

Modelling, singular perturbation and bifurcation analyses of bitrophic food chains

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1 Modelling, singular perturbation and bifurcation
2 analyses of bitrophic food chains

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5 **Abstract**

6 Two predator-prey model formulations are studied: for the classical Rosenzweig-
7 MacArthur (RM) model and the Mass Balance (MB) chemostat model. When the
8 growth and loss rate of the predator is much smaller than that of the prey these mod-
9 els are slow-fast systems leading mathematically to singular perturbation problem.
10 In contradiction to the RM-model, the resource for the prey are modelled explicitly
11 in the MB-model but this comes with additional parameters. These parameter val-
12 ues are chosen such that the two models become easy to compare. In both models a
13 transcritical bifurcation, a threshold above which invasion of predator into prey-only
14 system occurs, and the Hopf bifurcation where the interior equilibrium becomes un-
15 stable leading to a stable limit cycle. The fast-slow limit cycles are called relaxation
16 oscillations which for increasing differences in time scales leads to the well known
17 degenerated trajectories being concatenations of slow parts of the trajectory and fast
18 parts of the trajectory. In the fast-slow version of the RM-model a canard explosion
19 of the stable limit cycles occurs in the oscillatory region of the parameter space.
20 To our knowledge this type of dynamics has not been observed for the RM-model
21 and not even for more complex ecosystem models. When a bifurcation parameter
22 crosses the Hopf bifurcation point the amplitude of the emerging stable limit cycles
23 increases. However, depending of the perturbation parameter the shape of this limit
24 cycle changes abruptly from one consisting of two concatenated slow and fast episodes
25 with small amplitude of the limit cycle, to a shape with large amplitude of which
26 the shape is similar to the relaxation oscillation, the well known degenerated phase
27 trajectories consisting of four episodes (concatenation of two slow and two fast).

28 The canard explosion point is accurately predicted by using an extended asymptotic
29 expansion technique in the perturbation and bifurcation parameter simultaneously
30 where the small amplitude stable limit cycles exist. The predicted dynamics of the
31 MB-model is in a large part of the parameter space similar to that of the RM-model.
32 However, the fast-slow version of MB-model does not predict a canard explosion
33 phenomenon.

34 *Keywords:*

35 Aggregation methods; Asymptotic series expansion; Canard; Geometrical Singular
36 Perturbation theory; Predator-prey models

37 *Mathematics Subject Classification:* 34E17 - 37G15 - 92D25 - 92D40

1 Introduction

There is already a long tradition in modelling predator–prey systems under various environmental conditions. In some realistic cases there are differences in the order of magnitudes of the ingestion and growth rates of the two populations leading to so called fast-slow dynamical systems. Various mathematical analyses techniques have been used to analyse these models. Here we focus on the application of perturbation techniques when the processes of the two population occur at different time-scales.

The starting point is the Rosenzweig-MacArthur (RM) model [44] where the prey population grows logistically and the predator-prey interaction is described by the Holling type II functional response. This predator-prey system is mathematically described by two ordinary differential equations, (ODE)s, for the prey and the predator population. This model does not obey mass conservation law, however. Therefore we study also a version where additionally the prey population consumes abiotic nutrients. The resulting model is called the Mass Balance (MB) model where mass conservation is obeyed. This type of model is common practice in modeling food chains in a chemostat reactor which have been studied extensively: we refer to [45, 24]. These systems consist minimally of a nutrient, a prey and a predator. Consequently, the description of the dynamics involves three ODEs. The resulting three dimensional model is reduced to a two dimensional model for prey and predator populations when realistic assumptions are made.

For both types of models it is well known that the long-term dynamics is either a stable equilibrium (boundary: prey only, or interior: predator-prey) or a stable predator-prey limit cycle. For the RM-model, in [19] it was proved that the coexistence equilibrium is globally stable and in [4] that the periodic solution is unique thus a globally stable limit cycle and in [31] a detailed bifurcation analysis is performed.

Nutrient enrichment leads to the risk of extinctions when fluctuating densities during the limit cycle reach low values, called the “paradox of enrichment” [43]. Mathematically the first transition occurs at a transcritical bifurcation and the second at a Hopf bifurcation. This holds for both types of model the RM and MB-model.

When the growth and loss rate of the predator is much smaller than that of the prey, the system becomes a so called slow–fast system. These rates for the predator are multiplied by a perturbation parameter. These systems have been studied intensively in the literature, the RM-model with fast-slow dynamics in [35, 42, 41, 5, 11]. Slow-fast systems can naturally be identified, are often encountered in ecology. This is almost a rule when behavioral and population dynamics are considered at the same time. But also interactions between two populations like plankton and fish, plants and insects, herbs and trees are classical examples of systems with two time scales (see [41]). Another example where there are differences in the order of magnitudes of the ingestion and growth rates is a food chain of sewage-bacterium-worms often found in wastewater treatment plants (see [40]). The worm is the water nymph *Nais elinguis*, a oligochaete species. In a previous paper [25] we took advantage of these different time scales to apply aggregation methods in order to simplify the models for the dynamics of the wastewater treatment plant system.

Using a perturbation technique often the slow variables are frozen with the calculation

80 of the equilibria of the fast system but better approximations are obtained by asymptotic
 81 expansions [18, 16]. When the perturbation parameter becomes small the resulting limit
 82 cycle is called the *relaxation oscillation*, see [15], where the periodic orbits are phase plane
 83 curves with both fast and slow parts of the trajectory.

84 When the time-scales differences are very large, that is with small positive perturbation
 85 parameter, the presence of the Hopf bifurcation indicates the possible occurrence of so
 86 called *canards*. In physics this has been studied extensively for the van der Pol equations
 87 [47, 10, 6, 3, 8, 28, 29, 2]. More recently, in [37, 16] geometric singular perturbation
 88 techniques [12] have been studied for application in biological practice, including these
 89 slow-fast predator-prey systems. In this theory *invariant manifolds* play an important role
 90 in the study of structural stability of dynamical systems or, when a degeneracy occurs,
 91 in understanding the nature of bifurcations. A trajectory is an example of an invariant
 92 manifold. Using this approach we will find that similar to the van der Pol equations case
 93 also for the RM-model application of asymptotic expansions [3, 2] for the critical manifolds
 94 leads to a divergent expansion. Nevertheless we will show that we are still able to compute
 95 for which bifurcation parameter values a canard explosion occurs.

