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Indirect taxis drives spatio-temporal patterns in an extended Schoener's intraguild predator–prey model

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A B S T R A C T

In Schoener's model of intraguild-predation a prey–predator interaction is mixed with the competition of the prey and the predator for food resource supplied to a system with a constant rate. In this work the model is extended to examine the impact of indirect prey taxis which counts for the movement of predator towards the odor released by prey rather than directly towards gradient of prey density (prey taxis) and indirect predator taxis which refers to prey movement opposite to the gradient of a chemical released by predator. The constant coexistence steady state in the model was shown earlier to be globally stable when Schoener's O.D.E. model is generalized to reaction–diffusion or even prey taxis system. Existence of global-in-time solutions to Schoener's model with indirect prey taxis is proved for any space dimension while for the case of indirect predator taxis only in 1D. This study reveals that sufficiently large value of taxis sensitivity parameter disturbs the stability of the coexistence steady state giving rise to pattern formation governed by the Hopf bifurcation. Numerical simulations illustrate emergence of taxis driven spatio-temporal periodic patterns.

1. Introduction

We consider Schoener's type predator–prey model [1] describing so called intraguild predation in which both predator and prey exploit competitively a common food resource which is available at some constant rate and shared between the predator and the prey. There are many examples of such an ecological interplay and we refer to [2] for the biological background with detailed description of Schoener's O.D.E. model and to [3,4] for mathematical results on extensions of the model to the case of reaction–diffusion or prey-taxis systems. In this work Schoener's model is extended to study the impact of indirect prey taxis which counts for indirect movement of predator towards the odor released by prey rather than directly towards gradient

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of prey (prey taxis) as well as predator taxis which refers to the movement of prey in the opposite direction to the gradient of chemical released by predator (c.f. [5–8]).

If N and P represent the densities of prey and predator distributed in domain $\Omega \subset I\!R^n$ with smooth boundary, W the concentration of chemo-attractant released by prey and U the concentration of chemical released by predator then the following system defined in $\Omega \times (0\,,+\infty)$ is an extension of Schoener's kinetic model:

$$\begin{cases} P_t = d_1 \Delta P - \chi \nabla \cdot (P \nabla W) + P\Big(\dfrac{bc}{cP+eN} + dN - \delta_1\Big)\,, \\ N_t = d_2 \Delta N + \xi \nabla \cdot (N \nabla U) + N\Big(\dfrac{be}{cP+eN} - dP - \delta_2\Big)\,, \\ W_t = d_3 \Delta W + \alpha_w N - \beta W\,, \\ U_t = d_3 \Delta U + \alpha_u P - \beta U\,, \end{cases} \tag{1}$$

with homogeneous Neumann boundary condition and initial conditions

$$\partial_\nu P = \partial_\nu N = \partial_\nu W = \partial_\nu U = 0 \quad \text{on} \quad \partial\Omega \times (0\,,\infty) \tag{2}$$

$$P(\cdot,0) = P_0\,, N(\cdot,0) = N_0\,, W(\cdot,0) = W_0\,, U(\cdot\,,0) = U_0\,. \tag{3}$$

where ∂_ν denotes derivative with respect to outer normal vector ν at the boundary $\partial\Omega$. In the sequel we shall separately consider the following two models:

$$\begin{aligned} &\text{Schoener's model with indirect prey taxis defined by setting in (1)–(3) :} \\ &\xi = 0\,, \alpha_u = 0\,, \chi > 0\,, \end{aligned} \tag{4}$$

$$\begin{aligned} &\text{Schoener's model with indirect predator taxis defined by setting in (1)–(3) :} \\ &\chi = 0\,, \alpha_w = 0\,, \xi > 0\,. \end{aligned} \tag{5}$$

In (1) d_i are diffusion coefficients, χ and ξ are chemotactic sensitivity coefficients, b represents a constant inflow of resources units, c and e are the conversion coefficients of the resource into number of offspring per population density unit for predator and prey respectively, δ_i are death rates, d is a predation coefficient proportional to the encounter rate, $\alpha_w\,, \alpha_u$ chemical production rates and β is a chemical degradation rate. Following [3,4] for simplicity we assume that in P-equation a conversion coefficient of the prey biomass into the number of predator's offspring equals 1.

