NOISE AND PRODUCTIVITY DEPENDENCE
OF SPATIOTEMPORAL PATTERN FORMATION
IN A PREY-PREDATOR SYSTEM

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ABSTRACT. The spatiotemporal pattern formation in a prey-predator dynamics is studied numerically. External noise as well as the productivity of the prey population control emergence, symmetry and stability of as well as transitions between structures. Diffusive Turing structures and invasion waves are presented as example.

1. **Introduction.** Recently, a number of papers has been published about pattern formation in minimal prey-predator models [1, 2, 3, 4] that were originally formulated by Scheffer [5] as models of phytoplankton-zooplankton dynamics. Routes to local chaos through seasonal oscillations of parameters have been extensively studied with several models [6, 7, 8, 9, 10]. Deterministic chaos in uniform parameter models and data of systems with three or more interacting plankton species have been studied as well [11]. The emergence of diffusion-induced spatio-temporal chaos along a linear nutrient gradient has been found by Pascual [12] in Scheffer's model without fish predation. Chaotic oscillations behind propagating diffusive prey-predator invasion fronts have been presented in [13, 14].
Recently, it has been shown that the appearance of chaotic spatio-temporal oscillations in a prey-predator system is a somewhat more general phenomenon and must not be attributed to front propagation or to an inhomogeneity of environmental parameters [14, 15].

In this paper we focus on the influence of prey productivity and external noise on the spatio-temporal pattern formation of interacting populations in a uniform environment. The model by Scheffer [5] is used as an example.

2. **Standing waves driven by deterministic and noisy initial conditions.**
The Scheffer model for the prey-predator dynamics of phytoplankton X_1 and zooplankton X_2 in time t and two spatial dimensions (x, y) reads with dimensionless quantities, scaled following [12]

$$\frac{\partial X_1}{\partial t} = r X_1 (1 - X_1) - \frac{aX_1}{1 + bX_1} X_2 + d_1 \Delta X_1 , \tag{1}$$

$$\frac{\partial X_2}{\partial t} = \frac{aX_1}{1 + bX_1} X_2 - m(x, y, t) X_2 - \frac{g^2 X_2^2}{1 + h^2 X_2^2} f + d_2 \Delta X_2 . \tag{2}$$

In preceding papers, the dynamics of the top predator, *i.e.*, the planktivorous fish f was modelled by a set of certain rules, cf. [16]. Here, we come back to the original description with fish as a control parameter. The parameter ranges for the emergence of diffusion- and/or advection-induced instabilities of a spatially homogeneous stationary solution against supercritical wave perturbations have been derived and given in detail, cf. [2, 4, 17, 18]. The differential-diffusion induced Turing instabilities and structures will be studied first.

2.1. **Parameter set I.** The following set of model parameters has been chosen for the simulations described in this section, cf. [4]:

$$r = 1 , \ a = 8.0 , \ b = 11.905 , \ g = 1.434 , \ h = 0.857 , \ \overline{m} = 0.49 , \ f = 0.093 ,$$
$$L = 100 , \ x, y \in [0, L] , \ d_1 = 2.8 \times 10^{-5} , \ d_2 = 5.6 \times 10^{-3} ,$$

where $\overline{m}$ is the spatiotemporal mean of the noisy predator mortality rate $m(x, y, t)$.

The environmental noise will be incorporated following an idea by Steele and Henderson [19]: The value of m will be chosen randomly at each point and each unit time step from a truncated normal distribution between $I = \pm 5\%$ and 45% of $\overline{m}$, *i.e.*

$$m(x, y, t) = \overline{m} \left[1 + I - \texttt{rndm} (2I) \right] \tag{3}$$

with $\texttt{rndm} (z)$ as a random number between 0 and z.

The interactions have been integrated with a Runge-Kutta scheme of 4th order whereas the diffusion terms have been computed with explicit and, in order to check the results, with semi-implicit (ADI) methods [20].

2.2. **Simulations I.** The simulations in [4] started with different symmetric and asymmetric initial conditions without noise. A sample pattern is shown in Fig. 1. There, a circular wave of supercritical wave number in the center has destabilized the spatially homogeneous species distribution, resulting in that funny fully symmetric 5-eyes pattern. Here and furtheron, the prey pattern is displayed on a greyscale from black ($X_1 = 0$) to white ($X_1 = 1$).

Besides the strong conditions on the difference of the diffusion coefficients, the symmetry and polarity of Turing patterns has long been a reason to question the role of those instabilities and structures in biodynamics because nature is not that symmetric in mathematical sense. We will see now how a little noise changes the
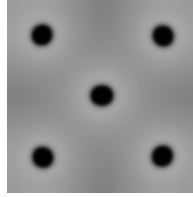
FIGURE 1. Symmetric Turing structure after perturbation of the homogeneous solution with a central circular wave of supercritical wave number, cf. [4]. Neumann boundary conditions.

patterns completely. The same initial perturbation wave is used, however, the predator mortality rate is subject to increasing noise. The result is seen in Fig. 2.

