

Analysis of two generic spatially extended predator-prey models

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Abstract

We present the analysis of two reaction-diffusion systems modeling predator-prey interactions with the Holling Type II functional response and logistic growth of the prey. Initially we undertake the local analysis of the systems, deriving conditions on the parameters that guarantee a stable limit cycle in the reaction kinetics, and construct arbitrary large invariant regions in the equal diffusion coefficient case. We then provide an *a priori* estimate that leads to the global well-posedness of the classical (nonnegative) solutions, given any nonnegative L^∞ - initial data. In order to verify the biological wave phenomena of solutions and the theoretical results, numerical experiments are undertaken in two space dimensions using a Galerkin finite element method with piecewise linear continuous basis functions.

Key words: predator-prey interaction, Holling type II functional response, reaction-diffusion system, invariant region, global existence, classical solution, limit cycle, *a priori* estimate

1 Introduction

In this paper we study a class of generic spatially extended predator-prey systems in ecology, modeled 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 behavior. Spatiotemporal dynamics includes spiral waves, target patterns and chaos [15,16,19]. The study

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of such spatiotemporal dynamics is an intensive area of research and there are still many unanswered questions concerning these solution types (e.g. [19],[21],[33]).

We focus on reaction-diffusion systems modeling predator-prey interactions with the following general form (cf. [32], [21, page 71], [18, page 84])

$$\begin{cases} \frac{\partial u}{\partial t} = \delta_1 \Delta u + r u \left(1 - \frac{u}{w}\right) - p v h(ku) & \text{in } \Omega_T := \Omega \times (0, T), \\ \frac{\partial v}{\partial t} = \delta_2 \Delta v + q v h(ku) - s v & \text{in } \Omega_T, \\ u(\mathbf{x}, 0) = u_0(\mathbf{x}), \quad v(\mathbf{x}, 0) = v_0(\mathbf{x}), \quad \mathbf{x} \in \Omega \\ \frac{\partial u}{\partial \boldsymbol{\nu}} = \frac{\partial v}{\partial \boldsymbol{\nu}} = 0 & \text{on } \partial\Omega \times (0, T), \end{cases} \quad (1.1)$$

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 $\delta_1, \delta_2, r, w, p, k, q$, 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) $\lim_{x \rightarrow \infty} h(x) = 1$,
- (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’ [10]. Type II functional responses are the most frequently studied functional responses, and are well-documented in empirical studies (see [36,14,8] 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 (1.1) 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

$$\begin{cases} \frac{\partial u}{\partial t} = \Delta u + u(1 - u) - v h(au) & \text{in } \Omega_T := \Omega \times (0, T), \\ \frac{\partial v}{\partial t} = \delta \Delta v + b v h(au) - c v & \text{in } \Omega_T, \\ u(\mathbf{x}, 0) = u_0(\mathbf{x}), \quad v(\mathbf{x}, 0) = v_0(\mathbf{x}), \quad \mathbf{x} \in \Omega \\ \frac{\partial u}{\partial \nu} = \frac{\partial v}{\partial \nu} = 0 & \text{on } \partial\Omega \times (0, T), \end{cases} \quad (1.2)$$

where the parameters $a, b, c,$ and $\delta,$ are real and strictly positive. In this paper we focus on the following specific type II functional responses with positive parameters $\alpha, \beta,$ and γ

$$h(\eta) = h_1(\eta) = \frac{\eta}{1 + \eta} \quad (\eta = au), \quad \text{with } a = 1/\alpha, b = \beta, c = \gamma, \quad (1.3a)$$

$$h(\eta) = h_2(\eta) = 1 - e^{-\eta} \quad (\eta = au), \quad \text{with } a = \gamma, c = \beta, b = \alpha\beta, \quad (1.3b)$$

due originally to Holling [11] and Ivlev [13] respectively. Thus the two types of kinetics covered by our work are

$$\begin{aligned} \text{(i)} : \quad & f(u, v) = u(1 - u) - \frac{uv}{u + \alpha}, \quad g(u, v) = \frac{\beta uv}{u + \alpha} - \gamma v, \\ \text{(ii)} : \quad & f(u, v) = u(1 - u) - v(1 - e^{-\gamma u}), \quad g(u, v) = \beta v(\alpha - 1 - \alpha e^{-\gamma u}). \end{aligned}$$