It follows from earlier works [3,4] that neither diffusion nor prey taxis is capable to destabilize the unique homogeneous steady state which exists for some range of parameters. Contrary to the aforementioned extensions this work shows that in Schoener's model extended to account for indirect prey taxis or indirect predator taxis for sufficiently big chemotaxis sensitivity coefficients the steady state destabilizes giving rise to spatio-temporal patterns based on the Hopf bifurcation mechanism. Moreover, we provide a model example of a system in which the Hopf bifurcation appears for a reaction–diffusion system with taxis in the case when it is not possible to hold for the corresponding O.D.E. At last we notice that the existence of classical solutions for the full system (1) with $\xi, \chi > 0$ seems to be an open problem and in the light of [9] it is expected to hold for its parabolic–elliptic approximation.

2. Existence of global-in-time solutions

It turns out that proving existence of global in time solutions to each of the problems demands substantially different arguments and leads to restriction of space dimension to $n = 1$ for the case of Schoener's model with indirect predator taxis. This is due to the lack of L^∞ estimates on the predator density P while in the case of Schoener's model with indirect prey taxis the L^∞ estimate on prey density

N follows easily from the comparison principle. Note that assuming the logistic term in the P-equation (not present in the original Schoener's model) would lead to the global existence of solutions for $n = 2$ using similar arguments as in [7]. It is also worth noticing that contrary to Schoener's model with prey taxis [4] no restriction on the chemotactic sensitivity χ is needed to ensure global existence of solution. By $\|\cdot\|_p$ the standard norm in the space $L^P(\Omega)$ is denoted while $W^{k,p}(\Omega)$ denotes the Sobolev space.

Theorem 1. *Suppose that initial functions $N_0, P_0, W_0, U_0 \in W^{1,r}(\Omega)$, $r > n$. There exist unique global-in-time classical solutions (N, P, W) to problem (1)–(3) with (4) for all $n \geq 1$ and (N, P, U) to problem (1)–(3) with (5) for $n = 1$. The solutions are L^∞-bounded and satisfy boundary conditions and initial conditions in (2), (3) such that*

$$(N,P,W)\,,(N,P,U) \in \left(C([0\,,T) : W^{1,r}(\Omega)) \cap C^{2,1}(\bar{\Omega}\times(0\,,T))\right)^3 \quad \textit{for any } T>0\,.$$

Proof. Since both problems have the structure of a quasilinear parabolic system with a normally elliptic operator in the main part having upper-triangular structure the existence and uniqueness of maximal classical solutions $(N,P,W)\,,(N,P,U) \in \left(C([0\,,T_{max}) : W^{1,r}(\Omega)) \cap C^{2,1}(\bar{\Omega}\times(0\,,T_{max}))\right)^3$ satisfying boundary and initial conditions (2),(3) follows from Amann's theory [10, Theorems 14.4 &14.6] (see e.g. [6] for details) which has been already applied for similar problems in many papers. The non-negativity of solutions easily follows from the maximum principle. Moreover in this case it is known that a uniform in time L^∞-bound for the solution is enough to warrant that $T_{max} = +\infty$.

We are in the position to obtain a uniform L^1-bound for each of problems under consideration. On multiplying W-equation in problem (1)–(3) with (4) by $\frac{\delta_2}{2\alpha_w}$ and then integrating the equations over Ω using the boundary condition (2) we obtain upon summing up the equations

$$\begin{aligned} &\frac{d}{dt}\left(\int_\Omega P dx + \int_\Omega N dx + \frac{\delta_2}{2\alpha_w}\int_\Omega W dx\right) \\ &\leq -\delta_1 \int_\Omega P dx - \frac{\delta_2}{2}\int_\Omega N dx - \frac{\delta_2 \beta}{2\alpha_w}\int_\Omega W dx + b|\Omega| \\ &\leq -\min\left\{\delta_1\,, \frac{\delta_2}{2}\,, \beta\right\}\left(\int_\Omega P dx + \int_\Omega N dx + \frac{\delta_2}{2\alpha_w}\int_\Omega W dx\right) + b|\Omega|\,. \end{aligned} \tag{6}$$