96 Bifurcation analysis results show that in the MB-model the singularity in the limiting
 97 time-scale differences is completely different from that in the RM-model where the prey
 98 grows logistically. Only local bifurcations occur and therefore continuation of equilibrium
 99 and limit cycles gives a full picture of the long-term dynamics.

100 2 The RM bitrophic food chain model

101 A standard two-level food chain model from the field of theoretical biology is the scaled
 102 Rosenzweig-MacArthur system (1963). The RM-model reads in dimensionless form derived
 103 in the Appendix A:

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

$$\frac{dx_2}{dt} = x_2 \left(\frac{c_1 a_1 x_1}{1 + b_1 x_1} - d_1 \right), \quad (1b)$$

104 with $x_i(t) \in \mathbb{R}_+$, $t \geq 0$, $i = 1, 2$, respectively the size of the prey and predator population.
 105 The first part of (1a) models that the prey population grows logistically in absence of the
 106 predator. The hyperbolic relationship $a_1 x_1 / (1 + b_1 x_1)$ is called the Holling type II functional
 107 response. This expression occurs in both equations and models the consumption of the
 108 prey population by the predator population. Parameter $a_1 > 0$ is the searching rate for
 109 the prey and $b_1 > 0$ the product of the handling time of the prey by the predator and
 110 the searching rate. The ratio of the first term of (1b) and the last term on the right-hand
 111 sides of (1a) is the efficiency $c_1 > 0$. The last term of (1b) is death rate $d_1 > 0$ of the
 112 predator population but it can also model other biological processes of which the loss rate
 113 is proportional to the population size similar to maintenance.

114 For a description of the state variables and the biological meaning of the parameters of
the predator-prey model the reader is referred to Table 1.

Table 1: List of parameters and state variables and their reference values. We take the efficiency c_1 and death rate d_1 both proportional to the positive perturbation parameter ε . For numerical studies we take that parameter a_1 co-varies with b_1 via $a_1 = 5/3 b_1$, hence handling time is $3/5$ and the values for parameters $c = d = 1$ for the RM-model and $D = e_1 = 1$ for the MB-model. This is without loss of generality.

parameter	ref.values	Interpretation
t	$[0, \infty)$	Fast time variable
τ	$[0, \infty)$	Slow time variable
x_0	$[0, \infty)$	Nutrient density
x_1	$[0, \infty)$	Prey biomass density
x_2	$[0, \infty)$	Predator biomass density
x_r	$(0, \infty)$	Nutrient concentration in reservoir
a_1	$a_1 = 5/3 b_1$	Searching rate
b_1	3,4 or 8	Handling time \times searching rate
$c_1 = \varepsilon c$	$c = 1$	Conversion efficiency
$d_1 = \varepsilon d$	$d = 1$	Death rate
e_1	1	Conversion efficiency
$D_1 = \varepsilon D$	$D = 1$	Dilution rate
ε	$[0, 1]$	Perturbation parameter

115
116 The set of equations analysed extensively in the literature that form a model with
117 slow-fast dynamics reads

$$\frac{dx_1}{dt} = f(x_1, x_2, \varepsilon) = x_1 \left(1 - x_1 - \frac{a_1 x_2}{1 + b_1 x_1} \right), \quad (2a)$$

$$\frac{dx_2}{dt} = \varepsilon g(x_1, x_2, \varepsilon) = \varepsilon x_2 \left(\frac{a_1 x_1}{1 + b_1 x_1} - 1 \right), \quad (2b)$$

118 with $x_i \in \mathbb{R}$, $i = 1, 2$. We introduced $c_1 = \varepsilon c$ and $d_1 = \varepsilon d$ and toke for both parameters
119 their reference value 1. The efficiency is again the ratio of the first term of (2b) and the
120 last term on the right-hand sides of (2a) and is now equal to ε .

121 The functions $f : \mathbb{R}^3 \rightarrow \mathbb{R}$ and $g : \mathbb{R}^3 \rightarrow \mathbb{R}$ are of class smooth enough. The time-scale
122 separation parameter ε is introduced in the model to implement trophic time diversification.
123 For $\varepsilon \ll 1$ this is called a fast-slow system.

124 In the mathematical literature, factor ε is treated as a perturbation parameter, justified
125 and described by the ratio between the linear death rate of the predator and the linear
126 growth rate of the prey in [42, 16]. That is, only when the prey reproduce much faster than
127 the predators and the predator is, in comparison, not so efficient, when the ratio ε becomes

128 a small parameter. For, the efficiency $c_1 = \varepsilon c$, where c is of order 1 (with a reference value
 129 1) is proportional to the perturbation parameter ε .

130 The Holling type II hyperbolic relationship is derived by a time scale argument using
 131 a time budget modelling spend on searching for and handling of prey individuals by a
 132 predator individual. The ratio of these two terms is called the assimilation efficiency in
 133 ecology literature and the yield in the microbiology literature. When the units of both
 134 state variables equal then consequently $\varepsilon < 1$ means that there is a smaller than 100%
 135 biomass conversion, as is always the case in nature. We assume that the formed products
 136 during this conversion process, have no effects on other processes underlying model (2). In
 137 general, however, a very small conversion efficiency is not supported in the literature.

138 Observe that also the predator loss rate is multiplied by the same factor ε in order to
 139 facilitate coexistence. In other words when predators efficiency is low they also have to
 140 have a low loss rate in order to survive. Therefore the parameter ε affects two processes,
 141 mass conversion from prey biomass into predator biomass and the predator loss rate.

142 2.1 Existence and stability analysis of equilibria and limit cycles

143 In model (2) there are only three free parameters, namely a_1 , b_1 and ε which scales the
 144 efficiency and predator loss rate. The following stability analysis is classical for $\varepsilon > 0$ and
 145 therefore we recall some results regarding the dynamics of (2) and report some interesting
 146 results when $\varepsilon \rightarrow 0$ and $\varepsilon = 0$

147 The one-parameter bifurcation diagram with varying b_1 where $\varepsilon = 1$ and a_1 co-varies
 148 with b_1 via $a_1 = 5/3 b_1$, is shown in Fig. 1 for parameter b_1 as free parameter. The three
 149 relevant equilibria zero- E_0 , boundary- E_1 and interior equilibrium E_2 and the limit cycle
 150 L_2 are summarized in Table 2 and the bifurcation curves the transcritical bifurcation TC
 151 and Hopf bifurcation H in Table 3. In [19] it was proved that the coexistence equilibrium
 152 E_2 is globally stable and in [4] that the periodic solution is unique thus a globally unique
 153 stable limit cycle L_2 . The numerical bifurcation results show that the limit cycle for
 154 parameter values above the supercritical Hopf bifurcation is stable and that the minimum
 155 values become very small for large b_1 . This phenomenon is related to the “paradox of
 156 enrichment” [43], because extinction due to stochastic fluctuations is likely.