The system of ODEs, i.e. the spatially homogeneous system (1.2) with either kinetics, has been well studied [18,21,5]. The ODE system corresponding to Kinetics (i) is sometimes called the Rosenzweig-MacArthur model [28], 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 recent SIAM Review paper for plankton dynamics [19] modelled by (1.2) with Kinetics (i). For additional recent studies of the system (1.2) concerning biological wave phenomena and chaos, see [2,9,17,22–26,31,33–35].

This paper provides a mathematical basis for computational studies of the systems, both from a numerical analysis [7] and a biological perspective [6]. 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 (Section 3). In Section 4 we also provide an L^∞ - *a priori* estimate that leads to global well-posedness of the classical, nonnegative

solutions. Finally, in Section 5, we present the results of some numerical experiments using a standard Galerkin finite element method with piecewise linear continuous basis functions that illustrates the theoretical behaviour and wave phenomena of solutions.

2 Preliminaries

We use the standard notation for the Sobolev spaces $W^{m,p}(\Omega)$, $m \in \mathbb{N}$, $p \in [1, \infty]$, with associated norms and semi-norms given by

$$\|u\|_{m,p} := \left(\sum_{0 \leq |\alpha| \leq m} \|D^\alpha u\|_{0,p}^p \right)^{1/p}, \quad |u|_{m,p} := \left(\sum_{|\alpha|=m} \|D^\alpha u\|_{0,p}^p \right)^{1/p},$$

respectively, where D^α is the standard multi-index notation for the mixed (generalized) partial derivatives of order $|\alpha|$ ($\alpha \in \mathbb{N} \cup \{0\}$). When $p = 2$, $W^{m,2}(\Omega)$ is denoted $H^m(\Omega)$ with norm $\|\cdot\|_m$ and semi-norm $|\cdot|_m$, and if additionally $m = 0$, $W^{0,2}(\Omega) \equiv L^2(\Omega)$. The usual $L^2(\Omega)$ inner product over Ω with norm $\|\cdot\|_0$ is denoted by (\cdot, \cdot) . Another standard Banach space we use is $L^\infty(\Omega)$, with associated essential supremum norm

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

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

We use a simple L^p injection result, namely

$$\|u\|_{0,q} \leq |\Omega|^{1/q-1/p} \|u\|_{0,p}, \quad \text{for } 1 \leq q \leq p \leq \infty, \quad (2.1)$$

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

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

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

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

In order to derive an *a priori* estimate we use the following Grönwall lemma in differential form: let $E(s) \in W^{1,1}(0, t)$ and $Q(s), P(s), R(s) \in L^1(0, t)$, where all functions are nonnegative. Then,

$$\frac{dE}{ds} + P(s) \leq R(s)E(s) + Q(s) \quad \text{a.e. in } [0, t] \quad (2.3a)$$

implies

$$E(t) + \int_0^t P(\tau) d\tau \leq e^{\Lambda(t)} E(0) + e^{\Lambda(t)} \int_0^t Q(\tau) d\tau, \quad (2.3b)$$

where $\Lambda(t) := \int_0^t R(\tau) d\tau$.

