumann boundary condition case.

It will facilitate our analysis to express Equation (1) in nondimensional form via the rescaling of variables

$$\tilde{u} = \frac{u}{w}, \quad \tilde{v} = v\left(\frac{p}{r\, w}\right), \quad \tilde{t} = r\, t, \quad \tilde{x}_i = x_i \left(\frac{r}{\delta_1}\right)^{1/2},$$

and rescaling of parameters

$$a = k\, w, \quad b = \frac{q}{r}, \quad c = \frac{s}{r}, \quad \delta = \frac{\delta_2}{\delta_1}.$$

This leads to (after dropping the tildes) the nondimensional problem.

Find the prey $u(\mathbf{x}, t)$ and predator $v(\mathbf{x}, t)$ densities such that

$$\frac{\partial u}{\partial t} = \Delta u + u(1 - u) - v\, h(au) \quad \text{in} \quad \Omega_T := \Omega \times (0, T),$$

$$\frac{\partial v}{\partial t} = \delta \Delta v + b\, v\, h(au) - c\, v \quad \text{in} \quad \Omega_T,$$

$$u(\mathbf{x}, 0) = u_0(\mathbf{x}), \quad v(\mathbf{x}, 0) = v_0(\mathbf{x}), \quad \mathbf{x} \in \Omega \tag{2}$$

$$\frac{\partial u}{\partial \boldsymbol{\nu}} = \frac{\partial v}{\partial \boldsymbol{\nu}} = 0 \quad \text{on} \quad \partial \Omega \times (0, T),$$

where the parameters a, b, c, and δ are real and strictly positive. In this paper, we focus on the following specific type II functional responses with positive parameters α, β, and γ

$$h(\eta) = h_1(\eta) = \frac{\eta}{1 + \eta} \quad (\eta = au), \quad \text{with } a = 1/\alpha, b = \beta, c = \gamma, \tag{3a}$$

$$h(\eta) = h_2(\eta) = 1 - e^{-\eta} \quad (\eta = au), \quad \text{with } a = \gamma, c = \beta, b = \alpha\beta, \tag{3b}$$

due originally to Holling [12] and Ivlev [14], respectively. Thus, the two types of kinetics covered by our work are

(i) $f(u, v) = u(1 - u) - (uv/(u + \alpha))$, $\quad g(u, v) = (\beta uv/(u + \alpha)) - \gamma v$,
(ii) $f(u, v) = u(1 - u) - v(1 - e^{-\gamma u})$, $\quad g(u, v) = \beta v(\alpha - 1 - \alpha e^{-\gamma u})$.

The system of ordinary differential equations (ODEs), i.e. the spatially homogeneous system (2) with either kinetics, has been well studied [6,20,24]. The ODE system corresponding to kinetics (i) is sometimes called the Rosenzweig–MacArthur model [31] and has been used in many studies to fit ecological data. There are fewer studies in the literature concerning the 'spatially extended' reaction–diffusion system. One notable exception is a SIAM Review paper for plankton dynamics [21] modelled by Equation (2) with kinetics (i). For additional recent studies of system (2) concerning biological wave phenomena and chaos, see [2,10,18,25–29,34,36–38].

This paper provides a mathematical basis for computational studies of the systems, both from a numerical analysis [8] and a biological perspective [7]. To this end, we use linear stability analysis and well-known dynamical systems theory to derive conditions on the parameters that guarantee biologically meaningful equilibria and prove the existence of an arbitrary large invariant region in phase space for the case when the diffusion coefficients are equal (Section 3). In Section 4, we also provide an L^∞ *a priori* estimate that leads to global well-posedness of the classical, nonnegative solutions in either the equal or distinct diffusion coefficient case. In Section 5, we present the results of some numerical experiments using the Galerkin finite-element method with piecewise linear continuous basis functions, which illustrates the wave phenomena of solutions with some interesting biological implications. Finally, in Section 6, we discuss the wider applicability of the technique used to obtain an L^∞-estimate and provide some comments on how this estimate can be mimicked in the discrete case.

2. Preliminaries

We use standard notation for the Banach space $L^p(\Omega)$, $1 \le p < \infty$, with norm

$$\|u\|_{0,p} := \left(\int_\Omega |u(x)|^p \, dx \right)^{1/p}.$$

For $p = \infty$, $L^\infty(\Omega)$ is the Banach space with associated essential supremum norm

$$\|u\|_{0,\infty} \equiv \|u\|_{L^\infty(\Omega)} := \inf\{M : |u(x)| \le M \quad \text{a.e. on } \Omega\}.$$

Spaces consisting of vector-valued functions are denoted in bold face.