157 For the stability analysis of equilibria we need the Jacobian matrix evaluated at point
 158 (x_1, x_2) ([27]), which reads

$$\mathbf{J} = \begin{pmatrix} 1 - x_1 - \frac{a_1 x_2}{1+b_1 x_1} + x_1 \left(\frac{a_1 x_2 b_1}{(1+b_1 x_1)^2} - 1 \right) & -\frac{a_1 x_1}{1+b_1 x_1} \\ \varepsilon x_2 \left(\frac{a_1}{1+b_1 x_1} - \frac{a_1 x_1 b_1}{(1+b_1 x_1)^2} \right) & \varepsilon \left(\frac{a_1 x_1}{1+b_1 x_1} - 1 \right) \end{pmatrix}. \quad (3)$$

159 In E_0 the Jacobian matrix is

$$\mathbf{J}_0 = \begin{pmatrix} 1 & 0 \\ 0 & -\varepsilon \end{pmatrix}. \quad (4)$$

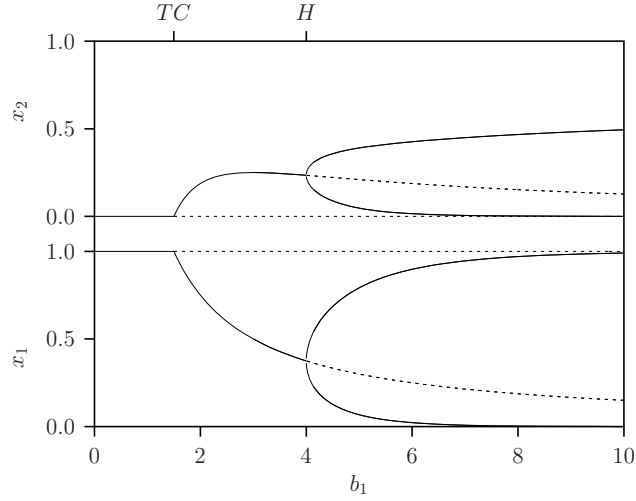


Figure 1: One-parameter bifurcation diagram for b_1 and $a_1 = 5/3 b_1$ of the RM-system (1) with $\varepsilon = 1$. The equilibria E_1 (below TC) and E_2 (between TC and H) as well as the maximum and minimum values for the limit cycle L_2 (above H) are shown. Note that the critical values where the bifurcations TC and H occur in this diagram are independent of ε since the expression for the real parts of the eigenvalues of the Jacobian matrix do not depend on ε .

Table 2: Equilibria of RM-model (2) and MB-model (54).

Equilibria	System composition
RM-model	
$E_0 = (0, 0)$	Extinction
$E_1 = (1, 0)$	Prey-only
$E_2 = (x_1^*, x_2^*) = \left(\frac{1}{a_1 - b_1}, \frac{a_1 - b_1 - 1}{(a_1 - b_1)^2}\right)$	Prey-predator
MB-model	
$E_0 = (0, 0)$	Extinction
$E_1 = (1, 0)$	Prey-only
$E_2 = (x_1^*, x_2^*) = \left(\frac{1}{a_1 - b_1}, \frac{a_1 - b_1 - 1}{\varepsilon(a_1 - b_1)^2 + a_1 - b_1}\right)$	Prey-predator

Table 3: Bifurcation curves for RM-model (2) and MB-model (54). Note that for RM-model the expression are independent of ε . The arrow indicates the transition of the steady states that occurs when the parameter crosses the bifurcation point.

Bifs.	$a_1(b_1, \varepsilon)$	b_1 ($a_1 = 5/3 b_1$)	Interpretation
RM-model			
TC	$a_1 = b_1 + 1$	1.5	$E_1 \rightarrow E_2$
H	$a_1 = \frac{b_1(b_1+1)}{b_1-1}$	4	$E_2 \rightarrow L_2$
MB-model			
TC	$a_1 = b_1 + 1$	1.5	$E_1 \rightarrow E_2$
H	$a_1 = \frac{2\varepsilon b_1^2 + 1 + \sqrt{4b_1^2\varepsilon(\varepsilon+1)+1}}{2\varepsilon(b_1-1)}$	$b_1 = \frac{4\varepsilon + \sqrt{16\varepsilon^2 + 15\varepsilon}}{(2\varepsilon)}$	$E_2 \rightarrow L_2$

160 The eigenvalues are the diagonal elements and the E_0 is always unstable. At the boundary
 161 equilibrium E_1 the Jacobian matrix reads

$$\mathbf{J}_1 = \begin{pmatrix} -1 & -\frac{a_1 - b_1 - 1}{1 + b_1} \\ 0 & \varepsilon \left(\frac{a_1 - b_1 - 1}{a_1} \right) \end{pmatrix}. \quad (5)$$

162 The eigenvalues are again the diagonal elements and E_1 is stable when $a_1 - b_1 - 1 < 0$ and
 163 unstable when $a_1 - b_1 - 1 > 0$. The equality gives the transcritical bifurcation TC where
 164 $b_1 = a_1 - 1$ or for the reference value $a_1 = 5/3 b_1$ we have $b_1 = 3/2$.

