Modeling, singular perturbation and bifurcation analyses of bitrophic food chains dynamics including canard explosion

Bob W. Kooi

Dept. Theoretical Biology, VU University, de Boelelaan 1085, 1081 HV Amsterdam, The Netherlands



bob.kooi@vu.nl
http://www.bio.vu.nl/thb/

### Outline

- Introduction
- Rosenzweig-MacArthur predator-prey model
- RM<sub>1</sub> model, variable efficiency
- RM<sub>2</sub>-model, constant efficiency
- MB nutrient-prey-predator model
- Conclusions

- The predator-prey systems are modelled using ordinary differential equations, one for each trophic level
- Two model formulations (RM) and (MB) are studied in detail and the consequences for the application of the analysis methods when the time scales of the trophic levels differ a lot

- In the classical Rosenzweig-MacArthur (RM) model in absence of the predator the prey grows logistically and nutrients are not modelled
  - Fast-slow dynamics,
  - Singular perturbation technique,
  - Canards
- In mass balance (MB) chemostat model this nutrient is explicitly modelled
  - Bifurcation analysis

# Canard: Van der Pol equation (Eckhaus 1983)





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# Rosenzweig-MacArthur predator-prey model $RM_1$ -model, variable efficiency

$$\frac{dx_1}{dt} = f(x_1, x_2, \varepsilon) = x_1(1 - x_1 - \frac{a_1 x_2}{1 + b_1 x_1})$$
$$\frac{dx_2}{dt} = \varepsilon g(x_1, x_2, \varepsilon) = \varepsilon x_2(\frac{a_1 x_1}{1 + b_1 x_1} - 1)$$

	<b>T</b> 1 1 1
parameter	Interpretation
t	Time variable
$x_1$	Prey density
$x_2$	Predator biomass density
$a_1$	Searching rate
$b_1$	Searching rate $\times$ handling time
ε	Efficiency and predator death rate

The hyperbolic relationship

$$F_{x_1,x_2} = \frac{a_1 x_1}{1 + b_1 x_1}$$

is called

- Ecology: Holling type II functional response
- Biochemistry: Michaelis-Menten kinetics

Derivation using time-scale separation: seaching and feeding is much faster than population physiological processes, such as growth

Here the parameters are:

 $a_1 = b$ ; searching rate

 $b_1 = b/k$ ; searching rate × handling time

We will often fix  $a_1 = 5/3 b_1$ 

The biological interpretation of  $\varepsilon$  is the yield in Microbiology, or assimilation efficiency in Ecology and here besides a time-scale parameter also predator death rate factor

When the units of both state variables (biomasses of the populations) are equal we have  $\varepsilon < 1$ . This means the there is a smaller than 100% biomass conversion: as is always the case in nature

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RM<sub>1</sub> predator-prey model, variable efficiency

$$\frac{dx_1}{dt} = x_1 \left( 1 - x_1 - \frac{a_1 x_2}{1 + b_1 x_1} \right)$$

$$\frac{dx_2}{dt} = \varepsilon x_2 \Big( \frac{a_1 x_1}{1 + b_1 x_1} - 1 \Big)$$

parameter	Interpretation
t	Time variable
$x_1$	Prey biomass density
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$b_1$	Searching rate $ imes$ handling time
ε	Efficiency and predator death rate

#### Bifurcation analysis of $RM_1$ predator-prey model

$\frac{dx_1}{dt}$	$= x_1(1)$	$(-x_1 - \frac{a_1 x_2}{1 + b_1 x_1})$		
$\frac{dx_2}{dt}$	$=\varepsilon x_{2}(\frac{a_{1}x_{1}}{1+b_{1}x_{1}}-1)$			
	Bifur	Bifurcation Description		
	TC	Transcritical bifurcation: invasion through boundary equilibrium		
	T	Tangent bifurcation: collapse of the system		
	Н	Hopf bifurcation: origin of (un)stable limit cycle		