We use a simple L^p injection result, namely

$$\|u\|_{0,q} \le |\Omega|^{1/q-1/p} \|u\|_{0,p}, \quad \text{for } 1 \le q \le p \le \infty, \tag{4}$$

provided Ω is a bounded domain, and recall from Adams [1, Theorem 2.8] the following result: if $u \in L^p(\Omega)$ for $1 \le p < \infty$ and if there is a constant K such that for all p

$$\|u\|_{0,p} \le K,$$

then $u \in L^\infty(\Omega)$ and

$$\|u\|_{0,\infty} \le K.$$

We recall Young's inequality: for any $\varepsilon > 0, a, b \ge 0$ and $m, n > 1$

$$ab \le \varepsilon^{m/n} \frac{a^m}{m} + \frac{1}{\varepsilon} \frac{b^n}{n}, \quad \frac{1}{m} + \frac{1}{n} = 1. \tag{5}$$

Another useful inequality, valid for arbitrary $a, b \ge 0, 0 < p < 1$, is [30]

$$2^{p-1}(a^p + b^p) \le (a + b)^p \le a^p + b^p. \tag{6}$$

For notational convenience, we express the predator–prey system (2) in the following vector form after taking $\mathbf{u} := (u, v)^{\mathrm{T}}$:

$$\mathbf{u}_t = D\Delta\mathbf{u} + \mathbf{f}(\mathbf{u}), \quad \text{in} \quad \Omega_T, \tag{7a}$$

$$\mathbf{u}(\mathbf{x}, 0) = \mathbf{u}_0(\mathbf{x}), \quad \mathbf{x} \in \Omega, \quad \frac{\partial\mathbf{u}}{\partial\boldsymbol{\nu}} = \mathbf{0} \quad \text{on} \quad \partial\Omega \times (0, T), \tag{7b}$$

where

$$\mathbf{f}(\mathbf{u}) \equiv \begin{pmatrix} f(u, v) \\ g(u, v) \end{pmatrix} := \begin{pmatrix} u(1 - u) - v\,h(au) \\ b\,v\,h(au) - c\,v \end{pmatrix}, \quad D := \begin{pmatrix} 1 & 0 \\ 0 & \delta \end{pmatrix}. \tag{7c}$$

Throughout, we let C denote a finite, positive constant, possibly depending on $T_{\max}, \Omega, u_0$, and v_0, which may change from expression to expression.

3. Local analysis

We provide some details of the local dynamics of the reaction–diffusion system. This provides conditions on the parameters necessary for the solutions to have biologically meaningful equilibria and is also an aid in the correct choice of parameters when numerically simulating solutions of the full reaction–diffusion system (Section 5). We also provide a geometric construction of an 'invariant region' in phase space that allows us to deduce additional conditions on the parameters necessary for limit cycle kinetics in the positive quadrant of the phase space.

We focus on dynamics in the region $u > 0, v > 0$, corresponding to biologically meaningful solutions. The nullclines of kinetics (i) and (ii) (Section 1) are the solution curves corresponding to the equations $f = 0$ and $g = 0$. From linear stability analysis one finds that in both the cases we have saddle points at $(0, 0)$ and $(1, 0)$. There is also an equilibrium point (u^*, v^*) (stable or

unstable) corresponding to the coexistence of prey and predators given by

$$u^* = \frac{\alpha\gamma}{\beta - \gamma}, \quad v^* = (1 - u^*)(u^* + \alpha), \quad \beta > \gamma \quad \text{and} \quad \alpha < \frac{\beta - \gamma}{\gamma}, \tag{8}$$

$$u^* = -\frac{1}{\gamma}\ln\left(\frac{\alpha - 1}{\alpha}\right), \quad v^* = \frac{u^*(1 - u^*)}{1 - e^{-\gamma u^*}}, \quad \alpha > 1 \quad \text{and} \quad \gamma > -\ln\left(\frac{\alpha - 1}{\alpha}\right), \tag{9}$$

for kinetics (i) and (ii), respectively. Note that in both cases, we have $b > c$. The conditions on the parameters follow from $0 < u^* < 1$, which is necessary for the stationary point to be in the region $u > 0, v > 0$. For appropriate choices of the parameters, the kinetics of the system have a stable limit cycle surrounding the unstable stationary point (u^*, v^*), i.e. the densities of predators and prey cycle periodically in time. To find conditions that guarantee limit cycle kinetics in the positive quadrant of phase space, we first need the concept of an 'invariant' region for the spatially homogeneous situation:

DEFINITION 3.1 (invariant region for the ODE) *We define a positively invariant region corresponding to the spatially homogeneous version of system* (2), *to be a closed subset* $\mathbb{B}$ *of the phase-space* $\mathbb{R}^2$, *s.t. if the initial data* (u_0, v_0) *lies in* $\mathbb{B}$, *then the solution* $(u(t; u_0, v_0), v(t; u_0, v_0))$ *lies in* $\mathbb{B}$ *for all* $t > 0$ *for which the solution exists.*

After proving the existence of an invariant region that contains (u^*, v^*), we apply a standard theory of dynamical systems.