165 At the equilibrium E_2 the Jacobian matrix reduces to

$$\mathbf{J}_2 = \begin{pmatrix} \frac{a_1(b_1-1) - b_1(1+b_1)}{a_1((a_1-b_1))} & -1 \\ \varepsilon \left(\frac{a_1 - b_1 - 1}{a_1} \right) & 0 \end{pmatrix}. \quad (6)$$

The complex pair of eigenvalues $\lambda_{1,2}$ of the Jacobian matrix evaluated at the equilibrium
 E_2 read

$$\lambda_{1,2}(b_1, \varepsilon) = \mu(b_1) \pm i\omega(b_1, \varepsilon). \quad (7)$$

166 We calculated the following real $\mu \in \mathbb{R}$ and imaginary $\omega \in \mathbb{R}$ parts as functions of parameter
 167 ε and b_1 where $a_1 = 5/3 b_1$

$$\Delta(b_1, \varepsilon) = (\text{Tr } \mathbf{J}_2)^2 - 4 \det \mathbf{J}_2 = \frac{-144 + 72b_1 - 9b_1^2 - 60b_1\varepsilon + 40\varepsilon b_1^2}{25b_1^2}, \quad (8)$$

$$\mu(b_1, \varepsilon) = \frac{3(b_1 - 4)}{10b_1} \pm \frac{1 - \text{sgn } \Delta(b_1, \varepsilon)}{2} \sqrt{|\Delta(b_1, \varepsilon)|}, \quad (9)$$

$$\omega(b_1, \varepsilon) = \pm \frac{1 + \text{sgn } \Delta(b_1, \varepsilon)}{2} \sqrt{|\Delta(b_1, \varepsilon)|}. \quad (10)$$

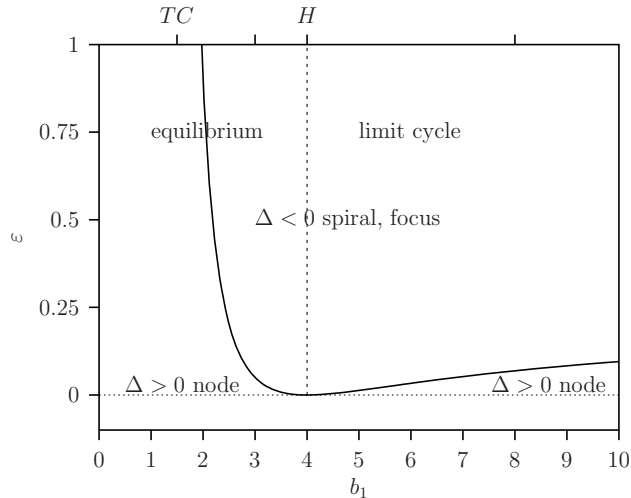


Figure 2: Focus bifurcation where $\Delta = 0$ curve for ε vs b_1 .

168 In Fig. 2 the curve where $\Delta(b_1, \varepsilon) = 0$ is plotted in the (b_1, ε) parameter space. This
 169 curve separates regions where the equilibrium is a node $\Delta > 0$ (two real eigenvalues) or
 170 a spiral or focus $\Delta < 0$ (two conjugated complex eigenvalues). At $\Delta = 0$ there are two
 171 equal real eigenvalues. From this figure we conclude that for $\varepsilon = 1$ and $b_1 = 3$ or $b_1 = 8$
 172 the equilibria are foci while for $\varepsilon = 0.01$ the equilibria are nodes, stable and unstable,
 173 respectively.

174 The positions of the bifurcations TC and H are independent of the parameter ε . This
 175 is not true for the so called first Lyapunov coefficient ℓ^1 which determines whether the
 176 Hopf bifurcation is supercritical or subcritical, that is whether the emerging limit cycles
 177 are stable or unstable, respectively.

178 At the Hopf bifurcation with $b_1 = 4$ we have for $\varepsilon > 0$ a zero real part $\mu(4) = 0$
 179 and the positive imaginary part equal to the determinant of the Jacobian matrix \mathbf{J}_2 :
 180 $\omega(4) = \sqrt{\det \mathbf{J}_2} = 1/2 \sqrt{\varepsilon}$, for the two conjugated complex eigenvalues. The square root of
 181 the ratio $\mu(b_1)/\omega(b_1)$ measures the amplitude of the limit cycle that emerge for the Hopf
 182 bifurcation for $b_1 > 4$. Evaluation of this ratio just above $b_1 = 4$ gives that the oscillatory
 183 dynamics for values is as with the Hopf bifurcation till the canard explosion occurs.

184 The derivative $d\mu/db_1(b_1)|_{b_1=4} = 3/40 > 0$ at the Hopf bifurcation equilibrium is posi-
 185 tive and therefore the transversality condition for applying the normal form theorem [31,
 186 Theorem (3.3)] is satisfied. Using a similar procedure in Maple, [32] described in [31], the
 187 first Lyapunov coefficient ℓ^1 is evaluated as

$$\ell^1 = -\frac{16}{75} \frac{14\varepsilon + 1}{\varepsilon^{3/2}}. \quad (11)$$

188 Since ℓ^1 is negative for $\varepsilon > 0$, the Hopf bifurcation is supercritical. Note that for $\lim \varepsilon \rightarrow$
 189 0 we have $\ell^1 \rightarrow -\infty$. That is, the first Lyapunov coefficient ℓ^1 becomes unbounded.

190 Furthermore, in the limiting case $\varepsilon = 0$ at the Hopf bifurcation where $b_1 = 4$ with $\mu(4) = 0$
 191 we get together with $\omega(4) = 1/2 \sqrt{\varepsilon} = 0$ that this point becomes a degenerated bifurcation
 192 where both eigenvalues are zero as in a Bogdanov-Takens bifurcation point. Exploration
 193 of these facts can be done with a blow-up technique [8, 9] which is beyond the scope of
 194 this paper.

195 2.2 Phase-space analysis

196 In this section we discuss results in the phase-space of simulation in time. These results
 197 where in all simulations the same initial conditions are used, are shown in Fig. 3 and Fig. 4:

- 198 • Left panels of Fig. 3: for $b_1 = 3$, in the region between the transcritical TC and Hopf
 199 H bifurcation in Fig. 1 where equilibrium E_2 is stable,
- 200 • Fig. 4: for $b_1 = 4$ at the Hopf bifurcation,
- 201 • Right panels of Fig. 3: for $b_1 = 8$ above the Hopf bifurcation in Fig. 1 where equilib-
 202 rium E_2 is unstable.