#### Literature ( $\varepsilon = 1$ ):

Yu. A Kuznetsov, *Elements of Applied Bifurcation Theory*, Applied Mathematical Sciences 112, Springer-Verlag, 2004

# $\label{eq:RM1-model} \begin{array}{l} \mathsf{RM}_1\text{-model} \\ \mathsf{One-parameter\ diagram\ } x_i \ \mathrm{vs\ } b_1\text{:} \ a_1 = 5/3\,b_1\text{,} \ \epsilon = 1 \end{array}$



Transcritical TC, Hopf H bifurcations

#### Equilibrium points

Equi. Eigenvalues  

$$E_0 \quad (x_1^*, x_2^*) = (0, 0)$$
  
 $\lambda_1 = 1, \ \lambda_2 = -\varepsilon$   
 $E_1 \quad (x_1^*, x_2^*) = (1, 0)$   
 $\lambda_1 = -1, \ \lambda_2 = -\varepsilon(a_1 - b_1 - 1)/(1 + b_1)$ 

Transcritical TC when  $\lambda_2 = 0$  and using  $a_1 = 5/3 b_1$ 

 $a_1 = b_1 + 1 \Rightarrow b_1 = 1.5$ 

independent of  $\varepsilon$ 

#### Equilibrium points

Equi. Eigenvalues

$$E_2 \quad (x_1^*, x_2^*) = \left(\frac{1}{a_1 - b_1}, \frac{a_1 - b_1 - 1}{(a_1 - b_1)^2}\right)$$
$$\lambda_1 = \frac{a_1 b_1 - a_1 - b_1 - b_1^2 + \sqrt{\Delta}}{2(a_1^2 - a_1 b_1)}, \ \lambda_2 = \frac{a_1 b_1 - a_1 - b_1 - b_1^2 - \sqrt{\Delta}}{2(a_1^2 - a_1 b_1)}$$

where

$$\Delta = a_1^2 b_1^2 - 2a_1^2 b_1 - 2a_1 b_1^3 + (a_1 + b_1)^2 + 2b_1^3 + b_1^4 - 4\varepsilon (3a_1^2 b_1^2 - a_1^4 + a_1^3 + 3b_1 a_1^3 - 2a_1^2 b_1 + a_1 b_1^3 + a_1 b_1^2)$$

Hopf H when Re  $\lambda_{1,2}=0$  and using  $a_1=5/3\,b_1$ 

$$a_1 = \frac{b_1(b_1+1)}{b_1-1} \Rightarrow b_1 = 4$$

independent of  $\varepsilon$ 

Note that  $\varepsilon$  does **not** occur in the expression for the real part of the eigenvalues. So in the parameter space the qualitative change of the stability is independent of  $\varepsilon$ .

 $\varepsilon$  does occur in the expression for the imaginary part  $\Delta$ . Therefore in the parameter space the change from node to focus where  $\Delta = 0$  does depend on  $\varepsilon$ .



transcritical TC, Hopf H bifurcations  $\Delta < 0$  focus (complex eigenvalues)  $\Delta > 0$  node (real eigenvalues)

RM<sub>1</sub> predator-prey system  
Transient dynamics for  

$$b_1 = 3,8$$
 where  $a_1 = 5/3b_1$  and  $\varepsilon = 1,0.01$ 

$$\frac{dx_1}{dt} = f(x_1, x_2, \varepsilon) = x_1 \left( 1 - x_1 - \frac{a_1 x_2}{1 + b_1 x_1} \right)$$
$$\frac{dx_2}{dt} = \varepsilon g(x_1, x_2, \varepsilon) = \varepsilon x_2 \left( \frac{a_1 x_1}{1 + b_1 x_1} - 1 \right)$$

