Predator-prey model with diffusion and indirect prey-taxis.

Dariusz WRZOSEK
Institute of Applied Mathematics and Mechanics
University of Warsaw

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Micro and Macro systems in life sciences
Będlewo

Plan

- Basic population model of a single population
- Predator prey model with prey taxis
- Two predator prey models with indirect prey taxis
- Constant and non-constant steady states
- Stabilization of solutions

based on a joint work with

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Basic population model

Logistic equation

$v(t)$ – population density at time $t \geq 0$
λ- birth rate
K –caring capacity
F - consumption rate (mortality)

$$v_t(t) = \lambda v(t)\left(1 - \frac{v(t)}{K}\right) - Fv(t)$$

If $\lambda > F$ there is the unique stable steady state

$$\bar{v} = K\left(1 - \frac{F}{\lambda}\right)$$

Predator-prey model with (direct) prey taxis

Predator searching strategy is the superposition of random dispersion and directed movement towards the gradient of prey density

u–predator density
v–prey density

$$\begin{aligned} u_t &= d_u \Delta u - div(\chi u \nabla v) + f_1(u, v), && x \in \Omega,\ t > 0 \\ v_t &= \varepsilon \Delta v + \lambda v(1 - \tfrac{v}{k}) - f_2(u\, v), && x \in \Omega,\ t > 0 \end{aligned}$$

introduced by **Kareiva and Odell (1987)**
studied by **J. Lee, M. Lewis and T. Hillen (2009)**
survey paper **A. Jungel (2010)**

Question: Could predator-prey interaction lead to pattern formation and occurrence of prey aggregations?

Two Models of indirect prey taxis (IPT)

Predator searching strategy is the superposition of random dispersion and directed movement towards the gradient of some chemical indicating the presence of prey :

Model IPT1: released by injured prey during capturing.

Model IPT2: released by prey itself ”smell of prey”.

Model IPT1

u–predator density
v–prey density
w– chemical released by injured prey (chemoattractant)

Nondimesionalized version of IPT1 model:

$$\begin{aligned} u_t &= \Delta u - div(\chi u \nabla w), && x \in \Omega,\ t > 0 \\ w_t &= d_w \Delta w - w + \alpha v F(u), && x \in \Omega,\ t > 0 \\ v_t &= \lambda v(1 - v) - v F(u), && x \in \Omega,\ t > 0 \end{aligned}$$

with mortality of prey due to the activity of predator.
Effect of spacial grouping of predators:

$$F(u) = \frac{F_m u}{1 + u}$$

proposed by **C. Cosner et al. (1999)**,
no-flux boundary conditions and nonnegative initial data

Model IPT2

w– chemical released by prey ”smell of prey”’(chemoattractant)

$$
\begin{aligned}
u_t &= \Delta u - div(\chi u \nabla w), && x \in \Omega,\ t > 0\\
w_t &= d_w \Delta w - \mu w + \alpha v, && x \in \Omega,\ t > 0\\
v_t &= \lambda v(1 - v) - vF(u), && x \in \Omega,\ t > 0
\end{aligned}
$$

Foraging of planktivorous fish on zooplankton

- **Z.M Gliwicz, D.W.** *Predation-Mediated Coexistence of Large- and Small-Bodied Daphnia at Different Food Levels.* American Naturalist (2008).
- **Z.M Gliwicz, P. Maszczyk, J. Jablonski, D.W.** *Patch exploitation by planktivorous fish and the concept of aggregation as an antipredation defense in zooplankton.* Limnol. Oceanogr (2013).