In the case of problem (1)–(3) with (5) we proceed similarly multiplying the U-equation by $\frac{\delta_1}{2\alpha_u}$. Solving the differential inequality (6) with respect to $\xi(t) = (\int_\Omega P dx + \int_\Omega N dx + \frac{\delta_2}{2\alpha_w}\int_\Omega W dx)$ in the case of problem (1)–(3) with (4) and with respect to $\xi_1(t) = \left(\int_\Omega P dx + \int_\Omega N dx + \frac{\delta_1}{2\alpha_u}\int_\Omega U dx\right)$ in the case of problem (1)–(3) with (5) we deduce that there exists a constant $M > 0$ such that

$$\sup_{t\in[0\,,T_{max})} (\|N(t)\|_1 + \|P(t)\|_1 + \|W(t)\|_1 + \|U(t)\|_1) \leq M\,. \tag{7}$$

Next we consider the following prototype for the last equation in both problems

$$u_t = d_3 \Delta u - \beta u + f\,, \quad f \in C([0\,,T_{max}); L^q(\Omega)) \cap C(\bar{\Omega}\times(0\,,T_{max})) \tag{8}$$

with homogeneous Neumann boundary condition and initial condition $u_0 \in W^{1,r}(\Omega)\,, r > n$. By standard estimates of analytic semigroup theory (see e.g. [6, Lemma 2.3]) we infer that for some $\tau > 0$ and $C > 0$

$$\|\nabla u(\cdot,t)\|_p \leq C(1 + \sup_{t\in[0,T_{max})} \|f(\cdot,t)\|_q) \quad \text{for} \quad t \in [\tau\,,T_{max}) \tag{9}$$

provided

$$\frac{1}{2} + \frac{n}{2}\Big(\frac{1}{q} - \frac{1}{p}\Big) < 1\,, \quad \text{for} \quad p \in (1,\infty] \ \text{ and } \ q \in [1,\infty)\,. \tag{10}$$

The remaining part of the proof of the global existence of solutions splits.

Let us first consider an easier case of problem (1)–(3) with (4). To this end we notice that due to the embedding $W^{1,r}(\Omega) \subset C(\bar{\Omega})$ by the comparison with O.D.E. we obtain that

$$\sup_{t\in[\tau\,,T_{max})}\{\|N(t)\|_\infty\} \le \max\{\|N_0\|_\infty\,,\frac{b}{\delta_2}\} \tag{11}$$

and setting in (8) $f = \alpha_w N$ with $q > n$ and $p = \infty$ we infer that $\sup_{t\in[\tau\,,T_{max})}\{\|\nabla W(t)\|_\infty\} < \infty$ and then adjusting the Moser–Alikakos iteration for the P-equation in much the same way as in the proof of [6, Theorem 1.1] we obtain that $\sup_{t\in[0\,,T_{max})}\{\|P(t)\|_\infty\} < C_1$ where C_1 depends on the uniform L^1-bound in (7). It follows that in fact $T_{max} = +\infty$ for problem (1)–(3) with (4). To prove a uniform L^∞-bound of solution to problem (1)–(3) with (5) we shall first show that $\sup_{t\in[0\,,T_{max})}\{\|P(t)\|_2\} < \infty$ which is the first step to deduce the L^∞-estimate on ∇U in the case $n = 1$. The Gagliardo–Nirenberg inequality in the following form (see e.g. [7, Lemma 3.3]) will be used twice

$$\|v\|_4^4 \le C_{G-N}\Big(\|\nabla v\|_2^2\,\|v\|_1^2 + \|v\|_1^4\Big) \quad \text{for} \quad v \in W^{1,2}(\sigma_1\,,\sigma_2) \tag{12}$$

where $\Omega = (\sigma_1\,,\sigma_2) \subset I\!R$ is an interval. On multiplying the P-equation by P for problem (1)–(3) with (5) we use first the Hölder inequality and next the Gagliardo–Nirenberg inequality (12) to obtain

$$\begin{aligned}&\frac{1}{2}\frac{d}{dt}\int_\Omega P^2dx + d_1\int_\Omega |\nabla P|^2dx + \delta_1\int_\Omega P^2dx = bc\int_\Omega Pdx + d\int_\Omega NP^2dx \le \\ &\le bc\int_\Omega Pdx + \|N\|_2\|P\|_4^2 \le bc\int_\Omega Pdx + \frac{d^2}{4\varepsilon}\int_\Omega N^2dx + \varepsilon C_{G_N}(\|\nabla P\|_2^2\|P\|_1^2 + \|P\|_1^4)\,.\end{aligned}$$