Nullclines:  $f(x_1, x_2, \varepsilon) = 0$  and  $g(x_1, x_2, \varepsilon) = 0$ 



# $RM_1$ predator-prey system Transient dynamics for $b_1 = 4$

$$\frac{dx_1}{dt} = x_1 \left( 1 - x_1 - \frac{a_1 x_2}{1 + b_1 x_1} \right)$$
$$\frac{dx_2}{dt} = \varepsilon x_2 \left( \frac{a_1 x_1}{1 + b_1 x_1} - 1 \right)$$

For these parameter values the equilibrium is at the Hopf bifurcation point H



Transient dynamics reveals two critical points in the fasespace where:  $x_2$  is parameter

- Point where nullcline of f intersects the vertical axis at  $x_1 = 0$ Transcritical bifurcation
- Top of nullcline f at  $(\overline{x}_1, \overline{x}_2)$ :  $df/dx_1 = 0$ Tangent bifurcation at op of nullcline

Singular perturbation problem when  $\varepsilon \rightarrow 0$ : Fast-slow system

#### fast system

$$\frac{dx_1}{dt} = f(x_1, x_2, \varepsilon)$$
$$\frac{dx_2}{dt} = \varepsilon g(x_1, x_2, \varepsilon)$$

$$\varepsilon \to 0$$
$$\frac{dx_1}{dt} = f(x_1, x_2, 0)$$
$$\frac{dx_2}{dt} = 0$$

*slow* system  $\tau = \varepsilon t$ 

$$\varepsilon \frac{dx_1}{d\tau} = f(x_1, x_2, \varepsilon) \qquad \qquad \varepsilon \to 0 \\ 0 = f(x_1, x_2, 0) \\ \frac{dx_2}{d\tau} = g(x_1, x_2, \varepsilon) \qquad \qquad \frac{dx_2}{d\tau} = g(x_1, x_2, 0)$$

reduced system

evolution of the slow variable on  $f(x_1, x_2, 0) = 0$ 



Geometric singular perturbation techniques (N. Fenichel 1997, G. Hek 2010)



#### Geometric singular perturbation techniques

critical manifolds:

$$\mathcal{M}_0^0 = \left\{ (x_1, x_2) | x_1 = 0, x_2 \ge 0 \right\}$$
$$\mathcal{M}_0^1 = \left\{ (x_1, x_2) | x_2 = \frac{1}{a_1} (1 - x_1) (1 + b_1 x_1), x_1, x_2 \ge 0 \right\}$$

Both critical manifolds are normally hyperbolic except in a small part around the fold point indicated  $(\overline{x}_1, \overline{x}_2)$  at the top of the parabola

Geometric singular perturbation techniques

Fenichel (1979) theorem for small nonzero  $\varepsilon$ :  $\mathcal{M}_0$  persists as a  $\mathcal{M}_{\varepsilon}$  manifold with a slow flow on it

On the stable (unstable) side of  $\mathcal{M}_0$ ,  $\mathcal{M}_{\varepsilon}$  is an attracting (repelling) slow invariant manifold

Later we will see that this is not always true (canards)

## Delayed bifurcation

In order to calculate the value where in the limit  $\varepsilon = 0$ the trajectory leaves the vertical axis fast, we can use an equation derived in Rinaldi and Muratori (1992):

#### Literature

S. Rinaldi and S. Muratori. Slow fast limit-cycles in predator prey models. *Ecological Modelling*, 61(3-4):287–308, 1992.

F. Campillo and C. Lobry. Effect of population size in a predator-prey model. *Ecological Modelling* 246:1–10, 2012.

## Slow fast limit-cycles (Rinaldi and Muratori 1992)

SLOW-FAST LIMIT CYCLES IN PREDATOR-PREY MODELS





Approximations techniques slow manifolds,  $x_2 = q_{\varepsilon}(x_1)$ 

Using its invariance the perturbed manifold  $\mathcal{M}^1_\varepsilon$  can be described as a graph