LEMMA 3.1 *The trapezoidal region* $\mathcal{T} \in [0, \infty)^2$ *defined by*

$$\mathcal{T} := \left\{ (u, v) : u \leq \bar{u}, \quad v \leq \frac{b}{c}\bar{u}(1 + c) - bu, \quad u \geq 0, \quad v \geq 0 \right\}, \quad \bar{u} \geq 1, \tag{10}$$

is positively invariant for the spatially homogeneous predator–prey system corresponding to Equation (2), *with either kinetics* (i) *or* (ii) *(Figure 1).*

Proof Observe that the reaction kinetics do not point out of $\mathcal{T}$ along $u = 0, v = 0$, and $u = \bar{u}$. To show that this is also true along the line $v = (b/c)\bar{u}(1 + c) - bu$, set $G(u, v) := v - (b/c)\bar{u}(1 +$
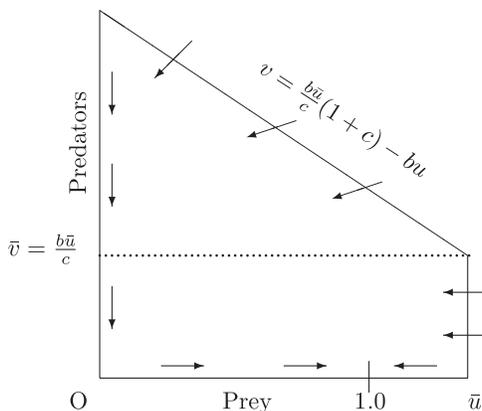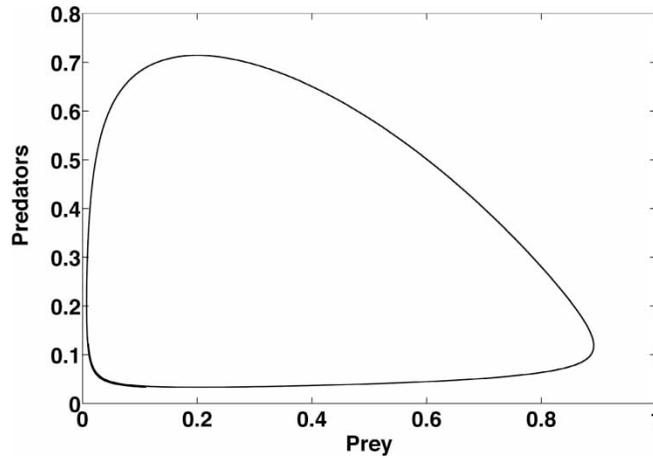

Figure 1. Invariant region $\mathcal{T}$.

Figure 2. Limit cycle for Equation (2) with kinetics (i). Parameter values: $\alpha = 1/5, \beta = 1.0, \gamma = 1/2$.

$c) + bu$ and denote the outward normal to $\mathcal{T}$ along this line by $\partial G := (\partial G/\partial u, \partial G/\partial v)^{\mathrm{T}} = (b, 1)^{\mathrm{T}}$. Then denoting the vector of reaction kinetics by $\mathbf{f} = (f, g)^{\mathrm{T}}$, we have

$$\partial G \cdot \mathbf{f}|_{v=(b/c)\bar{u}(1+c)-bu} = b(1+c)(u - \bar{u}) - bu^2 \leq 0,$$

as $0 \leq u \leq \bar{u}$, which proves the assertion. ∎

By choosing $\bar{u} \geq 1$ sufficiently large, we see that $\mathcal{T}$ will contain any point in $[0, \infty)^2$, thus the invariant region is arbitrarily large.

We derive simple conditions on the parameters that ensures the equilibrium point, given by Equation (8) or (9), is either an unstable node or an unstable focus, and thus by the well-known Poincaré–Bendixson theorem [43, Theorem 1.1.19], there exists a stable limit cycle solution surrounding this point (Figure 2).

PROPOSITION 3.1 *With the condition that*

$$\alpha < \frac{\beta - \gamma}{\beta + \gamma}, \quad (\beta > \gamma) \tag{11}$$

in the kinetics (i) *case, and the condition*

$$\gamma > \frac{2 \ln(1 - 1/\alpha)}{(1 - \alpha) \ln(1 - 1/\alpha) - 1}, \quad (\alpha > 1) \tag{12}$$

in the kinetics (ii) *case, the spatially homogeneous predator–prey system corresponding to Equation* (2) *contains a stable limit cycle in the positive quadrant of phase space. Furthermore, the limit cycle contains the equilibrium point (u^*, v^*), which is an unstable node or focus.*

Proof Define

$$A := \left. \begin{pmatrix} f_u & f_v \\ g_u & g_v \end{pmatrix} \right|_{(u^*, v^*)},$$

then the direct calculation leads to

$$\mathrm{tr}\, A = \gamma \left[\frac{1}{\beta} - \frac{\alpha(\beta + \gamma)}{\beta(\beta - \gamma)} \right], \quad |A| = \frac{\gamma}{\beta}(\beta - \gamma - \alpha\gamma),$$

for kinetics (i), and

$$\operatorname{tr} A = \frac{1}{\gamma}\left[(\alpha - 1)\left(\ln\left(1 - \frac{1}{\alpha}\right)\right)^2 + (\alpha\gamma - \gamma + 2)\ln\left(1 - \frac{1}{\alpha}\right) + \gamma\right],$$

$$|A| = \frac{\beta}{\gamma}(1 - \alpha)\ln\left(1 - \frac{1}{\alpha}\right)\left[\ln\left(1 - \frac{1}{\alpha}\right) + \gamma\right],$$

for kinetics (ii). Now it follows from the conditions on the parameters given in Equations (8) and (9) that we have $|A| > 0$ in both cases. Furthermore, with condition (11) in the kinetics (i) case and Equation (12) in the kinetics (ii) case, it also follows that $\operatorname{tr} A > 0$; thus, the equilibrium point (u^*, v^*) is an unstable node or focus [42, p. 107]. Thus, after noting Lemma 3.1, it follows from the Poincaré–Bendixson theorem that there exists a limit cycle solution in the positive quadrant of phase space surrounding the unstable equilibrium point. ∎

Note that Equations (11) and (12) imply the conditions on the parameters given in Equations (8) and (9), respectively. We also note that the invariant region defined by Equation (10) provides additional information concerning the boundedness of solutions and is also applicable to the full reaction–diffusion system (Section 4).