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

$$ab \leq \varepsilon^{m/n} \frac{a^m}{m} + \frac{1}{\varepsilon} \frac{b^n}{n}, \quad \frac{1}{m} + \frac{1}{n} = 1. \quad (2.4)$$

Another useful inequality, valid for arbitrary $a, b \geq 0$, $0 < p < 1$, is [27]

$$2^{p-1}(a^p + b^p) \leq (a + b)^p \leq a^p + b^p. \quad (2.5)$$

For notational convenience we express the predator-prey system (1.2) in the following vector form after taking $\mathbf{u} := (u, v)^T$:

$$\mathbf{u}_t = D\Delta\mathbf{u} + \mathbf{f}(\mathbf{u}), \quad \text{in } \Omega_T, \quad (2.6a)$$

$$\mathbf{u}(\mathbf{x}, 0) = \mathbf{u}_0(\mathbf{x}) \quad \mathbf{x} \in \Omega, \quad \frac{\partial \mathbf{u}}{\partial \nu} = \mathbf{0} \quad \text{on } \partial\Omega \times (0, T), \quad (2.6b)$$

$$\text{where } \mathbf{f}(\mathbf{u}) \equiv \begin{pmatrix} f(u, v) \\ g(u, v) \end{pmatrix} := \begin{pmatrix} u(1-u) - v h(au) \\ b v h(au) - c v \end{pmatrix}, \quad D := \begin{pmatrix} 1 & 0 \\ 0 & \delta \end{pmatrix}. \quad (2.6c)$$

Throughout we let C denote a finite, positive constant, possibly depending on T_{max} , Ω , 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 will allow us to give conditions on the parameters necessary for solutions to have biologically meaningful equilibria and will also be an aid in the correct choice of parameters when numerically simulating solutions of the full reaction-diffusion system (see 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 phase space.

We focus on dynamics in the region $u > 0, v > 0$, corresponding to biologically meaningful solutions. The nullclines of Kinetics (i) and Kinetics (ii) (see Section 1) are the solution curves corresponding to the equations $f = 0$ and $g = 0$. From linear stability analysis one finds that in both 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

$$u^* = \frac{\alpha\gamma}{\beta - \gamma}, \quad v^* = (1 - u^*)(u^* + \alpha), \quad \beta > \gamma \ \& \ \alpha < \frac{\beta - \gamma}{\gamma}, \quad (3.1)$$

$$u^* = -\frac{1}{\gamma} \ln\left(\frac{\alpha - 1}{\alpha}\right), \quad v^* = \frac{u^*(1 - u^*)}{1 - e^{-\gamma u^*}}, \quad \alpha > 1 \ \& \ \gamma > -\ln\left(\frac{\alpha - 1}{\alpha}\right), \quad (3.2)$$

for Kinetics (i) and Kinetics (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 (1.2), 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 standard theory of dynamical systems.

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

$$\mathcal{T} := \left\{ (u, v) : u \leq \bar{u}, \quad v \leq \frac{b}{c}\bar{u}(1+c) - bu, \quad u \geq 0, \quad v \geq 0 \right\}, \quad \bar{u} \geq 1, \quad (3.3)$$

is positively invariant for the spatially homogeneous predator-prey system corresponding to (1.2), with either Kinetics (i) or Kinetics (ii) (see 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 $v = \frac{b}{c}\bar{u}(1+c) - bu$, set $G(u, v) := v - \frac{b}{c}\bar{u}(1+c) + bu$, and denote the outward normal to \mathcal{T} along this line by $\partial G := (\partial G/\partial u, \partial G/\partial v)^T = (b, 1)^T$. Then denoting the vector of reaction kinetics by $\mathbf{f} = (f, g)^T$ we have