Choosing suitable ε and using (7) we can find C_1 such that

$$\frac{1}{2}\frac{d}{dt}\int_\Omega P^2dx + \delta_1\int_\Omega P^2dx \le C_1\Big(1 + \int_\Omega N^2dx\Big)\,. \tag{13}$$

Next observe that setting in (8) $f = \alpha_u P\,, n = 1$ and $q = 1$ it follows that for any $p \in [1\,,\infty)$ condition (10) is satisfied and hence

$$\sup_{t\in[\tau\,,T_{max})}\{\|\nabla U(t)\|_p\} < \infty \quad \text{for any} \quad p \in [1\,,\infty)\,. \tag{14}$$

On multiplying the N-equation in problem (1)–(3) with (5) by N and using twice the Young inequality with ε and ε' and then the Gagliardo–Nirenberg inequality (12) we arrive at

$$\begin{aligned}&\frac{1}{2}\frac{d}{dt}\int_\Omega N^2dx + d_2\int_\Omega |\nabla N|^2dx + \delta_2\int_\Omega N^2dx = be\int_\Omega Ndx - d\int_\Omega NP^2dx - \xi\int_\Omega N\nabla U\nabla Ndx \\ &\le be\int_\Omega Ndx + \varepsilon\int_\Omega |\nabla N|^2dx + C_\varepsilon\|N\|_4^2\|\nabla U\|_4^2 \\ &\le be\int_\Omega Ndx + \varepsilon\int_\Omega |\nabla N|^2dx + C_\varepsilon\varepsilon'\|N\|_4^4 + C_\varepsilon C_{\varepsilon'}\|\nabla U\|_4^4 \\ &\le be\int_\Omega Ndx + \varepsilon\int_\Omega |\nabla N|^2dx + C_\varepsilon\varepsilon' C_{G_N}\Big(\Big(\int_\Omega |\nabla N|^2dx\Big)\|N\|_1^2 + \|N\|_1^4\Big) + C_\varepsilon C_{\varepsilon'}\|\nabla U\|_4^4\,.\end{aligned}$$

Choosing suitable ε and ε' and using (7) and (14) for $p = 4$ we get

$$\frac{1}{2}\frac{d}{dt}\int_\Omega N^2dx + \delta_2\int_\Omega N^2dx \le C_1'$$

where C_1' depends on M. It follows that there exists a constant C_2' such that

$$\sup_{t\in[0\,,T_{max})}\{\|N(t)\|_2\} < C_2'.$$

Combining this with (13) we infer that there exists a constant C_2'' such that

$$\sup_{t\in[0\,,T_{max})}\{\|P(t)\|_2\} < C_2'.$$

It remains to use again the regularity result for (8) with $f = \alpha P$ whence for $q = 2$ we may set in (10) $p = \infty$. Hence, $\sup_{t\in[\tau\,,T_{max})}\{\|\nabla U(t)\|_\infty\} < \infty$ and to find the uniform in time L^∞-bound on N in problem (1)–(3) with (5) the Moser–Alikakos iterative technique may be used again. Owing the L^∞-bound on N the uniform estimate on P follows from (7) and the classical paper by Alikakos [11] which completes the proof. □

3. Stability of the constant coexistence steady state and occurrence of the Hopf bifurcation

The constant steady state $\bar{E} = (\bar{N}, \bar{P}, \bar{W})$ with

$$\bar{P} = -\frac{\delta_2}{d} + \frac{be}{e\delta_1 - c\delta_2},\ \ \bar{N} = \frac{\delta_1}{d} - \frac{bc}{e\delta_1 - c\delta_2},\ \ \bar{W} = \frac{\alpha_w \bar{N}}{\beta} \tag{15}$$

is the unique coexistence steady state in model (1)–(3) with (4) under the condition

$$\frac{\delta_2}{ed} < \frac{b}{e\delta_1 - c\delta_2} < \frac{\delta_1}{cd} \tag{16}$$

which was found in [4] for O.D.E. system and extends by obvious reasons also for both models with an obvious modification $\bar{U} = \frac{\alpha_u \bar{P}}{\beta}$ in the place of $\bar{W}$ in the case of model (1)–(3) with (5).