$$\{(x_1, x_2) | x_2 = q_{\varepsilon}(x_1), x_1 \ge 0, x_2 \ge 0\}$$

This manifold is invariant when

$$\frac{dx_2}{dt} = \frac{dx_2}{dx_1}\frac{dx_1}{dt} = \frac{dq_{\varepsilon}}{dx_1}\frac{dx_1}{dt}$$

where  $x_2 = q_{\varepsilon}(x_1)$ 

This gives the following invariance condition after some algebraic manipulation

$$\frac{dq_{\varepsilon}}{dx_1}x_1((1-x_1)(1+b_1x_1)-a_1q_{\varepsilon}(x_1)) = \varepsilon q_{\varepsilon}(x_1)(x_1(a_1-b_1)-1)$$

The following power expansion is introduced:

$$x_2 = q_{\varepsilon}(x_1) = q_0(x_1) + \varepsilon q_1(x_1) + \varepsilon^2 q_2(x_1) + \dots$$

Gathering orders of  $\varepsilon$  results in an iterative procedure yielding the following coefficients  $q_i$ 

For 
$$\mathcal{O}(1)$$
:  
 $q_0 = \frac{(1 - x_1)(1 + b_1 x_1)}{a_1}$ 

Expression for  $q_0$  describes the critical manifold  $\mathcal{M}_0^1$  (a parabola)

For  $\mathcal{O}(\varepsilon)$ :

$$q_1 = q_0 \frac{(x_1(a_1 - b_1) - 1)}{x_1(2x_1b_1 + 1 - b_1)}$$

Note that at the top of the parabola we have

$$(\overline{x}_1, \overline{x}_2) = \left(\frac{b_1 - 1}{2b_1}, \frac{(b_1 + 1)^2}{4a_1b_1}\right)$$

with  $x_1 = \overline{x}_1$  the denominator is zero since

$$\frac{dq_{\varepsilon}}{dx_1}|_{\overline{x}_1} = 2\overline{x}_1b_1 + 1 - b_1 = 0$$

There is singularity

We will try to remove this singularity later on

For  $\varepsilon = 0$  the limit  $x_2 = q_0(x_1)$  prescribes the singular slow flow on  $\mathcal{M}_0^1$ 

$$\frac{dx_1}{dt} = x_1(1 - x_1 - \frac{a_1x_2}{1 + b_1x_1})$$

For  $\varepsilon \ll 1$  sufficiently small nonzero, the flow on the perturbed manifold  $\mathcal{M}^1_{\varepsilon}$  can be approximated by inserting  $x_2 = q_{\varepsilon}(x_1)$  with  $q_{\varepsilon}(x_1)$  power expansion approximation

In order to simulate the model we solve the uncoupled system

$$\frac{d\tilde{x}_1}{dt} = \tilde{x}_1 \left( 1 - \tilde{x}_1 - \frac{a_1 q_{\varepsilon}(\tilde{x}_1)}{1 + b_1 \tilde{x}_1} \right) \quad \text{master}$$
$$\frac{d\tilde{x}_2}{dt} = \varepsilon q_{\varepsilon}(\tilde{x}_1) \left( \frac{a_1 \tilde{x}_1}{1 + b_1 \tilde{x}_1} - 1 \right) \quad \text{slave}$$

where the initial values are chosen as:  $\tilde{x}_1 = x_1(0)$  and  $\tilde{x}_2 = q_{\varepsilon}(x_1(0))$   $a_1 = 5/3 b_1$ , where  $b_1 = 3$ power approximation  $\varepsilon = 0.1$ 






$$a_1 = 5/3 b_1$$
, where  $b_1 = 8$   
 $x_2 = q_{\varepsilon}(x_1)$ ,  $\varepsilon = 0.1$ ,  $\varepsilon = 0.01$ 



Discussion of the canards very close to the unstable equilibrium point where  $b_1$  is beyond the Hopf bifurcation at  $b_1 = 4$ 