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

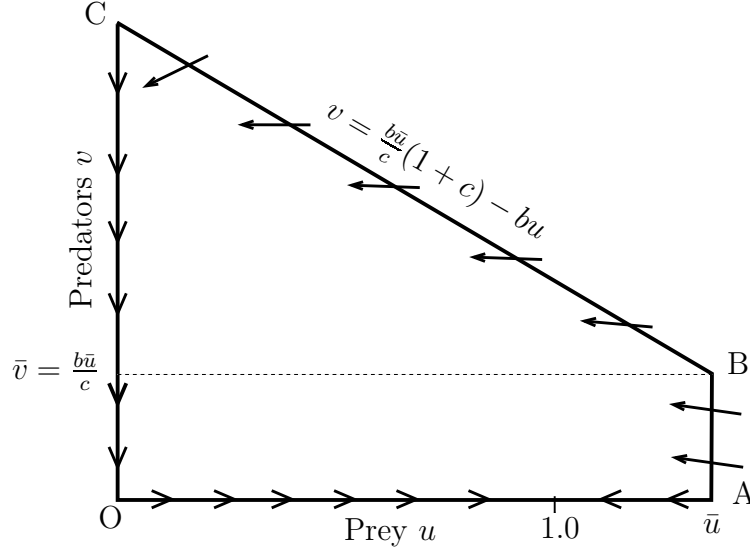


Fig. 1. Invariant region \mathcal{T}

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

Remark 3.1 *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 (3.1) or (3.2), is either an unstable node, or an unstable focus, and thus by the well-known Poincaré-Bendixson theorem there exists a stable limit cycle solution surrounding this point (see Figure 2).

Proposition 3.1 *With the condition that*

$$\alpha < \frac{\beta - \gamma}{\beta + \gamma}, \quad (\beta > \gamma) \quad (3.4)$$

in the Kinetics (i) case, and the condition

$$\gamma > \frac{2 \ln(1 - \frac{1}{\alpha})}{(1 - \alpha) \ln(1 - \frac{1}{\alpha}) - 1}, \quad (\alpha > 1) \quad (3.5)$$

in the Kinetics (ii) case, the spatially homogeneous predator-prey system corresponding to (1.2) 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

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

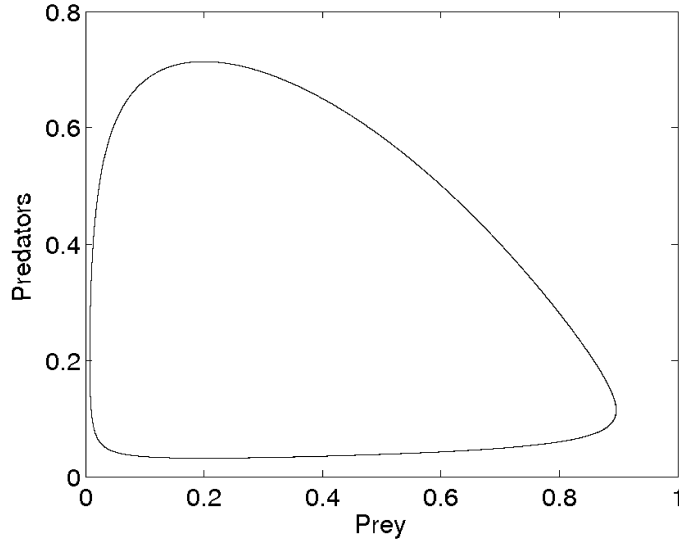


Fig. 2. Limit cycle for (1.2) with Kinetics (i). Parameter values: $\alpha = 1/5$, $\beta = 1.0$, $\gamma = 1/2$.

then direct calculation leads to

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

for Kinetics (i), and

$$\begin{aligned} \text{tr } A &= \frac{1}{\gamma} \left[(\alpha - 1) \left(\ln\left(1 - \frac{1}{\alpha}\right) \right)^2 + (\alpha\gamma - \gamma + 2) \ln\left(1 - \frac{1}{\alpha}\right) + \gamma \right], \\ |A| &= \frac{\beta}{\gamma} (1 - \alpha) \ln\left(1 - \frac{1}{\alpha}\right) \left[\ln\left(1 - \frac{1}{\alpha}\right) + \gamma \right], \end{aligned}$$

for Kinetics (ii). Now it follows from the conditions on the parameters given in (3.1) and (3.2) that we have $|A| > 0$ in both cases. Furthermore, with condition (3.4) in the Kinetics (i) case, and (3.5) in the Kinetics (ii) case, it also follows that $\text{tr } A > 0$, thus the equilibrium point (u^*, v^*) is an unstable node or focus (e.g. [38, p.107]). Thus after noting Lemma 3.1, it follows from the Poincaré-Bendixson theorem [39, Theorem 1.1.19] that there exists a limit cycle solution in the positive quadrant of phase space surrounding the unstable equilibrium point. \square