4. Well–posedness

Results from semigroup theory and an *a priori* estimate are used to prove the global existence and uniqueness of the classical solutions of the predator–prey system (2). The proof of global existence of solutions from the local existence in the equal diffusion coefficient case is a straightforward application of the invariant region method of Smoller [40]. In the distinct diffusion coefficient case, the proof of global existence requires additional theory as the only admissible invariant regions are products of intervals [40] and thus the invariant region method of Smoller is *inapplicable* in this case.

DEFINITION 4.1 (invariant region for the partial differential equation (PDE))   *We define a positively invariant region corresponding to the reaction–diffusion system* (2), *to be a closed subset $\mathbb{B}$ of the phase-space $\mathbb{R}^2$, s.t. if the initial data $(u_0(\mathbf{x}), v_0(\mathbf{x}))$ lies in $\mathbb{B}$ for all $\mathbf{x}$ in Ω, then the solution $(u(\mathbf{x}, t; u_0, v_0), v(\mathbf{x}, t; u_0, v_0))$ lies in $\mathbb{B}$ for all $\mathbf{x}$ and all $t > 0$ for which the solution exists.*

THEOREM 4.1   *Assume Ω is a bounded, open domain in $\mathbb{R}^d$, $d \leq 3$, with a boundary $\partial\Omega$ of class $C^{2+\nu}$, $\nu > 0$. Let $\boldsymbol{u}_0$ be nonnegative initial data in $\boldsymbol{L}^\infty(\Omega)$. Then, there exists a unique nonnegative classical solution of the predator–prey system* (2) *with the functional response* (3a) *or* (3b) *for all $(\mathbf{x}, t) \in \Omega \times [0, \infty)$. Furthermore, if $\delta = 1$, then the region $\mathcal{T}$ defined by Equation* (10) *is positively invariant for the system* (2).

Proof   The local existence of solutions is based on the well-known semigroup theory. After noting that f and g (Equation (7c)) are continuously differentiable and from the assumptions on the initial data, it follows immediately from Proposition 1 in [13] that Equation (2) has a unique classical solution (u, v), for $(\mathbf{x}, t) \in \Omega \times [0, T_{\max})$. Moreover, if $T_{\max} < \infty$ then

$$\lim_{t \uparrow T_{\max}} \sup_{\mathbf{x} \in \Omega}\{|u(\mathbf{x}, t)| + |v(\mathbf{x}, t)|\} = \infty. \tag{13}$$

To prove the nonnegativity of solutions, observe that the reaction kinetics satisfy

$$f(0, v), \ g(u, 0) \ge 0 \quad \text{for all } u, v \ge 0, \tag{14}$$

and by assumption the initial data $(u_0(\mathbf{x}), v_0(\mathbf{x}))$ are in $[0, \infty)^2$ for all $\mathbf{x} \in \Omega$. Thus, by a maximum principle [40, Lemma 14.20], the solution $(u(\mathbf{x}, t), v(\mathbf{x}, t))$ lies in $[0, \infty)^2$ for all $\mathbf{x} \in \Omega$ and for all $t > 0$ for which the solution of Equation (2) exists. In other words, $[0, \infty)^2$ is positively invariant for the system. To prove global existence of solutions from local existence in the equal diffusion coefficient case, we use the invariant region method of Smoller [40]. From Theorem 4.3 of [4] (alternatively, Theorem 14.13 of [40]) it follows that the invariant region $\mathcal{T}$ (10) is also invariant for the full PDE system (2). The invariant region yields an L^∞ *a priori* bound that contradicts nonglobal existence as solutions either exist for all time, or blow-up in the sup-norm in finite time [3] (Equation (13)).

In order to obtain global existence and uniqueness from local existence and uniqueness (in either the equal or distinct diffusion coefficient case) we present an *a priori* estimate contradicting the nonglobal existence. Note first that nonnegative classical solutions (u, v) exist on $\Omega \times [0, T_{\max})$. Thus, we can multiply the first equation in (2) by u^q and the second equation in Equation (2) by v^q for any $q \ge 1$ and apply Young's inequality (5) with $\varepsilon = 1, n = (q + 1)/q$, and $m = q + 1$, to yield

$$u^q u_t + v^q v_t = \frac{1}{(q + 1)} \frac{\partial}{\partial t}(u^{q+1} + v^{q+1}),$$

$$u^q f(u, v) + v^q g(u, v) \le \frac{1}{(q + 1)} C_q(u^{q+1} + v^{q+1}), \tag{15}$$

where $C_q := \max\{2q + 1, (q + 1)(b - c) + 1\}$. Integrating by parts over Ω, multiplying through by $q + 1$, and discarding nonessential positive terms on the LHS leads to

$$\frac{\mathrm{d}}{\mathrm{d}t} \left(\|u\|_{0,q+1}^{q+1} + \|v\|_{0,q+1}^{q+1} \right) \le C_q \left(\|u\|_{0,q+1}^{q+1} + \|v\|_{0,q+1}^{q+1} \right).$$