The linearization of model (1)–(3) with (4) at the steady state $\bar{E}$ leads to the following stability matrix

$$J_j(\bar{E}) = \begin{pmatrix} j_{11} - d_1 h_j & j_{12} & \chi \bar{P} h_j \\ j_{21} & j_{22} - d_2 h_j & 0 \\ 0 & \alpha_w & -\beta - d_3 h_j \end{pmatrix} \tag{17}$$

where $\{h_j\}_{j=1}^{\infty}$ are positive eigenvalues of the Laplace operator $-\Delta$ on Ω with Neumann boundary conditions and

$$j_{11} = -\frac{bc^2\bar{P}}{(c\bar{P} + e\bar{N})^2} < 0,\ \ j_{12} = \Big(d - \frac{ebc}{(c\bar{P} + e\bar{N})^2}\Big)\bar{P}\,, \tag{18}$$

$$j_{21} = -\frac{ebc\bar{N}}{(c\bar{P} + e\bar{N})^2} - d\bar{N} < 0,\ \ j_{22} = -\frac{e^2 b\bar{N}}{(c\bar{P} + e\bar{N})^2} < 0\,. \tag{19}$$

Notice that for $j = 0$ there is $h_j = 0$ and the system reduces to the O.D.E case. The characteristic polynomial to (17) reads

$$\lambda^3 + \phi_j^1 \lambda^2 + \phi_j^2 \lambda + \phi_j^3 = 0\,, \tag{20}$$

where

$$\begin{aligned}
\phi_j^1 &= -\mathrm{tr} J_j(\bar{E}) = (\beta - j_{11} - j_{22}) + (d_1 + d_2 + d_3)h_j := \alpha_0 + \alpha_1 h_j,\\
\phi_j^2 &= (j_{11}j_{22} - j_{12}j_{21} - j_{11}\beta - j_{22}\beta) + (-j_{11}(d_2 + d_3) - j_{22}(d_1 + d_3) + \beta(d_1 + d_2))h_j\\
&\quad + (d_1d_2 + d_1d_3 + d_2d_3)h_j^2 := \beta_0 + \beta_1 h_j + \beta_2 h_j^2,\\
\phi_j^3 &= (j_{11}j_{22}\beta - j_{12}j_{21}\beta) + (j_{11}j_{22}d_3 - j_{12}j_{21}d_3 - j_{11}\beta d_2 - j_{22}\beta d_1 - j_{21}\alpha_w \chi \bar{P})h_j\\
&\quad + (-j_{11}d_2d_3 - j_{22}d_1d_3 + \beta d_1 d_2)h_j^2 + d_1d_2d_3h_j^3,\\
&\quad := \gamma_0 + \gamma_1 h_j + \gamma_2 h_j^2 + \gamma_3 h_j^3 - \chi j_{21}\alpha \bar{P} h_j := \phi_j^{3,1} + \chi \phi_j^{3,2},
\end{aligned}$$

where $\phi_j^{3,1} = \gamma_0 + \gamma_1 h_j + \gamma_2 h_j^2 + \gamma_3 h_j^3$ and $\phi_j^{3,2} = -j_{21}\alpha_w \bar{P} h_j > 0$. It can be checked using (18)–(19) that the coefficients $\alpha_j,\ \beta_j,\ \gamma_j$ defined above are strictly positive provided $j_{12} \geq 0$. It follows that

$\phi_j^3 = -detJ_j(\bar{E}) = \phi_j^{3,1} + \chi\phi_j^{3,2} > 0$. By substituting the steady state coordinates (15) to j_{12} in (18) we find that

$$j_{12} > 0 \quad \text{iff} \quad \frac{b}{e\delta_1 - c\delta_2} < \frac{\sqrt{b}}{\sqrt{ecd}} \tag{21}$$

and combining it with the upper bound in (16) we infer that condition

$$\delta_1^2 e < bcd \tag{22}$$

implies $j_{12} > 0$. Notice that $\phi_j^1, \phi_j^2, \phi_j^3 > 0$ and the last Routh–Hurwitz stability criterion reads

$$\Phi_j := \phi_j^1\phi_j^2 - \phi_j^3 = \phi_j^1\phi_j^2 - \phi_j^{3,1} - \chi\phi_j^{3,2}. \tag{23}$$