Remark 3.2 *We note that (3.4) and (3.5) imply the conditions on the parameters given in (3.1) and (3.2) respectively.*

Remark 3.3 *Instead of using the aid of an invariant region to prove the existence of a stable limit cycle in the reaction kinetics, we could have tried to implement the Kolmogorov Theorem [5, Theorem 5.1], which gives conditions for stable equilibrium points or limit cycles of the predator-prey system.*

Although the theorem is applicable to the predator-prey system with Kinetics (i), the necessary conditions are not entirely fulfilled in the Kinetics (ii) case. Furthermore, the invariant region defined by (3.3) provides additional information concerning the boundedness of solutions and is also applicable to the full reaction-diffusion system (see next section).

4 Well-posedness

We use results from semigroup theory and an *a priori* estimate to prove the global existence and uniqueness of the classical solutions of the predator-prey system (1.2).

Definition 4.1 (Invariant region for the PDE) We define a positively invariant region corresponding to the reaction-diffusion system (1.2), 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 \mathbf{u}_0 be nonnegative initial data in $\mathbf{L}^\infty(\Omega)$. Then there exists a unique nonnegative classical solution of the predator-prey system (1.2) with the functional response (1.3a) or (1.3b) for all $(\mathbf{x}, t) \in \Omega \times [0, \infty)$. Furthermore, if $\delta = 1$, then the region \mathcal{T} defined by (3.3) is positively invariant for the system (1.2).

Proof. The local existence of solutions is based on well-known semigroup theory. After noting that f and g (see (2.6c)) are continuously differentiable and the assumptions on the initial data it follows immediately from Proposition 1 in [12] that (1.2) has a unique classical solution (u, v) , for $(\mathbf{x}, t) \in \Omega \times [0, T_{max})$. Moreover, if $T_{max} < \infty$ then

$$\lim_{t \uparrow T_{max}} \sup_{\mathbf{x} \in \Omega} \{|u(\mathbf{x}, t)| + |v(\mathbf{x}, t)|\} = \infty. \quad (4.1)$$

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

$$\hat{f}(0, v), \hat{g}(u, 0) \geq 0 \quad \text{for all } u, v \geq 0,$$

and by assumption the initial data $(u_0(\mathbf{x}), v_0(\mathbf{x}))$ is in $[0, \infty)^2$ for all $\mathbf{x} \in \Omega$. Thus by a maximum principle (see e.g., [37, 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 (1.2) 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 is straightforward. From Theorem 4.3 of [4] (alternatively, Theorem 14.13 of [37]) it follows that the invariant region \mathcal{T}

(3.3) is also invariant for the full PDE system (1.2). The invariant region yields an L^∞ - *a priori* bound which contradicts non-global existence as solutions either exist for all time, or blow-up in the sup-norm in finite time [3] (see (4.1)). The proof of global existence results in the distinct diffusion coefficient case requires additional theory as the only admissible invariant regions are products of intervals [37].