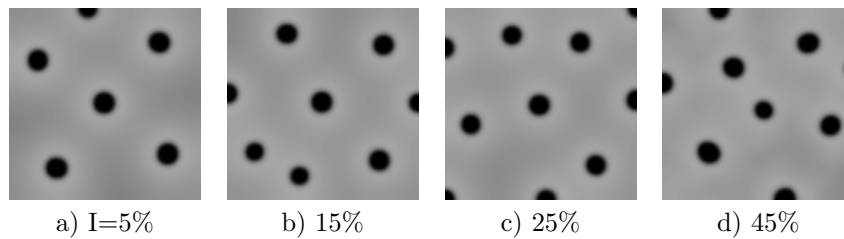a) I=5%   b) 15%   c) 25%   d) 45%

FIGURE 2. Destruction of the polar and symmetric Turing structures in Fig. 1 for noisy predator mortality with increasing noise intensity.

The pattern symmetry is immediately disturbed and the 5-eyes pattern disappears step by step. Finally, we have an asymmetric Turing pattern even with varying sizes of the empty (black) patches.

For the next simulations, we have chosen randomized initial conditions, *i.e.*, the homogeneous stationary solution subject to increasing noise intensities like the predator mortality in Eq. 3 but not to a macroscopic perturbative wave.

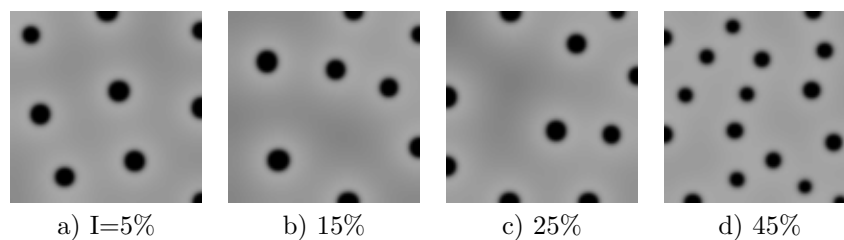a) I=5%   b) 15%   c) 25%   d) 45%

FIGURE 3. Nonpolar and asymmetric Turing structures for random initial conditions with increasing noise intensity.

Without the control of the initial perturbation wave, no characteristic pattern is formed. As before, increasing noise generates more empty prey patches on a

biologically reasonable time scale. However, it must be mentioned that it is still open whether the shown patterns are transient and will change for large times. Howsoever, the disturbing symmetry of diffusion-induced Turing patterns has been overcome by some noise which is present everywhere in natural systems. Furthermore, noise has induced transitions between different structures what has also been shown in a previous paper [16].

3. **Travelling waves driven by noise and prey productivity.** Now, the impact of noise and prey productivity on travelling population waves is studied. In order to create those waves, we have chosen another set of parameters and a certain initial condition.

3.1. **Parameter set II.** The following set of model parameters has been chosen for the simulations described in this section, cf. [4, 12]:

$$r = 1 \ , \ a = b = 5 \ , \ g = h = 10 \ , \ \overline{m} = 0.6 \ , \ f = 0.4 \ ,$$

$$L = 100 \ , \ x, y \in [0, L] \ , \ d_1 = d_2 = 5 \times 10^{-2} \ .$$

These parameters guarantee the existence of a stable limit cycle in the system. Any perturbation of spatially homogeneous oscillations will generate waves. However, an even more sophisticated initial condition is used, following previously published results [15, 21, 22, 23].

3.2. **Simulations II.** Two localized prey patches of different spatial size at their carrying capacity with smaller inner predator patches serve as wave generator, cf. Fig. 4 for average productivity $r = 1$ of the prey. The resulting two excitation cen-
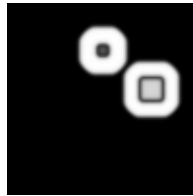

FIGURE 4. The wave generator for average prey productivity $r = 1$ and zero noise at t=15, cf. [22]. Periodic boundary conditions.

ters generate concentric population waves and after some time they unite. Chaotic dynamics occurs behind the slower predator fronts [13, 15]. Due to the periodic

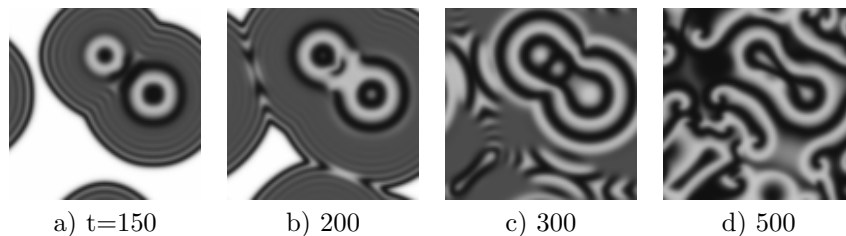a) t=150   b) 200   c) 300   d) 500

FIGURE 5. Development of complex wave pattern for average productivity and zero noise.

boundary conditions the utmost wave fronts collide, break up and eventually form spirals. This is shown in Fig. 5 for 500 time steps.