- First simulation of transient dynamics
- Thereafter bifurcation diagram  $x_i$  vs  $b_1>$  4 of  $\mathsf{RM}_1$  model where  $\varepsilon\ll 1$
- Finally power expansion in  $\varepsilon$  of q and of bifurcation parameter  $b_1$  is introduced now near the Hopf bifurcation point

RM<sub>1</sub>-model:  $a_1 = 5/3b_1$ ,  $\varepsilon = 0.01$ , A:  $b_1 = 4.0402$ , B:  $b_1 = 4.0404$ , C: 4.0405, D: 4.042





One-parameter diagram  $x_i$  vs  $b_1$ ,  $\varepsilon = 0.01$ 

Hopf H bifurcation



#### Literature on Canards not complete

M. Diener. The canard unchained or how fast/slow dynamical problems bifurcate, *The Mathematical Intelligencer*, 6, 38-49, 1984.

F. Dumortier, R. Roussarie. *Canard cycles and center manifolds*, Memoires of the AMS, 557, 1996.

W. Eckhaus. *Relaxation oscillations including a standard chase on French ducks; in Asymptotic Analysis II*, Springer Lecture Notes Math. 985, 449-494, 1983.

N. Fenichel. Geometric singular perturbation theory, *JDE* 31, 53-98, 1979.

J-M. Ginoux, J. Llibre, Flow curvature method applied to canard explosion, *arXiv:1408.4894v1* [mathDS 21 Aug 2014], 2014.

M. Brons. An iterative method for the canard explosion in general planar systems. *Discrete and continuous dynamical systems*, 250:77–83, 2013.

M. Canalis-Durand. Formal expansion of van der pol equation canard solutions are Gevrey. In E. Beno<sup>^</sup>, editor, *Dynamic Bifurcation*, pages 28–39. Springer, 1990.

#### Literature on Canards in Ecology

S. Rinaldi and A. Gragnani. Destabilizing factors in slow–fast systems. *Ecol Model*, 180:445–460, 2004.

F. Campillo, C. Lobry. Effect of population size in a predator-prey model, *Ecological Modelling*, 246:1-10, 2012.

#### Where is the maximal canard location?

Power expansion now near the Hopf bifurcation point in  $\varepsilon$ of  $r(x_1, \varepsilon)$ 

$$x_2 = r(x_1, \varepsilon) = r_0(x_1, \varepsilon) + \varepsilon r_1(x_1, \varepsilon) + \varepsilon^2 r_2(x_1, \varepsilon) + \dots$$

and of bifurcation parameter  $b_1$ 

$$b_1(\varepsilon) = b_{10} + \varepsilon b_{11} + \varepsilon^2 b_{12} + \dots$$

where  $r_j$  and  $b_j$ ,  $j = 1 \cdots$  are independent of  $\varepsilon$  and are fixed by an invariance condition at the Hopf bifurcation point by equality order by order of powers of  $\varepsilon$  Equating  $\mathcal{O}(1)$  terms yields:

$$r_0 = \frac{(1 - x_1)(1 + b_{10}x_1)}{5/3 \, b_{10}}$$

Equating  $\mathcal{O}(\varepsilon)$  terms yields:

$$r_{1} = \frac{(1 - x_{1})(-3b_{10} + 3b_{11}x_{1}(b_{10} - 1) - 6b_{11}x_{1}^{2}b_{10} - x_{1}b_{10}^{2} + 2x_{1}^{2}b_{10}^{3})}{b_{10}^{2}(1 + 2x_{1}b_{10} - b_{10})x_{1}}$$
  
$$b_{10} = 4$$

However  $1 + 2x_1b_{10} - b_{10} = 0$  evaluated at  $b_{10} = 4$  and equilibrium  $x_1 = x_1^* = \overline{x}_1$  at Hopf bifurcation point

Determine  $b_{11}$  so that besides denominator also numerator is zero

This gives  $b_{11} = 100/27$ 

In a similar way we can get higher order approximations

For  $\varepsilon = 0.01$  we calculated for the second order term  $b_1(\varepsilon) = b_{10} + \varepsilon b_{11} + \varepsilon^2 b_{12} + \dots$ 

$$b_1(\varepsilon) = 4 + \varepsilon 100/27 + \varepsilon^2 58700/2187 = 4.04018$$