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Existence of solutions

$$W_N^{2,p}(\Omega) = \{w \in W_N^{2,p}(\Omega) : \frac{\partial w}{\partial \nu}(x) = 0\,,\ x \in \partial\Omega\}$$

Theorem

Assume that initial functions are nonnegative and for $p > n$, $u_0\,, v_0\,, \in W^{1,p}(\Omega)$ and $w_0 \in W_N^{2,p}(\Omega)$. Then there exist a unique solution $(u\,, w\,, v)$ to IPT model such that

$$u\,, v \in C([0\,,\infty); W^{1,p}) \quad \textit{and} \ \ w \in C([0\,,\infty); W_N^{2,p})\,.$$

Moreover, for any $T > 0$, $u\,, w \in C^{2,1}_{x,t}(\Omega \times (0\ T))$ and

$$u, w, v \geq 0 \quad on \quad \Omega \times (0\ T).$$

Proof is based on Banach fixed point theorem applied for integral formulation of the problem and theory of analytical semigroups.

Steady states and linearization

It follows from the non-flux boundary condition that

$$\langle u(t)\rangle := \frac{1}{|\Omega|}\int_{\Omega} u(x,t)dx = \langle u_0\rangle := \frac{M}{|\Omega|}, \quad \text{for} \quad t>0.$$

If $F(\bar{u}) < \lambda$ in each of the models there is only one constant steady state with positive components:

for IPT1; $P_1^1 = (\bar{u}\,, \bar{w}\,, \bar{v})$ with

$$\bar{u} = \langle u_0\rangle\ , \bar{w} = \frac{\alpha}{\mu}\left(1-\frac{F(\bar{u})}{\lambda}\right)F(\bar{u}), \bar{v} = 1-\frac{F(\bar{u})}{\lambda}\ ,$$

for IPT2; $P_1^2 = (\bar{u}\,, \bar{w}\,, \bar{v})$

$$\bar{u} = \langle u_0\rangle\,,\ \bar{w} = \frac{\alpha}{\mu}\left(1-\frac{F(\bar{u})}{\lambda}\right), \bar{v} = 1-\frac{F(\bar{u})}{\lambda}.$$

Trivial steady state

There is also a trivial steady state P_0 for both models:

$$\bar{u} = \langle u \rangle \, , \; \bar{w} = \bar{v} = 0 \, .$$

which is a unique space homogeneous steady state provided $F(\langle u_0 \rangle) \geq \lambda$.

Linearization and the eigenvalue problem

Linearization at a homogeneous steady state $(\bar{u}\,, \bar{w}\,, \bar{v})$ to Model IPT1 leads to the following eigenvalue problem

$$\begin{aligned} \Delta\varphi - \chi\bar{u}\Delta\psi &= \sigma\varphi, \\ d_w\Delta\psi - \mu\psi + \alpha\bar{v}F'(\bar{u})\varphi + \alpha F(\bar{u})\eta &= \sigma\psi, \\ -\bar{v}F'(\bar{u})\varphi + (F(\bar{u}) - \lambda)\eta &= \sigma\eta \end{aligned}$$

where $(\varphi\,, \psi\,, \eta) \in X_0 \times X \times Y$ and

$$\begin{aligned} X_0 = &\quad \{\varphi \in W^{2,p}(\Omega) \quad : \frac{\partial\varphi}{\partial\nu} = 0\,, \int_\Omega \varphi(x)dx = 0\}\,, \\ X = &\quad \{\varphi \in W^{2,p}(\Omega) \quad : \frac{\partial\psi}{\partial\nu} = 0\}\,, \qquad Y = L^2(\Omega)\,. \end{aligned}$$

Spectrum

Let $\{\lambda_n\}_{n=0}^{\infty}$ be the sequence of eigenvalues of operator $-\Delta$ with homogeneous Neumann boundary conditions defined on X

$$0 = \lambda_0 < \lambda_1 \leq \lambda_2 \leq \lambda_3 \leq \dots .$$

Let us define matrix

$$A_n = \begin{bmatrix} -\lambda_n & \chi \bar{u} \lambda_n & 0 \\ \alpha \bar{v} f_1 & -(d_w \lambda_n + \mu) & -\alpha f \\ \bar{v} f_2 & 0 & r \end{bmatrix}$$

where $f = F(\bar{u})$, $r = \lambda - f - 2\bar{v}\lambda$ and $f_1 = f_2 = F'(\bar{u})$ in Model IPT1 and $f_1 = 0$, $f_2 = F'(\bar{u})$ in the case of Model IPT2.