The resulting patterns look rather artificial and could also be a nonlinear reaction in a chemical lab. This changes again remarkably when we apply some noise to the mortality rate of the predator. The same time series as in Fig. 5 is shown for 15% noise in Fig. 6.

The mixing is enhanced and the structures look much more fuzzy and, therefore,
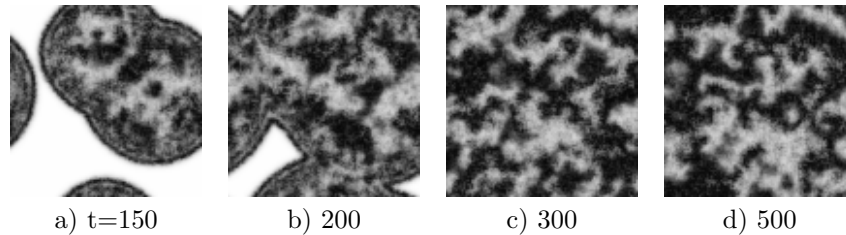

| a) t=150 | b) 200 | c) 300 | d) 500 |

FIGURE 6. Development of complex wave pattern for average productivity and 15% noise.

more realistic than without noise. Noise-induced transitions between different spatiotemporal patterns like in Ch. 2.2 cannot happen here because there are not any alternative stable pattern regimes.

Now, the role of the prey productivity in pattern formation is studied. At first, the productivity is halved. In the case without noise, *i.e.* in Fig. 7a, one can readily
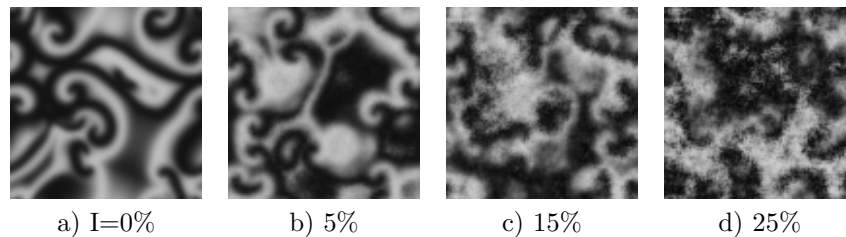

| a) I=0% | b) 5% | c) 15% | d) 25% |

FIGURE 7. Development of complex wave pattern for half average productivity $r = 0.5$ and increasing noise at t=750.

see that the scale of the structure has become much greater compared to average productivity in Fig. 5d. The opposite is true in the case of doubled productivity in Fig. 8a. The emerging wavy pattern is of much smaller scale. Therefore, it is much easier for the noise to blur the clear pattern contours.

4. **Conclusions.** A conceptual biomass-based prey-predator model of phytoplankton-zooplankton dynamics has been investigated for spatial and spatio-temporal dissipative pattern formation in a noisy environment.

It has turned out that noisy Turing structures loose their typical polarity and symmetry and, therefore, look much more biologically and ecologically realistic. The same is true for noisy wave patterns. Unrealistic contours are blurred and the
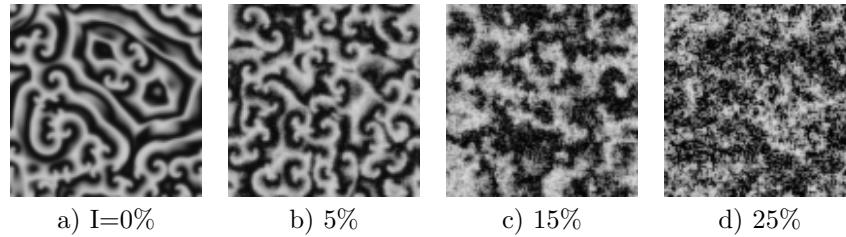
a) I=0%   b) 5%   c) 15%   d) 25%

FIGURE 8. Development of complex wave pattern for double average productivity $r = 2$ and increasing noise at t=750.

model patterns resemble natural spatiotemporal population structures much better. This is another support of coupled modelling, *i.e.*, even in relative physical uniformity, biologically controlled pattern formation processes should be superposed by some realistic noise.

In the case of Turing structures, it has been found again that noise can induce transitions between alternative stable spatial patterns.

Furthermore, it has been shown that the productivity of the prey population significantly determines the spatial scale of the emerging patterns. The higher the productivity the smaller is the scale and superposed noise enhances mixing better and better.

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