Let us denote

$$\Psi(h_j) = \phi_j^1\phi_j^2 - \phi_j^{3,1} = (\alpha_0\beta_0 - \gamma_0) + (\alpha_1\beta_0 + \alpha_0\beta_1 - \gamma_1)h_j + (\alpha_0\beta_2 + \alpha_1\beta_1 - \gamma_2)h_j^2 + (\alpha_1\beta_2 - \gamma_3)h_j^3$$

A straightforward calculation shows that all coefficients of the third order polynomial $\Phi(h_j)$ are positive. Now we are in a position to calculate the critical value of chemotaxis sensitivity parameter χ for the stability of the steady state $\bar{E}$. To this end from (23) we obtain

$$\chi_c = \min_{j\in\mathbb{N}_+} = \left\{\frac{\Psi(h_j)}{\phi_j^{3,2}}\right\} = \min_{j\in\mathbb{N}_+}\left\{\frac{\Psi(h_j)}{-j_{21}\alpha_w\bar{P}h_j}\right\}. \tag{24}$$

To see that $\chi_c > 0$ let us consider the function $\tilde{\Psi}(h_j) = \frac{\Psi(h_j)}{h_j}$. Since the coefficients of the polynomial Ψ are positive we infer that $\tilde{\Psi}(x) > 0 \quad \text{for } x > 0 \quad \text{and} \quad \lim_{x\to 0^+}\tilde{\Psi}(x) = \lim_{x\to+\infty}\tilde{\Psi}(x) = +\infty$, thus $\chi_c > 0$. Moreover, if

$$\tilde{\Psi}(h_j) \neq \tilde{\Psi}(h_k) \quad \text{for} \quad j \neq k \tag{25}$$

then of course the minimum is attained for a single $j = j_0$. To show the occurrence of Hopf bifurcation we use [12] and follow approach used in [8, Theorem 3.2]. Let $\lambda_1(\chi) \in \mathbb{R}$ and $\lambda_{2,3} = \sigma(\chi) \pm i\tau(\chi)$ be the roots of the characteristic polynomial (20). Then we have

$$\begin{aligned} -\phi_{j_0}^1 &= \mathrm{tr}J_{j_0}(\bar{E}) = 2\sigma(\chi) + \lambda_1(\chi), \\ \phi_{j_0}^2 &= \lambda_1\lambda_2 + \lambda_1\lambda_3 + \lambda_2\lambda_3 = \sigma(\chi)^2 + \tau(\chi)^2 + 2\sigma(\chi)\lambda_1(\chi), \\ -\phi_{j_0}^3(\chi) &= \det J_{j_0}(\bar{E}) = \Big(\sigma(\chi)^2 + \tau(\chi)^2\Big)\lambda_1(\chi). \end{aligned} \tag{26}$$

Notice that $\lambda_1(\chi) < 0$. Since $\sigma(\chi_c) = 0$ by (26) we have $\tau(\chi_c)^2 = \phi_{j_0}^2 > 0$ and upon differentiating each equation with respect to the bifurcation parameter χ we obtain

$$2\sigma'(\chi) + \lambda_1'(\chi) = 0, \tag{27}$$

$$2\sigma(\chi)\sigma'(\chi) + 2\tau(\chi)\tau'(\chi) + 2\sigma'(\chi)\lambda_1(\chi) + 2\sigma(\chi)\lambda_1'(\chi) = 0, \tag{28}$$

$$2\sigma(\chi)\sigma'(\chi)\lambda_1(\chi) + \sigma(\chi)^2\lambda_1'(\chi) + 2\tau(\chi)\tau'(\chi)\lambda_1(\chi) + \tau(\chi)^2\lambda_1'(\chi) = -\phi_{j_0}^{3,2}. \tag{29}$$

Evaluating the above functions at $\chi = \chi_c$ we infer from (27) that $\sigma'(\chi_c) = -\frac{1}{2}\lambda_1'(\chi_c)$ and reminding that $\sigma(\chi_c) = 0$ it follows from (28)–(29) that

$$0 = 2\tau(\chi_c)\tau'(\chi_c) + 2\sigma'(\chi_c)\lambda_1(\chi_c) \quad \text{and} \quad -\phi_{j_0}^{3,2} = 2\tau(\chi_c)\tau'(\chi_c)\lambda_1(\chi_c) + \tau(\chi_c)^2\lambda_1'(\chi_c).$$