Higher order terms can be calculated with symbolic algebra packages using the iterative scheme



Rosenzweig-MacArthur predator–prey model RM<sub>1</sub>-model, allochthonous prey input

$$\frac{dx_1}{dt} = \delta + f(x_1, x_2, \varepsilon) = \delta + x_1(1 - x_1 - \frac{a_1 x_2}{1 + b_1 x_1}),$$
  
$$\frac{dx_2}{dt} = \varepsilon g(x_1, x_2, \varepsilon) = \varepsilon x_2(\frac{a_1 x_1}{1 + b_1 x_1} - 1),$$

where  $\delta$  is a small allochthonous input rate of the prey population

Addition of this extra term removes the transcritical bifurcation at  $x_2 = 1/a_1$ 

It is structurally unstable with respect to such a perturbation

Focus only on Hopf bifurcation





Coefficients  $b_{1i}\varepsilon^i$  vs *i*,  $\varepsilon = 0.01$ power series is divergent!



The power series is divergent

Fortunately it has been shown that the summation up to the smallest term gives an optimal approximation. Indeed the result for  $\varepsilon = 0.01$  with allochthonous prey input where  $\delta = 0.001$  are very accurate



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RM<sub>2</sub> predator-prey model, constant efficiency

$$\frac{dx_1}{dt} = x_1 \left( 1 - x_1 - \varepsilon \frac{a_1 x_2}{1 + b_1 x_1} \right)$$
$$\frac{dx_2}{dt} = \varepsilon x_2 \left( \frac{a_1 x_1}{1 + b_1 x_1} - 1 \right)$$

This model has been studied in:

Hek. Geometric singular perturbation theory in biological practice. *Journal of Mathematical Biology*, 60:347–386, 2010.

However, without motivation for the extra  $\varepsilon$  factor

This term was suggested before in:

Kooi, Poggiale, Auger and Kooijman. Aggregation methods in food chains with nutrient recycling. *Ecological Modelling* 157:69-86. 2002.

Here we mention only the following results:

Transcritical bifurcation at  $b_1 = \frac{3}{2}$ Hopf bifurcation at  $b_1 = 4$ 

both bifurcation occur the same locations as in  $\mathsf{RM}_1$  model

Simulation results are shown which indicate unrealistic unbounded solutions when  $\varepsilon \to 0$ 

A:  $b_1 = 3, \varepsilon = 1$  B:  $b_1 = 8, \varepsilon = 1$ C:  $b_1 = 3, \varepsilon = 0.01$  D:  $b_1 = 8, \varepsilon = 0.01$ 



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# MB nutrient-prey-predator model

$$\frac{dx_0}{dt} = (x_r - x_0)\varepsilon d - a_0 x_0 x_1$$
$$\frac{dx_1}{dt} = a_0 x_0 x_1 - \varepsilon dx_1 - \varepsilon \frac{a_1 x_1 x_2}{1 + b_1 x_1}$$
$$\frac{dx_2}{dt} = \varepsilon \frac{a_1 x_1 x_2}{1 + b_1 x_1} - \varepsilon dx_2$$

parameter	Interpretation
t	Fast time variable
$x_0$	Nutrient density
$x_i$	Population biomass density
$x_r$	Nutrient concentration in reservoir
d	Dilution rate
$a_0$	Searching rate
$a_1$	Searching rate
$b_1$	Searching rate $\times$ handling time