This leads immediately to for a.e. $t \in [0, T_{\max})$

$$\|u(t)\|_{0,q+1}^{q+1} + \|v(t)\|_{0,q+1}^{q+1} \le \mathrm{e}^{C_q t} \left(\|u_0\|_{0,q+1}^{q+1} + \|v_0\|_{0,q+1}^{q+1} \right). \tag{16}$$

Now due to the assumptions on the initial data, there exist positive constants M_1 and M_2 such that $\|u_0\|_{0,\infty} \le M_1$ and $\|v_0\|_{0,\infty} \le M_2$. Raising both sides of Equation (16) to the power of $1/(q + 1)$ and recalling Equation (6) and the L^p injection result (4) with $p = \infty$ lead to

$$2^{-(q/(q+1))}(\|u(t)\|_{0,q+1} + \|v(t)\|_{0,q+1}) \le \mathrm{e}^{(C_q/(q+1))t}(\|u_0\|_{0,q+1} + \|v_0\|_{0,q+1})$$

$$\le |\Omega|^{(1/(q+1))}\mathrm{e}^{(C_q/(q+1))t}(\|u_0\|_{0,\infty} + \|v_0\|_{0,\infty})$$

$$\le M|\Omega|^{(1/(q+1))}\mathrm{e}^{(C_q/(q+1))t},$$

where $M := \max\{M_1, M_2\}$. Multiplying both sides by $2^{q/(q+1)}$ yields

$$\|u(t)\|_{0,q+1} + \|v(t)\|_{0,q+1} \le 2M|\Omega|\mathrm{e}^{\hat{C}t},$$

where $\hat{C} := \max\{2, b - c + 1\}$, and so by Theorem 2.8 of Adams [1] (Section 2), we have

$$\|u(t)\|_{0,\infty} + \|v(t)\|_{0,\infty} \equiv \sup_{\mathbf{x} \in \Omega}\{|u(\mathbf{x}, t)| + |v(\mathbf{x}, t)|\}$$

$$\le 2M|\Omega|\mathrm{e}^{\hat{C}t},$$

and so taking limits as t tends to $T_{\max}$ yields

$$\lim_{t \uparrow T_{\max}} \sup_{\mathbf{x} \in \Omega} \{|u(\mathbf{x}, t)| + |v(\mathbf{x}, t)|\} \leq 2M|\Omega|e^{\hat{C}T_{\max}} < C.$$

Thus, $T_{\max} = \infty$, otherwise we have a contradiction to Equation (13). ∎

5. Numerical solutions

In order to illustrate the theoretical results of the previous section and the typical biological wave phenomena of the predator–prey system, we present some numerical results in two space dimensions. The predator–prey system was solved using a 'lumped mass', semi-implicit (in time) Galerkin finite-element method with piecewise linear continuous basis functions. We prove in a separate numerical paper [8] the convergence and stability of the finite-element method employed here.

We employed a (uniform) right-angled triangulation of the square $\Omega = (0, 100) \times (0, 100)$, with space steps h, and numerically solved the predator–prey system (2) with kinetics (i) up to time T with uniform time steps Δt, so that $N := T/\Delta t$.
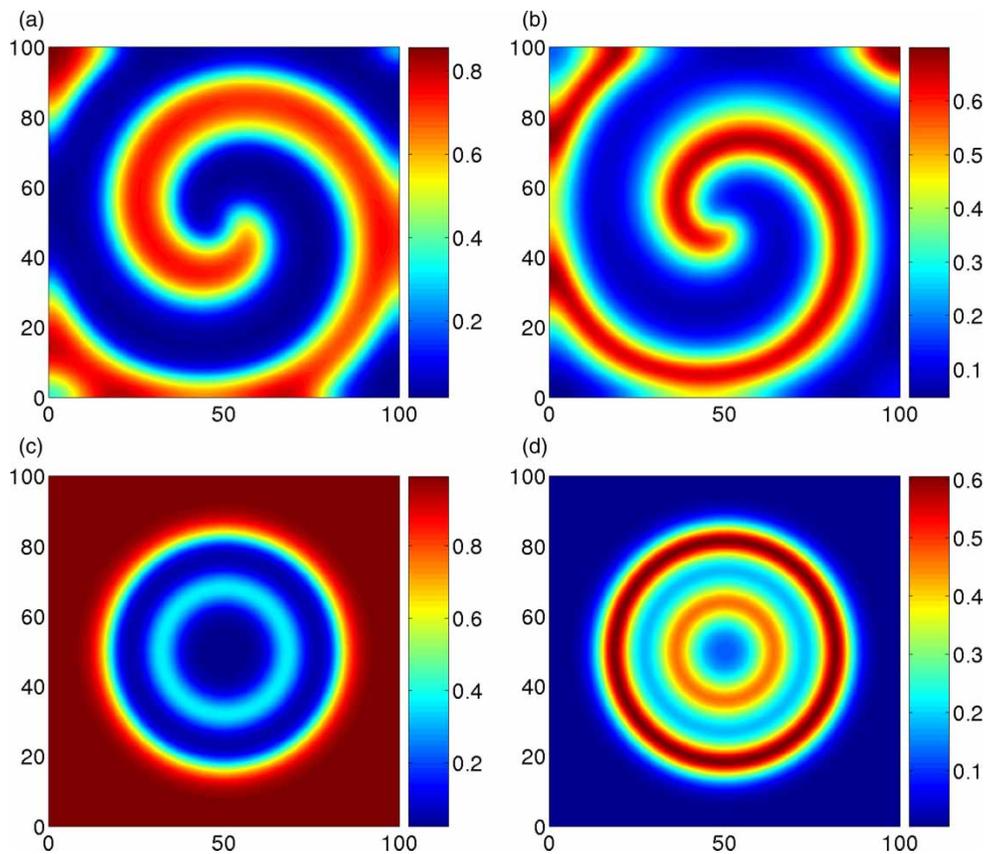