Proposition

A complex number σ is an eigenvalue to the linearized system if there exists $n \geq 1$ such that σ is an eigenvalue of matrix A_n or for $n = 0$, $\sigma \in \{-\mu , r\}$. Moreover spectrum of the linear operator consist only of eigenvalues.

Stability criterion

Theorem

Steady state P_1^1 in Model IPT1 is locally asymptotically stable if

$$\frac{\chi\alpha\bar{u}F'(\bar{u})}{\lambda} < (1+d_w)\min\left(\frac{2\mu}{\mu+F(\bar{u})}, 1\right).$$

Steady state P_1^2 in Model IPT2 is locally asymptotically stable if

$$\frac{\chi\alpha\bar{u}F'(\bar{u})}{\lambda} < (1+d_w)\frac{2\mu}{F(\bar{u})}.$$

There exists $\delta_0 > 0$ such that if $\sigma \in \mathrm{spec} A_n$ then $\mathrm{Re}\,\sigma < -\delta_0 < 0$. Steady state P_0 is unstable provided $\lambda \geq F(\bar{u})$. There is $K > 0$ such that steady states P_1^1 and P_1^2 are unstable provided

$$\frac{\chi\alpha\bar{u}}{\lambda} > K.$$

Non-constant steady states and reduced system

The stationary problem for IPT1 may be reduced to the system of two elliptic equations:

$$\begin{aligned} \Delta \bar{u} - div(\bar{u}\chi\nabla\bar{w}) &= 0, && x \in \Omega, \\ d_w\Delta\bar{w} - \mu\bar{w} + \alpha\left(1 - \frac{F(\bar{u})}{\lambda}\right)F(\bar{u}) &= 0, && x \in \Omega\,. \end{aligned}$$

with homogeneous Neumann boundary conditions.

Any solution of this system determines a solution of stationary IPT1 Model

linearization of the reduced system

Let us denote

$$\Gamma(u) = \left(1 - \frac{F(u)}{\lambda}\right) F(u)$$

and

$$\gamma := \Gamma'(\bar{u}) = \left(1 - \frac{2F(\bar{u})}{\lambda}\right) F'(\bar{u}).$$

Linearization at the constant steady state $(\bar{u}\,, \bar{w})$ leads to the following eigenvalue problem (**L)**

$$\begin{aligned} \Delta\phi - \chi\bar{u}\Delta\psi \quad &= \sigma\phi, \\ d_w\Delta\psi - \mu\psi + \alpha\gamma\phi \quad &= \sigma\psi\,. \end{aligned}$$

Linearization

Let us define matrix

$$B_n = \begin{bmatrix} -\lambda_n\,, & \chi\bar{u}\lambda_n \\ \alpha\gamma\,, & -\lambda_n d_w - 1 \end{bmatrix}$$

Proposition

A complex number σ is an eigenvalue iff there exists $n \geq 1$ such that σ is the eigenvalue to matrix B_n or $\sigma = -\mu$. Moreover, $\mathrm{Re}\,\sigma < 0$ iff

$$\lambda_1 > \frac{\alpha\gamma\chi\bar{u} - \mu}{d_w}\,.$$

Bifurcation for IPT1 model

If $\gamma > 0$ then it is convenient to choose χ as a bifurcation parameter and then we obtain the stability condition for the reduced problem

$$\lambda_1 > \frac{\alpha\gamma\chi\bar{u} - \mu}{d_w} \,.$$

Proposition

Assume 1-D case, $\gamma > 0$ *and fix* $M > 0$ *. Then for any* $\chi > \chi_1$ *there are non-constant steady states with mass M.*

we adapt result by **Xuefeng Wang** and **Quian Xu (2013)**

each component of such a non-constant steady state may be a monotone increasing or decreasing function. Using no-flux boundary condition and periodic extension or reflection of monotone function a non-monotone steady state may be constructed.