It is possible to decouple the system by introduction of the function

$$H(t) = x_0(t) + x_1(t) + x_2(t) - x_r \quad t \ge 0$$

It is easy to show that the equation for H models exponential decay and the final set of equations becomes with d = 1 and  $a_0 = 1$ 

$$\frac{dH}{dt} = -\varepsilon dH$$
  
$$\frac{dx_1}{dt} = \left(H + x_r - x_1 - x_2\right) x_1 - \varepsilon \left(x_1 + \frac{a_1 x_1 x_2}{1 + b_1 x_1}\right)$$
  
$$\frac{dx_2}{dt} = \varepsilon x_2 \left(\frac{a_1 x_1}{1 + b_1 x_1} - 1\right)$$

In order to be able to compare the three models  $RM_1$ ,  $RM_2$ and MB we make the following assumptions: H(0) = 0 and this gives:

$$\frac{dx_1}{dt} = x_1 \left( x_r - x_1 - x_2 - \varepsilon - \varepsilon \frac{a_1 x_2}{1 + b_1 x_1} \right)$$
$$\frac{dx_2}{dt} = \varepsilon x_2 \left( \frac{a_1 x_1}{1 + b_1 x_1} - 1 \right)$$

and 
$$x_r = 1 + \varepsilon$$
  

$$\frac{dx_1}{dt} = x_1 \left( 1 - x_1 - x_2 - \varepsilon \frac{a_1 x_2}{1 + b_1 x_1} \right)$$

$$\frac{dx_2}{dt} = \varepsilon x_2 \left( \frac{a_1 x_1}{1 + b_1 x_1} - 1 \right)$$





Transcritical TC, Hopf H bifurcations





Transcritical TC, Hopf H bifurcations







 $b_1 = 8$  and A: $\varepsilon = 1$ , B:  $\varepsilon = 0.1$ , C:  $\varepsilon = 0.01$ 



# MB<sub>1</sub>-model

One-parameter diagram  $x_i$  vs  $b_1$ :  $a_1 = 5/3 b_1$ ,  $\varepsilon = 0.01$ 



Transcritical TC, Hopf H bifurcations



Hopf  $H_{MB}$  MB model; Hopf  $H_{RM_{1,2}}$  RM<sub>1,2</sub> model; Transcritical TC all models

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## Conclusions (1)

- (RM<sub>1</sub>  $\Rightarrow$  RM<sub>2</sub>) Making the RM<sub>1</sub> model more realistic leads in fr RM<sub>2</sub> model to unrealistic unbounded solutions when  $\varepsilon \rightarrow 0$
- (RM<sub>2</sub>  $\Rightarrow$  MB) Introduction of dynamics of nutrients in the model leads to realistic solution and less complex dynamics when  $\varepsilon \rightarrow 0$

Conclusions (2)

- Integrated approach is important: Modelling, bifurcation analysis and perturbation theory
- Proper modelling gives perturbation parameter  $\varepsilon$  a biological interpretation not just a mathematical perturbation parameter
## Conclusions (3)

- In RM<sub>1</sub> model a canard occurs just above the Hopf bifurcation where the nullclines of the growth function f and g of the prey and predator populations intersect at the equilibrium point
- Power expansion also for a bifurcation parameter gives an approximation of the location where explosion occurs despide the fact that the series is divergent

## Thanks to

Jean-Christophe Poggiale (Marseille)

Pierre Auger (Paris)

Bas Kooijman (VU-Amsterdam)







Future work (together with Jean-Christophe Poggiale)

- Link between canards and blow-up techniques
- Link between maximal canard location and first Lyapunov coefficient

## Literature

M. Krupa and P. Szmolyan. Extending geometric singular perturbation theory to nonhyperbolic points - fold and canard points in two dimensions. *SIAM J. Math. Anal.*, 33(2):286–314, 2001.

C. Kuehn, *Multiple Time Scale Dynamics*, Applied Mathematical Sciences 191, Springer-Verlag, 2015

• Link between deterministic and stochastic modelling

## Literature

N, Stollenwerk, P.F. Sommer, B.W. Kooi, L. Mateus, P. Ghaffari, M. Aguiar. Hopf and torus bifurcations, torus destruction and chaos in population biology, in prep. 2016