Figure 3. Snapshots of approximate prey densities (left) and approximate predator densities (right) for the predator–prey system with kinetics (i). In all plots, $h = 1/2$, $\Delta t = 1/384$, $\delta = 1$, $\alpha = 1/5$, $\beta = 1$, $\gamma = 1/2$. In (a) and (b), $T = 200$, $u_0(x, y) = 0.02(x/100) + 0.19$, $v_0(x, y) = 0.02(100 - y)/100 + 0.31$; in (c) and (d) $T = 25$, $u_0(x, y) = 0.2$, and $v_0(x, y) = 0.32$ if $(x - 50)^2 + (y - 50)^2 < 25$ and zero otherwise.
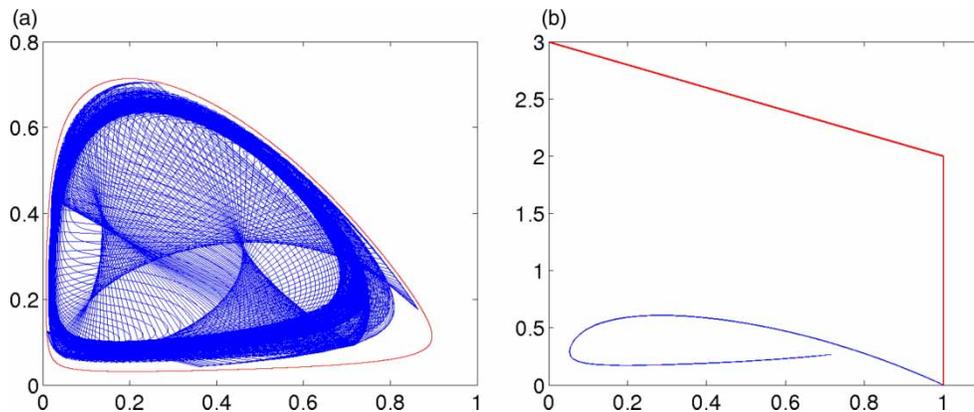
Figure 4. (Available in colour online). Plots of u against v at time T for all $\mathbf{x} \in \Omega$ (blue lines). (a) Corresponds to Figure 3(a) and (b), while (b) corresponds to Figure 3(c) and (d). The red lines indicate the limit cycle in (a) and the invariant region $\mathcal{T}$ in (b), respectively.

For the numerical experiments we chose initial conditions and parameter values that led to rotating spiral waves (Figure 3(a) and (b)) and expanding ring waves (Figure 3(c) and (d)). We also chose parameter values that satisfy condition (11) and thus there is a stable limit cycles in the reaction kinetics.

The finite-element formulation leads to a linear system of (sparse) algebraic equations, which we solved iteratively using the generalized minimal residual (GMRES) algorithm [33].

The results illustrated in Figure 3(a) and (b) did not require the use of preconditioners to solve the linear systems, while in Figure 3(c) and (d) we used preconditioners resulting from incomplete LU factorization [32] of the coefficient matrices. As these experiments employed equal diffusion coefficients, it follows from the theory of Smoller [40] that the limit cycle and the trapezoidal region $\mathcal{T}$ (Equation (10)) are invariant for the full PDE system. Thus, as the initial data used to generate the spiral wave solutions lie within the limit cycle, and the initial data used to generate the ring wave lie within the region $\mathcal{T}$, solutions remain trapped in these regions for all time (Figure 4(a) and (b)).

6. Conclusions and discussion

In this paper, we present the analysis of two generic spatially extended predator–prey systems in ecology. Initially, we consider the local dynamics of the system and derive conditions on the parameters that guarantee a stable limit cycle in the reaction kinetics. We then prove the global well-posedness of the classical nonnegative solutions, in either the equal or distinct diffusion coefficient case, with the aid of L^{∞}-uniform bounds. The results covering the unequal diffusion coefficients are important since in most terrestrial predator–prey systems the ratio of predator to prey dispersal rates is significantly greater than one. Numerical results are also provided, using the standard Galerkin finite-element method, leading to spiral waves and ring waves.

The biological wave phenomena illustrate that in the equal diffusion case, if the initial data are chosen inside the limit cycle of the reaction kinetics, or the invariant region $\mathcal{T}$, then solutions remain trapped in these regions for all time. Thus, in the absence of external influences, there are initial conditions that lead to spatial and temporal variations in densities of predators and prey that persist indefinitely. This has potentially important ecological implications. In natural resource management, if it is possible to create conditions that lead to a 'trapping region' in phase space for wildlife, then this could circumvent 'boom' or 'bust' scenarios.