203 In the top panels of Fig. 3 and Fig. 4 the f-nullcline where $f(x_1, x_2, \varepsilon) = 0$: $x_2 =$
 204 $(1 - x_1)(1 + b_1 x_1)/a_1$ and the g-nullcline where $g(x_1, x_2, \varepsilon) = 0$: $x_1 = 1/(a_1 - b_1)$, are
 205 shown. Both are independent of ε . The graph of the f-nullcline is part of a parabola where
 206 it intersects the horizontal axis $x_2 = 0$ at $x_1 = 1$ and of the g-nullcline is just a vertical
 207 line through the equilibrium point E_2 .

208 2.2.1 Stable interior equilibrium

209 With $b_1 = 3$, see Fig. 3a with $\varepsilon = 1$ and Fig. 3c with $\varepsilon = 0.01$, the equilibrium E_2 is stable
 210 and there is convergence to the stable point.

211 For low $\varepsilon = 0.01$ value shown in Fig. 3c, initially after starting above the nullcline the
 212 solution goes rapidly to the vertical axis. There is almost no prey population and hence
 213 the predator population diminishes approximately exponential with rate $d_1 = 1$:

$$\frac{dx_2}{d\tau} = -x_2, \quad (12)$$

214 where differentiation is with respect to the slow time variable $\tau = \varepsilon t$. The solution crosses
 215 the critical point $x_2 = 1/a_1$ the intersection with the nullcline and leaves the vertical
 216 axis moving fast toward the stable part of the nullcline. Because this happens below
 217 the critical point (intersection of parabola and vertical axis) this phenomenon is called
 218 a *delayed bifurcation* which is explained in [42]. Eventually the system converges to the
 219 stable equilibrium E_2 given in Table 2.

220 2.2.2 Hopf interior equilibrium

221 The equilibrium E_2 , see Table 2, at the Hopf bifurcation H coincides with the top of the
 222 f-nullcline parabola

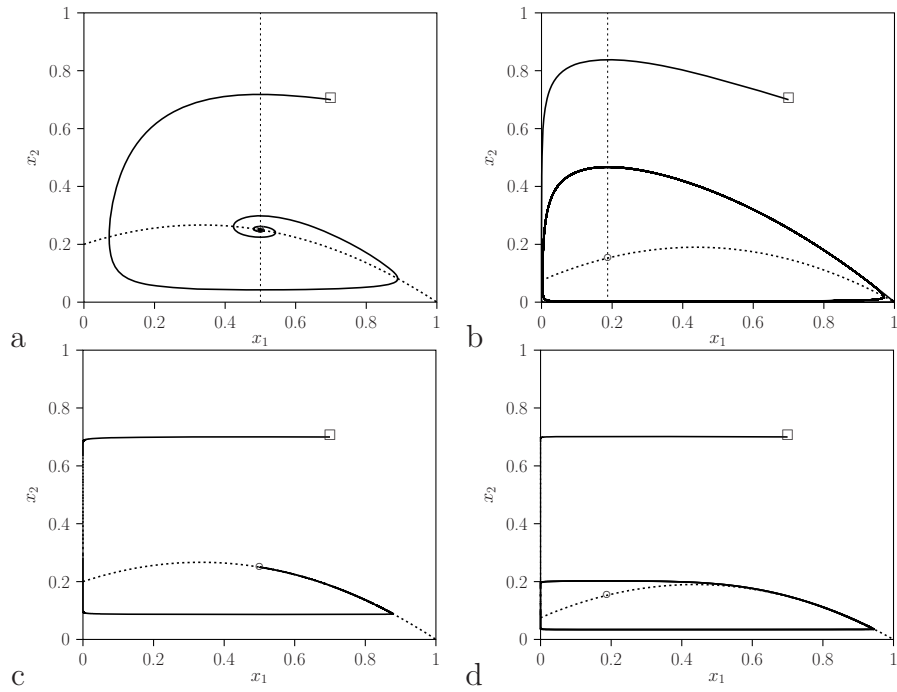


Figure 3: Phase-space analysis for system (2) describing the RM-model with $b_1 = 3$ (left panels) and $b_1 = 8$ (right panels) while $a_1 = 5/3 b_1$. Top panels (a,b): $\varepsilon = 1$ and bottom panels (c,d): $\varepsilon = 0.01$. (a): Spiral stable equilibrium E_2 , (b): stable limit cycle L_2 , (c): node stable equilibrium E_2 and (d): stable limit cycle L_2 .

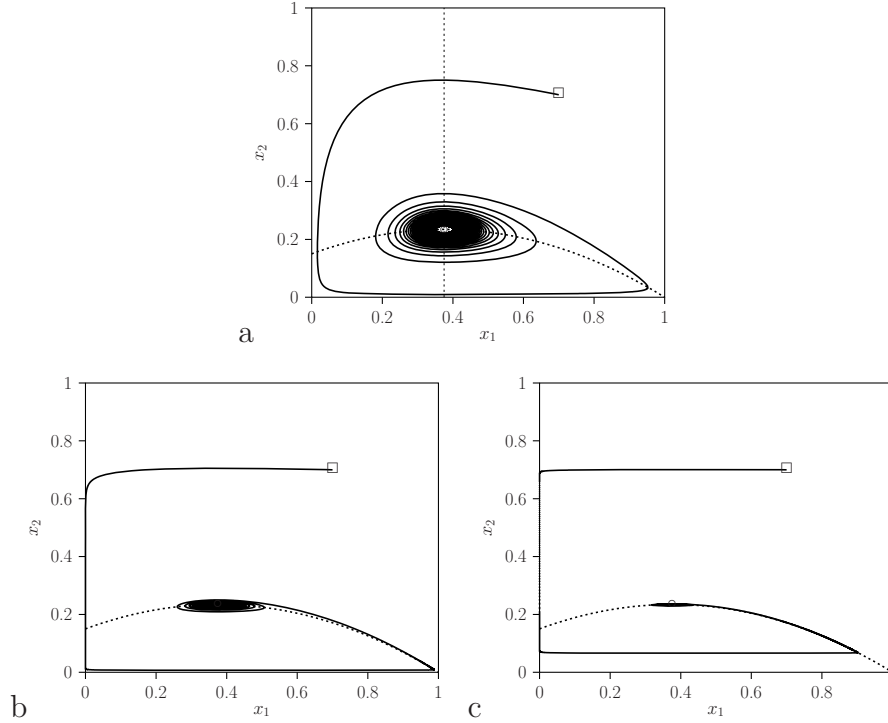


Figure 4: Phase-space analysis for system (2) describing the RM-model, $b_1 = 4$ and $a_1 = 5/3 b_1$, that is at the Hopf bifurcation point for three different values of ε : $\varepsilon = 1$ (a), $\varepsilon = 0.1$ (b) and $\varepsilon = 0.01$ (c).