In order to obtain global existence and uniqueness from local existence and uniqueness we present an *a priori* estimate contradicting non-global existence. Note first that nonnegative classical solutions (u, v) exist on $\Omega \times [0, T_{max})$. Thus we can multiply the 1st equation in (1.2) by u^q and the 2nd equation in (1.2) by v^q for any $q \geq 1$, and apply the Young's inequality (2.4) with $\varepsilon = 1$, $n = (q + 1)/q$, and $m = q + 1$, to yield

$$\begin{aligned} u^q u_t + v^q v_t &= \frac{1}{(q+1)} \frac{\partial}{\partial t} (u^{q+1} + v^{q+1}), \\ u^q f(u, v) + v^q g(u, v) &\leq \frac{1}{(q+1)} C_q (u^{q+1} + v^{q+1}), \end{aligned}$$

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

$$\frac{d}{dt} (\|u\|_{0,q+1}^{q+1} + \|v\|_{0,q+1}^{q+1}) \leq C_q (\|u\|_{0,q+1}^{q+1} + \|v\|_{0,q+1}^{q+1}).$$

Application of the Grönwall lemma (2.3a)-(2.3b) over $t \in [0, T_{max})$ leads to

$$\|u(t)\|_{0,q+1}^{q+1} + \|v(t)\|_{0,q+1}^{q+1} \leq e^{C_q t} (\|u_0\|_{0,q+1}^{q+1} + \|v_0\|_{0,q+1}^{q+1}). \quad (4.2)$$

Now due to the assumptions on the initial data there exists positive constants M_1 and M_2 such that $\|u_0\|_{0,\infty} \leq M_1$ and $\|v_0\|_{0,\infty} \leq M_2$. Raising both sides of (4.2) to the power of $1/(q + 1)$, recalling (2.5) and the L^p injection result (2.1) with $p = \infty$ leads to

$$\begin{aligned} 2^{-\left(\frac{q}{q+1}\right)} (\|u(t)\|_{0,q+1} + \|v(t)\|_{0,q+1}) &\leq e^{\left(\frac{C_q}{q+1}\right)t} (\|u_0\|_{0,q+1} + \|v_0\|_{0,q+1}) \\ &\leq |\Omega|^{\left(\frac{1}{q+1}\right)} e^{\left(\frac{C_q}{q+1}\right)t} (\|u_0\|_{0,\infty} + \|v_0\|_{0,\infty}) \\ &\leq M |\Omega|^{\left(\frac{1}{q+1}\right)} e^{\left(\frac{C_q}{q+1}\right)t}, \end{aligned}$$

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

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

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

$$\begin{aligned} \|u(t)\|_{0,\infty} + \|v(t)\|_{0,\infty} &\equiv \sup_{\mathbf{x} \in \Omega} \{|u(\mathbf{x}, t)| + |v(\mathbf{x}, t)|\} \\ &\leq 2M|\Omega|e^{\widehat{C}t}, \end{aligned}$$

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

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

Thus $T_{max} = \infty$, otherwise we have a contradiction to (4.1). \square

Remark 4.1 *In addition to the approach given above we could have obtained global existence and uniqueness results from the theoretical framework presented in [20], which involves verifying ‘intermediate sum’ conditions and polynomial growth conditions on the kinetics. However, our approach via an a priori estimate is more direct, and has the advantage of providing important clues for the numerical analysis of the predator-prey system (see Estimate I in [7]).*

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 [7] the convergence and stability of the finite element method presented 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 (1.2) with Kinetics (i) up-to time T with uniform time steps Δt , so that $N := T/\Delta t$. We introduce S^h , the standard finite element space

$$S^h := \{v \in C(\overline{\Omega}) : v|_{\tau} \text{ is linear } \forall \tau \in \mathcal{T}^h\} \subset H^1(\Omega).$$

Let $\{x_i\}_{i=0}^J$ be the set of nodes of the triangulation. We introduce $\pi^h : C(\overline{\Omega}) \mapsto S^h$, the Lagrange interpolation operator, such that $\pi^h v(x_j) = v(x_j)$ for all $j = 0, \dots, J$. In order to formulate our finite element approximation of the reaction-diffusion system we define a discrete L^2 inner product on $C(\overline{\Omega})$ given by $(u, v)^h := \int_{\Omega} \pi^h(u(x)v(x)) dx$, which approximates the usual L^2 inner product $(u(x), v(x))$. The fully discrete finite element approximation of the predator-