By solving this system and making use of the equality $\lambda_1(\chi_c) = -\phi_{j_0}^1 = \mathrm{tr}J_{j_0}(\bar{E})$ we finally get

$$\lambda_1'(\chi_c) = \frac{-\phi_{j_0}^{3,2}}{(\phi_{j_0}^1)^2 + \phi_{j_0}^2} < 0, \text{ whence,} \quad \sigma'(\chi_c) > 0.$$

This verifies the transversality condition required for the occurrence of the Hopf-bifurcation at $\chi = \chi_c$. We thus proved the following theorem.

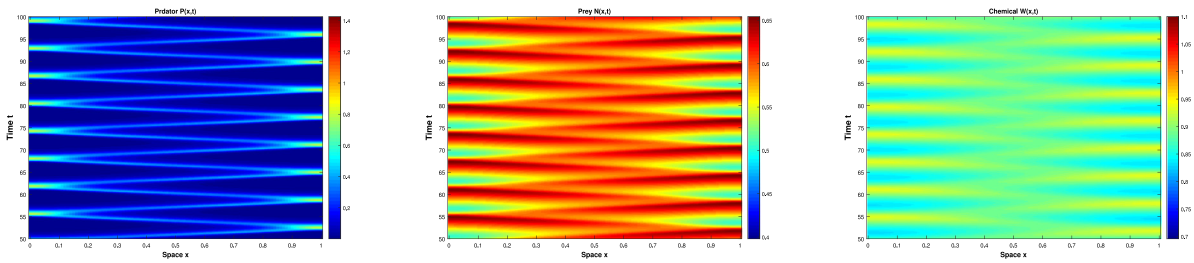
Theorem 2. *Under assumptions (22) the constant steady state $\bar{E}$ in problem (1)–(3) with (4) is locally asymptotically stable if $\chi < \chi_c$ defined in (24). If $\chi > \chi_c$ the steady state is unstable. At $\chi = \chi_c$ the Hopf bifurcation emerges provided (25) holds.*

Remark 1. Notice that for $h_j = 0$ (O.D.E case) as well as for $\chi = 0$ (reaction–diffusion case) the steady state $\bar{E}$ is linearly stable and moreover it is globally stable which was proved in [4] by means of suitable Lyapunov functional even in the case of prey taxis.

Remark 2. Following above computations we obtain the following stability matrix associated with indirect predator-taxis model (1)–(3) with (5) and the critical value of ξ_c:

$$J(\bar{E}) = \begin{pmatrix} j_{11} - d_1 h_j & j_{12} & 0 \\ j_{21} & j_{22} - d_2 h_j & -\xi \bar{N} h_j \\ 0 & \alpha & -\beta - d_3 h_j \end{pmatrix}, \quad \xi_c = \min_{j \in \mathbb{N}_+} \left\{ \frac{\Psi(h_j)}{(d_1 h_j - j_{11}) \alpha_u \bar{N} h_j} \right\}.$$

Remark 3. To illustrate numerically the pattern formation for model (1)–(3) with (4) we assume $\Omega = (0\,, 1)$ and fix model parameters as $b = 0.1$, $c = 0.2$, $d = 0.25$, $e = 0.15$, $\delta_1 = 0.3$, $\delta_2 = 0.1$, $\alpha = 1.5$, $\beta = 1, d_1 = 0.01$, $d_2 = 0.001$, $d_3 = 0.07$, $\chi = 1.5 > \chi_c$ with initial condition $(P_0\,, N_0\,, W_0) = (\bar{P} + 0.1 \cos \pi x\,, \bar{N} + 0.1 \cos \pi x\,, \bar{W} + 0.1 \cos \pi x)$ and steady state $\bar{E} = (\bar{P}\,, \bar{N}\,, \bar{W}) = (0.2, 0.4, 0.3)$. The figure below exhibits spatiotemporal periodic patterns emerging in the vicinity of the coexistence steady state $\bar{E}$:



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