$$(\bar{x}_1, \bar{x}_2)_T = \left(\frac{b_1 - 1}{2b_1}, \frac{(b_1 + 1)^2}{4a_1 b_1} \right). \quad (13)$$

223 At the Hopf point we have the equilibrium E_2

$$(x_1^*, x_2^*)_H = (\bar{x}_1, \bar{x}_2)_T = \left(\frac{3}{8}, \frac{15}{64} \right). \quad (14)$$

224 The simulation results for system (2) are shown in Fig. 4. These results show that the solu-
 225 tion finally converges very slowly to this, sometimes called a weakly attracting, equilibrium
 226 (14) at the top of the f-nullcline denoted by (13).

227 2.2.3 Unstable interior equilibrium

228 With $b_1 = 8$, see Fig. 3b,d equilibrium E_2 is unstable and there is no convergence to E_2
 229 but to a stable limit cycle L_2 .

230 For positive $\varepsilon = 0.01$ in Fig. 3d initially the dynamics is similar to that for the stable
 231 case shown in Fig. 3c. The dynamics on the unique stable limit cycle L_2 consists of four

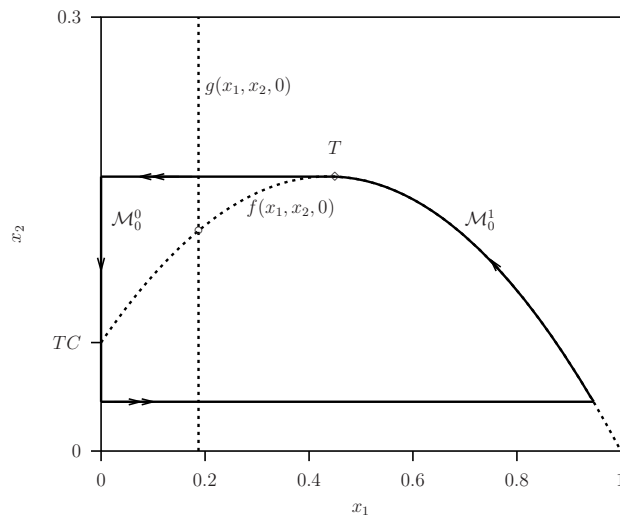


Figure 5: Fast (double arrow) and slow (single arrow) dynamics for system (2) describing the RM-model with $b_1 = 8$ where for $\lim \varepsilon \rightarrow 0$ the concatenated trajectories are the degenerated phase curves. The f-nullcline (parabola) and g-nullcline (vertical line through equilibrium) are shown. Point T is top of parabola given in (13) and TC is intersection point of f-nullcline and vertical axis.

232 concatenated episodes. Two parts of the trajectory where the predator population changes
 233 slowly and two parts of the trajectory where the predator population is almost constant
 234 and the prey population changes fast (the almost horizontal parts of the solution orbit).

235 2.2.4 Degenerate phase curves

236 With $b_1 > 4$ the limits of the limit cycles L_2 , the periodic *relaxation oscillations*, for
 237 $\lim \varepsilon \rightarrow 0$ are called *degenerated phase curves* shown in Fig. 5, see [14] It consists of
 238 four concatenated episodes (families of periodic sets). On two parts of the trajectory the
 239 dynamics is slow (single arrow): one along the vertical axis where the predator population
 240 decreases slowly and the other are along parts of the parabolic f-nullcline where the prey
 241 population decreases while the predator population increases slowly.
 242 On the other two parts of the trajectory the prey changes fast (double arrows) and the
 243 predator is constant: one from point T toward the vertical axis and one from this vertical
 244 axis to the point on the parabolic f-nullcline. This type of dynamics is discussed intensively
 245 in the ecological literature, we mention [42, 11] and references therein. These two episodes
 246 are connected by two fast episodes along the horizontal lines where the prey population
 247 size increases or decreases fast while the predator population is constant.

248 Starting slowly on the vertical axis above the f-nullcline, during the first episode, the
 249 solution orbit crosses the critical point TC and leaves this axis fast horizontally toward
 250 the parabola. Then it continues, during the second episode, slowly and during the third
 251 episode again along the parabola passing the top of the parabola point T given in (13).

252 Note that since $b_1 > 4$ the equilibrium E_2 indicated by the open circle in Fig. 5 on the
 253 f-nullcline, does not coincide with this non-hyperbolic point T . After crossing this point
 254 the solution orbit, during the forth episode, moves vastly horizontally toward the vertical
 255 axis again above the f-nullcline, and so on.

256 Note that the dynamics of the degenerate phase curves shown in Fig. 5 are indeed close
 257 to this for the RM-model in Fig. 3d where $b_1 = 8$ in both cases. However for the Hopf
 258 bifurcation $b_1 = 4$ case the resulting dynamics for small $\varepsilon \ll 1$ does not look like that of
 259 Fig. 5 and more importantly also not for b_1 slightly above the Hopf bifurcation. Therefore
 260 we focus in the next sections on the dynamics for parameter values where the unstable
 261 equilibrium E_2 is just above the Hopf bifurcation value.

262 3 Singular perturbation problem

263 In this section the singular perturbation technique is used to analyse the singular pertur-
 264 bation problem where $\varepsilon = 0$ in the RM-model (2). We will also analyse the quasi-steady
 265 state solution or the relaxation oscillation in detail. The reader is referred to [18, 21, 22]
 266 for introductions into perturbation analysis.

267 3.1 Heuristic introduction

268 We start with a short overview of singular perturbation techniques. Singular perturbation
 269 theory deals with systems of the *original* form (2) where $\varepsilon > 0$. When $\varepsilon \ll 1$ the system
 270 is a fast-slow system.