We could have obtained global well-posedness from the theoretical framework presented by Morgan [22], which involves verifying 'intermediate sum' conditions and polynomial growth conditions on the kinetics. The theoretical framework of Morgan applies to a wide variety of problems; however, there are many conditions to check and the theory does not specify how to choose the Lyapunov-type conditions. In contrast, our approach via an *a priori* estimate is more direct. Furthermore, the analysis in this paper can be extended to cover a class of problems that are sufficiently general to include various biological systems in addition to the predator–prey equations studied in this paper. For example, the setup covers reaction–diffusion equations modelling plankton–fish dynamics [19], biological pattern formation [23], competing species [5], and generic oscillatory phenomena [16]. With this simplified setup and a known Lyapunov-type condition, a single polynomial growth condition leads to global existence of the classical solutions.

Another advantage of deriving an L^∞ estimate is that it facilitates a numerical analysis of the reaction–diffusion system. Discretization of reaction–diffusion systems typically involves two separate stages. In the first step, application of the finite-element method (in space) leads to an initial value problem for a large system of ODEs. In the second step, we must choose an appropriate time-stepping technique, which can be challenging due to the stiffness of the ODEs and the particular structure of the nonlinearity. It is advantageous if the numerics of the semi-discrete and fully discrete problems mimic the behaviour of the continuous problem. To verify this, it is necessary to derive discrete stability estimates, which is an important step in proving error bounds for the semi-discrete and fully discrete problems. If we apply the standard Galerkin finite-element method with piecewise linear continuous basis functions, coupled with the technique of 'Mass Lumping' [41], the L^∞ estimate in our paper can be closely mimicked in the semi-discrete case [8, Estimate I] leading to a semi-discrete stability estimate. The L^∞ estimate can also be partially mimicked in the fully-discrete finite-element case leading to a fully discrete stability estimate [8, Estimate III]. The main difficulty in the numerical analysis is the lack of a discrete maximum principle; thus, there is no guarantee of the nonnegativity of the discrete solutions.

This paper provides a firm mathematical basis for the future study of spatiotemporal dynamics in predator–prey systems and paves the way for subsequent theoretical and numerical work.

References

[1] R.A. Adams, *Sobolev Spaces*, Pure and Applied Mathematics, Academic Press, New York, 1975.
[2] D. Alonso, F. Bartumeus, and J. Catalan, *Mutual interference between predators can give rise to Turing spatial patterns*, Ecology 83(1) (2002), pp. 28–34.
[3] J.M. Ball, *Remarks on blow-up and nonexistence theorems for nonlinear evolution equations*, Q. J. Math. 2(28) (1977), pp. 473–486.
[4] K.N. Chueh, C.C. Conley, and J.A. Smoller, *Positively invariant regions for systems of nonlinear diffusion equations*, Indiana Univ. Math. J. 26(2) (1977), pp. 373–392.
[5] S.-I. Ei, R. Ikota, and M. Mimura, *Segregating partition problem in competition-diffusion systems*, Interfaces Free Bound 1(1) (1999), pp. 57–80.
[6] H. Freedman, *Deterministic Mathematical Models in Population Ecology*, Monographs and Textbooks in Pure and Applied Mathematics, Vol. 57, Marcel Dekker, Inc., New York, 1980.
[7] M.R. Garvie, *Finite difference schemes for reaction-diffusion equations modelling predator-prey interactions in MATLAB*, Bull. Math. Biol. 69(3) (2007), pp. 931–956.
[8] M.R. Garvie and C. Trenchea, *Finite element approximation of spatially extended predatorprey interactions with the Holling type II functional response*, Numer. Math. 107 (2007), pp. 641–667.
[9] W. Gentleman, A. Leising, B. Frost, S. Strom, and J. Murray, *Functional responses for zooplankton feeding on multiple resources: A review of assumptions and biological dynamics*, Deep Sea Res. Part II 50 (2003), pp. 2847–2875.
[10] W.S.C. Gurney, A.R. Veitch, I. Cruickshank, and G. McGeachin, *Circles and spirals: Population persistence in a spatially explicit predator–prey model*, Ecology 79(7) (1998), pp. 2516–2530.
[11] C.S. Holling, *Some characteristics of simple types of predation and parasitism*, Can. Entomol. 91 (1959), pp. 385–398.
[12] C.S. Holling, *The functional response of predators to prey density and its role in mimicry and population regulation*, Mem. Entomol. Soc. Can. 45 (1965), pp. 1–60.

[13] S.L. Hollis, R.H. Martin, and M. Pierre, *Global existence and boundedness in reaction–diffusion systems*, SIAM J. Math. Anal. 18(3) (1987), pp. 744–761.

[14] V.S. Ivlev, *Experimental Ecology of the Feeding Fishes*, Yale University Press, New Haven, 1961.

[15] J.M. Jeschke, M. Kopp, and R. Tollrian, *Predator functional responses: Discriminating between handling and digesting prey*, Ecol. Monogr. 72(1) (2002), pp. 95–112.