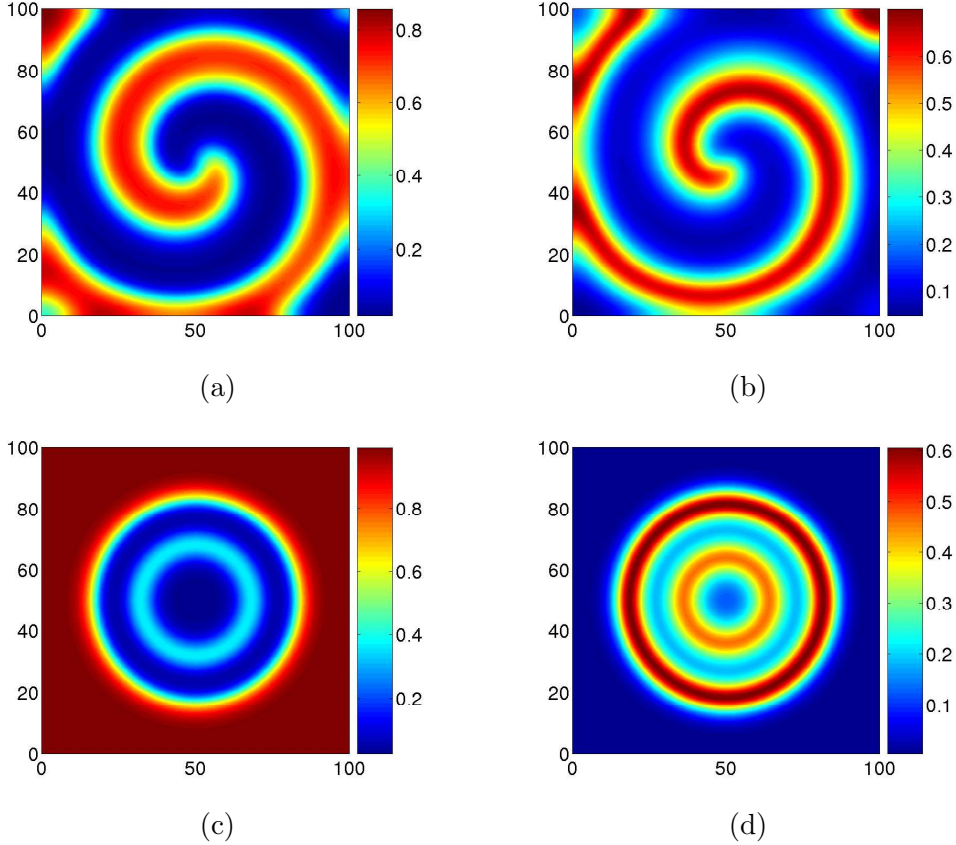


Fig. 3. Snapshots of approximate prey densities U^n (left) and approximate predator densities V^n (right). In all plots $h = 1/2$, $\Delta t = 1/384$, $\delta = 1$, $\alpha = 1/5$, $\beta = 1$, $\gamma = 1/2$. In (a)-(b) $T = 200$, $U^0 = \pi^h\{0.02(x/100) + 0.19\}$, $V^0 = \pi^h\{0.02(100 - y)/100 + 0.31\}$; in (c)-(d) $T = 25$, $U^0 = 0.2$, and $V^0 = 0.32$ if $(x - 50)^2 + (y - 50)^2 < 25$ and zero otherwise.