271 With $\varepsilon = 0$ we have the *fast system* also called called the *layer system*:

$$\frac{dx_1}{dt} = f(x_1, x_2(0), 0) = x_1 \left(1 - x_1 - \frac{a_1 x_2(0)}{1 + b_1 x_1} \right), \quad (15a)$$

$$\frac{dx_2}{dt} = 0. \quad (15b)$$

272 The predator populations remains constant hence the trajectories are the horizontal lines
 273 in Fig. 5.

274 With a change of time-scale, where $\tau = \varepsilon t$, we call the resulting system the *slow system*:

$$\varepsilon \frac{dx_1}{d\tau} = f(x_1, x_2, \varepsilon), \quad (16a)$$

$$\varepsilon \frac{dx_2}{d\tau} = \varepsilon g(x_1, x_2, \varepsilon). \quad (16b)$$

275 After substitution of $\varepsilon = 0$ we get

$$0 = f(x_1, x_2, 0), \quad (17a)$$

$$\frac{dx_2}{d\tau} = g(x_1, x_2, 0) = x_2 \left(\frac{a_1 x_1}{1 + b_1 x_1} - 1 \right). \quad (17b)$$

276 This differential algebraic equation (DAE) is called the *reduced system*. The trajectory is
 277 either part of the vertical axis where $x_2 = 0$ or part on the parabola, the other f-nullcline
 278 of the original system (2) in Fig. 5. However, in the fast-slow context these are the sets of
 279 equilibria of the fast layer-system (15) and then they are called *critical manifolds* where
 280 x_1 is acting as a parameter.

281 These heuristic results suggest the following approach for dealing with the two different
 282 time scales. The first step consists in setting $\varepsilon = 0$ which gives the set of fast equilibria
 283 of the fast system (15) yielding the algebraic equation (17a). This is the critical manifold
 284 which is the set of equilibria either at the vertical axis or the parabola where $f(x_1, x_2, 0) =$
 285 0.

286 From the results presented below in this section the parabolic critical manifold has two
 287 branches, one stable on the right-hand side (solid curve) and one unstable on the left-hand
 288 side (dashed curve) of point T in Fig. 5.

289 With good hypothesis (see below for the details), on the part of the parabola, $f(x_1, x_2, 0) =$
 290 0 is equivalent to $x_1 = p(x_2)$ and we can substitute x_1 by $p(x_2)$ in equation (17b). The
 291 result is the slow or reduced system

$$0 = f(p(x_2), x_2, 0), \quad \frac{dx_2}{d\tau} = g(p(x_2), x_2). \quad (18)$$

292 The differentiation is with respect to τ and the smooth functions f and g are defined in
 293 (2). Then the slow system becomes

$$\frac{dx_2}{d\tau} = x_2 \left(\frac{(a_1 - b_1)p(x_2) - 1}{b_1 p(x_2) + 1} \right), \quad x_1 = p(x_2) = \frac{1}{2b_1} (b_1 - 1 \pm \sqrt{(b_1 + 1)^2 - 4a_1 b_1 x_2}). \quad (19)$$

294 An alternative method is to use instead of $x_1 = p(x_2)$ of which the dynamics is described
 295 by the solution of (19), the inverse function $x_2 = q(x_1)$ also derived from (17a). This gives
 296 the relationship

$$x_2 = q(x_1) = \frac{1}{a_1} (1 - x_1)(1 + b_1 x_1), \quad (20)$$

297 and using (17b) the differential equation

$$\frac{dx_2}{d\tau} = g(x_1, q(x_1)) = \frac{dq}{dx_1} \frac{dx_1}{d\tau},$$

298 and we get formally

$$\frac{dx_1}{d\tau} = \frac{q(x_1)(a_1x_1 - (1 + b_1x_1))}{(1 + b_1x_1) dq/dx_1}, \quad \frac{dq}{dx_1} = \frac{1}{a_1} (b_1(1 - 2x_1) - 1). \quad (21)$$

299 Note that this expression is zero at point T given in (13). Hence the denominator of model
 300 (21) at that point T is zero. When the numerator is unequal zero, this means that the rate
 301 of change becomes unbounded at T which is a singular point of model (21). Only when in
 302 the special case b_1 is the Hopf bifurcation parameter value, point T is a limit point where
 303 the numerator is also zero. This is studied in the Appendix B.

304 3.2 Geometric singular perturbation techniques

305 We discuss the singular perturbation problem outlined in the previous section for the case
 306 where ε is not zero but small and positive: $0 < \varepsilon \ll 1$. Here we follow the geometric
 307 singular perturbation techniques.

308 Let us consider system (2) again. For $\varepsilon = 0$ the f-nullclines, the set $\{(x_1, x_2) | f(x_1, x_2, 0) =$
 309 $0, x_1 \geq 0, x_2 \geq 0\}$ consist of two types of critical manifolds, see Fig. 5

$$\mathcal{M}_0^0 = \{(x_1, x_2) | x_1 = 0, x_2 \geq 0\} \quad (22a)$$

$$\mathcal{M}_1^0 = \{(x_1, x_2) | x_2 = \frac{1}{a_1}(1 - x_1)(1 + b_1x_1), x_1, x_2 \geq 0\}. \quad (22b)$$

310 They form a set of equilibria of the fast system system (15). In the previous section we
 311 studied the dynamics for $\varepsilon = 0$ and now we will consider $0 < \varepsilon \ll 1$.

312 To that end, let us remind the statement of Fenichel's theorem. We consider differential
 313 system of the form:

$$\frac{dX}{dt} = F(X, Y, \varepsilon), \quad (23a)$$

$$\frac{dY}{dt} = \varepsilon G(X, Y, \varepsilon), \quad (23b)$$

$$\frac{d\varepsilon}{dt} = 0, \quad (23c)$$

314 where F and G are sufficiently smooth. We assume that the set $F(X, Y, 0) = 0$ can locally
 315 be written as $X = H(Y)$, which defines a critical manifold. If, for all Y in a given compact
 316 set \mathcal{D} , all the eigenvalues of $\frac{DF}{DX}(H(Y), Y, 0)$ have a non-vanishing real part, then the critical
 317 manifold is said *normally hyperbolic*. In this case, there exists ε_0 and a map p defined on
 318 $\mathcal{D} \times [0, \varepsilon_0[$ such that:

319 i) $H(Y) = p(Y, 0);$

320 ii) the graph of p is invariant under the flow associated to the original differential system
 321 (23);

322 iii) the graph of p is tangent to the central space associated to the linearisation of the
 323 system at $(H(Y), Y, 0)$.