[16] N. Kopell and L.N. Howard, *Plane wave solutions to reaction–diffusion equations*, Stud. Appl. Math. 42 (1973), pp. 291–328.

[17] N. Kopell and L.N. Howard, *Target patterns and spiral solutions to reaction–diffusion equations with more than one space dimension*, Adv. Appl. Math. 2(4) (1981), pp. 417–449.

[18] H. Malchow and S.V. Petrovskii, *Dynamical stabilization of an unstable equilibrium in chemical and biological systems*, Math. Comput. Model. 36 (2002), pp. 307–319.

[19] H. Malchow, B. Radtke, M. Kallache, A.B. Medvinsky, D.A. Tikhonov, and S.V. Petrovski, *Spatio-temporal pattern formation in coupled models of plankton dynamics and fish school motion*, Nonlinear Anal. Real. World Appl. 1 (2000), pp. 53–67.

[20] R.M. May, *Stability and Complexity in Model Ecosystems*, Princeton University Press, New Jersey, 1974.

[21] A.B. Medvinsky, S.V. Petrovskii, I.A. Tikhonova, H. Malchow, and B.-L Li, *Spatiotemporal complexity of plankton and fish dynamics*, SIAM Rev. 44(3) (2002), pp. 311–370.

[22] J. Morgan, *Global existence for semilinear parabolic systems*, SIAM J. Math. Anal. 20(5) (1989), pp. 1128–1144.

[23] J.D. Murray, *On pattern formation mechanisms for lepidopteran wing patterns and mammalian coat markings*, Phil. Trans. R. Soc. Lond. B 295 (1981), pp. 473–496.

[24] J.D. Murray, *Mathematical Biology*, Biomathematics Texts, Vol. 19, Springer, Berlin, 1993.

[25] M. Pascual, *Diffusion-induced chaos in a spatial predator–prey system*, Proc. R. Soc. Lond. B 251 (1993), pp. 1–7.

[26] S.V. Petrovskii and H. Malchow, *A minimal model of pattern formation in a prey–predator system*, Math. Comput. Model. 29 (1999), pp. 49–63.

[27] S.V. Petrovskii and H. Malchow, *Wave of chaos: New mechanism of pattern formation in spatio-temporal population dynamics*, Theor. Popul. Biol. 59 (2001), pp. 157–174.

[28] S.V. Petrovskii and H. Malchow, *Critical phenomena in plankton communities: KISS model revisited*, Nonlinear Anal. Real World Appl. 1 (2000), pp. 37–51.

[29] V. Rai and G. Jayaraman, *Is diffusion-induced chaos robust?* Curr. Sci. India 84(7) (2003), pp. 925–929.

[30] J. Rodrigues, *Obstacle Problems in Mathematical Physics*, North-Holland, Amsterdam, 1987.

[31] M.L. Rosenzweig and R.H. MacArthur, *Graphical representation and stability conditions for predator–prey interaction*, Am. Nat. 97 (1963), pp. 209–223.

[32] Y. Saad, *Iterative Methods for Sparse Linear Systems*, SIAM, Philadelphia, 2003.

[33] Y. Saad and M.H. Schultz, GMRES: *A generalized minimal residual algorithm for solving nonsymmetric linear systems*, SIAM J. Sci. Statist. Comput. 7(3) (1986), pp. 856–869.

[34] N.J. Savill and P. Hogeweg, *Competition and dispersal in predator–prey waves*, Theor. Popul. Biol. 56 (1999), pp. 243–263.

[35] J.A. Sherratt, *Periodic travelling waves in cyclic predator–prey systems*, Ecol. Lett. 4 (2001), pp. 30–37.

[36] J.A. Sherratt, M.A. Lewis, and A.C. Fowler, *Ecological chaos in the wake of invasion*, Proc. Natl Acad. Sci. 92 (1995), pp. 2524–2528.

[37] J.A. Sherratt, B.T. Eagan, and M.A. Lewis, *Oscillations and chaos behind predator–prey invasion: Mathematical artifact or ecological reality?* Phil. Trans. R. Soc. Lond. B 352 (1997), pp. 21–38.

[38] J.A. Sherratt, X. Lambin, C.J. Thomas, and T.N. Sherratt, *Generation of periodic waves by landscape features in cyclic predator–prey systems*, Proc. R. Soc. Lond. B 269 (2002), pp. 327–334.

[39] G.T. Skalski and J.F. Gilliam, *Functional responses with predator interference: Viable alternatives to the Holling type II model*, Ecology 82(11) (2001), pp. 3083–3092.

[40] J. Smoller, *Shock Waves and Reaction–Diffusion Equations*, Grundlehren der mathematischen Wissenschaften, Vol. 258, Springer-Verlag, New York, 1983.

[41] V. Thomée, *Galerkin Finite Element Methods for Parabolic Problems*, 2nd ed., Springer Series in Computational Mathematics, Vol. 25, Springer-Verlag, Berlin, 2006.

[42] P.N.V. Tu. *Dynamical Systems: An Introduction with Applications in Economics and Biology*, Springer-Verlag, Berlin, 1994.

[43] S. Wiggins, *Introduction to Applied Nonlinear Dynamical Systems and Chaos*, Texts in Applied Mathematics, Vol. 2, Springer-Verlag, New York, 1990.