Comparison of IPT models

Matrix B_n corresponding to the reduced IPT2 system has $\gamma = -\frac{\alpha}{\mu} F'(\bar{u}) < 0$. Then the space-homogeneous steady state is linearly locally asymptotically stable for all set of parameters and in particular it does not lose stability when χ is big enough. The constant solution to the reduced stationary IPT2 system is uniquely determined. Indeed, there is $\varrho > 0$ such that

$$u = \varrho e^{\chi w} .$$

Then any non-zero steady state satisfies the following semilinear elliptic equation

$$-\Delta w + \mu w + R(w) = 0 \quad \text{on} \quad \Omega$$

with no-flux boundary condition and $R(w) = \alpha(1 - \frac{F(\varrho e^{\chi w})}{\lambda})$. Since $w \longmapsto \mu w + R(w)$ for $w > 0$ is a strictly increasing function classical arguments for monotone operators may be applied.

Stabilization of solutions

Assumptions :

$$\lambda > F_m,$$

there exists a positive constant $\underline{v}_0 > 0$ such that the initial data v_0 satisfies

$$\underline{v}_0 \leq v_0(x) \leq 1$$

$$w_0(x) \geq 0\,,$$

$$M < \frac{2^7}{3^3}\left(\frac{\chi^2\alpha^2 F_m^2|\Omega|^2}{2d_w}\left(1+\frac{F_m^2}{\lambda\min\{\lambda\underline{v}_0,(\lambda-F_m)\}}\right)\right)^{-1}.$$

Stabilization of solutions

Theorem

Under assumptions above if $\Omega \subset \mathbb{R}$ is a bounded and open interval

$$\begin{aligned} u(\cdot,t) &\longrightarrow \quad \bar{u} \qquad \text{in } L^2(\Omega) \text{ as } t \to \infty, \\ v(\cdot,t) &\longrightarrow \quad \bar{v} \qquad \text{in } L^p(\Omega) \text{ as } t \to \infty, \\ w(\cdot,t) &\longrightarrow \quad \bar{w} \qquad \text{in } L^p(\Omega) \text{ as } t \to \infty\,, \end{aligned}$$

for any $p \in [1,\infty)$

crucial energy estimate for $N \leq 2$

We use the Sobolev embeddings and the Gagliardo-Nirenberg inequality to find:

$$\int_\Omega u(\ln u - 1) + \int_\Omega |\nabla w|^2 + \int_\Omega \left|\frac{\nabla v}{v}\right|^2 + \int_0^\infty \int_\Omega |\nabla w|^2 + \int_0^\infty \int_\Omega \frac{|\nabla u|^2}{1+u} \leq C$$

Space averaging for the long time.

$$\|u(\cdot,t) - \frac{1}{|\Omega|}\int_\Omega u(x,t)dx\|_2 \to 0$$

$$\|v(\cdot,t) - \frac{1}{|\Omega|}\int_\Omega v(x,t)dx\|_p \to 0$$

$$\|w(\cdot,t) - \frac{1}{|\Omega|}\int_\Omega w(x,t)dx\|_p \to 0$$

$$\text{as} \quad t \to +\infty\,.$$

We use results by **Friedman and Tello (2002).**

Main conclusions

- the presence of taxis in search strategy does not warrant formation of stationary patterns.
- even in the case of weak coupling between predator and prey the pattern formation of prey may result (e.g. if χ is large enough) solely from specific prey-predator interactions provided the search strategy of predator admits migration towards gradient of chemical released by prey injured during capturing.
- in the case of big density of predator the spatially homogeneous steady state may be unstable even if chemotaxis χ is small.

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