prey system can be written as follows: For $n = 1, \dots, N$ find $U^n, V^n \in S^h$ with initial densities $U^0 = \pi^h u_0(x)$, $V^0 = \pi^h v_0(x)$ such that

$$\begin{aligned} \frac{1}{\Delta t} (U^n - U^{n-1}, \chi^h)^h + (\nabla U^n, \nabla \chi^h) &= (U^n(1 - |U^{n-1}|) - \frac{U^{n-1}V^n}{|U^{n-1}|+\alpha}, \chi^h)^h, \\ \frac{1}{\Delta t} (V^n - V^{n-1}, \chi^h)^h + \delta (\nabla V^n, \nabla \chi^h) &= (\frac{\beta U^{n-1}V^n}{|U^{n-1}|+\alpha} - \gamma V^n, \chi^h)^h, \end{aligned}$$

for all $\chi^h \in S^h$. The finite element formulation leads to a linear system of (sparse) algebraic equations, which we solved iteratively using the GMRES algorithm [30].

For the numerical experiments we chose initial conditions and parameter values that led to rotating spiral waves and expanding ring waves (see Figure 3). We also chose parameter values that satisfy condition (3.4) and thus there is a stable limit cycles in the reaction kinetics (see Figure 2).

The results illustrated in Figures 3(a)-3(b) did not require the use of pre-

conditioners to solve the linear systems, while in Figures 3(c)-3(d) we used preconditioners resulting from Incomplete LU Factorization [29] of the coefficient matrices.

As these experiments employed equal diffusion coefficients, it follows from the theory of Smoller [37] that the limit cycle and the trapezoidal region \mathcal{T} (see (3.3)) are invariant for the full PDE system (see Section 4). Thus as the initial data used to generate the spiral wave solutions lies within the limit cycle, and the initial data used to generate the ring waves lies within the region \mathcal{T} , solutions remain trapped in these regions for all time (see Figure 4).

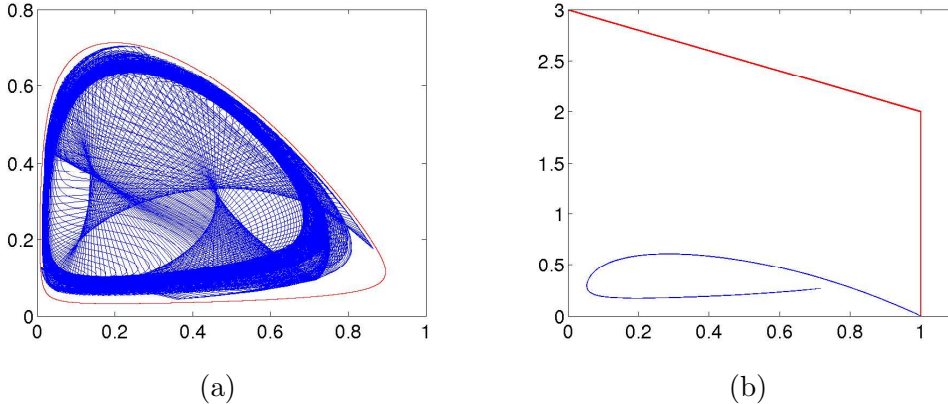


Fig. 4. Plot of u against v at times T for all $\mathbf{x} \in \Omega$ (blue lines). (a) corresponds to Figures 3(a)-3(b), while (b) corresponds to Figures 3(c)-3(d). The red lines indicate the limit cycle in (a) and the invariant region \mathcal{T} in (b) respectively.

6 Conclusions

In this paper we give an analysis of two generic spatially extended predator-prey systems in ecology. After considering the local dynamics of the system and deriving conditions on the parameters that guarantees a stable limit in the reaction kinetics we prove the global well-posedness of the classical (non-negative) solutions with the aid of an *a priori* estimate. Numerical results are also provided, using the standard Galerkin finite element method, leading to spiral waves and ring waves. These biological wave phenomena illustrate that in the equal diffusion case, if the initial data is 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.

This work provides an analytical framework for spatially extended predator-prey systems with the Holling Type II functional response and logistic growth of the prey, and paves the way for subsequent numerical work.

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