324 As a consequence, both critical manifolds \mathcal{M}_0^0 and \mathcal{M}_0^1 are normally hyperbolic and
 325 there exists ε_0 such that for $0 < \varepsilon < \varepsilon_0$, there are locally invariant manifolds $\mathcal{M}_\varepsilon^0$ and
 326 $\mathcal{M}_\varepsilon^1$ except in the neighborhood of point T $(x_1, x_2) = (\bar{x}_1, \bar{x}_2)$ and in the neighborhood
 327 of the intersection between \mathcal{M}_0^0 and \mathcal{M}_0^1 on the vertical axis. Indeed, at those points,
 328 the derivative of the fast part vanishes, which contradicts the assumptions of the theorem
 329 statement.

330 Using its invariance, the perturbed manifold $\mathcal{M}_\varepsilon^1$ can be approximated by asymptotic
 331 expansions in ε . It can be described as a graph

$$\{(x_1, x_2) | x_2 = q(x_1, \varepsilon), x_1 \geq 0, x_2 \geq 0\}. \quad (24)$$

332 This manifold is invariant when the following equality holds

$$\frac{dx_2}{dt} = \frac{dx_2}{dx_1} \frac{dx_1}{dt} = \frac{dq(x_1, \varepsilon)}{dx_1} \frac{dx_1}{dt}, \quad (25)$$

333 yields with equation (23) and $x_2 = q(x_1, \varepsilon)$:

$$\frac{\partial q(x_1, \varepsilon)}{\partial x_1} \frac{dx_1}{dt} = \varepsilon q(x_1, \varepsilon) \left(\frac{x_1(a_1 - b_1) - 1}{1 + b_1 x_1} \right). \quad (26)$$

334 Then (23) gives with $x_2 = q(x_1, \varepsilon)$ the invariance condition

$$\frac{\partial q(x_1, \varepsilon)}{\partial x_1} x_1 \left(1 - x_1 - \frac{a_1 q(x_1, \varepsilon)}{1 + b_1 x_1} \right) = \varepsilon q(x_1, \varepsilon) \left(\frac{x_1(a_1 - b_1) - 1}{1 + b_1 x_1} \right), \quad (27)$$

335 or using $1 + b_1 x_1 > 0$

$$\frac{\partial q(x_1, \varepsilon)}{\partial x_1} x_1 \left((1 - x_1)(1 + b_1 x_1) - a_1 q(x_1, \varepsilon) \right) = \varepsilon q(x_1, \varepsilon) (x_1(a_1 - b_1) - 1). \quad (28)$$

336 3.2.1 Asymptotic expansion

337 The following asymptotic expansion in ε is introduced:

$$q(x_1, \varepsilon) = q_0(x_1) + \varepsilon q_1(x_1) + \varepsilon^2 q_2(x_1) + \dots, \quad (29)$$

338 hence

$$\frac{\partial q}{\partial x_1} = \frac{dq_0}{dx_1} + \varepsilon \frac{dq_1}{dx_1} + \varepsilon^2 \frac{dq_2}{dx_1} + \dots . \quad (30)$$

339 Substitution into (28) gives

$$\begin{aligned} & \left(\frac{dq_0}{dx_1} + \varepsilon \frac{dq_1}{dx_1} + \varepsilon^2 \frac{dq_2}{dx_1} + \dots \right) x_1 \left((1-x_1)(1+b_1x_1) - a_1(q_0(x_1) + \varepsilon q_1(x_1) + \varepsilon^2 q_2(x_1) + \dots) \right) \\ & = \left(\varepsilon(q_0(x_1) + \varepsilon q_1(x_1) + \dots) \right) (x_1(a_1 - b_1) - 1) . \end{aligned} \quad (31)$$

340 Gathering orders of ε results for $\mathcal{O}(1)$ and assuming $x_1 > 0$ in:

$$q_0(x_1) = \frac{(1-x_1)(1+b_1x_1)}{a_1} , \quad \frac{dq_0}{dx_1} = \frac{b_1 - 1 - 2x_1b_1}{a_1} . \quad (32)$$

341 At $b_1 = 4$ we have $x_1 = (b_1 - 1)/(2b_1)$ and hence $dq_0/dx_1 = 0$.

342 For $\mathcal{O}(\varepsilon)$ and using an updated form of (28)

$$\frac{\partial q(x_1, \varepsilon)}{\partial x_1} x_1 a_1 (q_0 - q(x_1, \varepsilon)) = \varepsilon q(x_1, \varepsilon) (x_1(a_1 - b_1) - 1) , \quad (33)$$

343 gives

$$q_1(x_1) = q_0(x_1) \frac{(x_1(a_1 - b_1) - 1)}{-a_1 x_1 \frac{dq_0}{dx_1}} . \quad (34)$$

344 At $b_1 = 4$ the numerator and denominator are both zero. we have $x_1 = (b_1 - 1)/(2b_1)$ and
345 $dq_0/dx_1 = 0$ but also since it is a equilibrium $x_1(a_1 - b_1) - 1 = 0$.

346 For $\mathcal{O}(\varepsilon^2)$ in (33) gives

$$q_2(x_1) = q_1(x_1) \frac{\frac{dq_1}{dx_1} x_1 a_1 + x_1(a_1 - b_1) - 1}{-a_1 x_1 \frac{dq_0}{dx_1}} . \quad (35)$$

347 At point T we have $x_1 = \bar{x}_1 = (b_1 - 1)/(2b_1)$ where $dq_0/dx_1 = 0$. Consequently, at
348 that point the denominator in the expression for $q_i(\bar{x}_1), i > 0$ is zero. Therefore the
349 coefficients $q_i(\bar{x}_1), i > 0$ are unbounded when the numerator is not equal zero. Only when
350 the parameter $b_1 = 4$ is at the Hopf bifurcation the numerator is zero and the coefficients
351 $q_i(\bar{x}_1)$ remain finite.

352 **3.2.2 Asymptotic expansion in phase space**

353 The expression for q_0 describes the critical manifold \mathcal{M}_0^1 . This expression is the inverse
 354 (when it exists) of $p(x_2)$ in (19). The voluminous expressions for the higher order q_i , $i > 1$
 355 coefficients obtained by equating the $\mathcal{O}(\varepsilon^i)$ terms on the left- and right-hand side of the
 356 invariance condition (28), are not given here but are available using Maple, [32]. This
 357 yields the approximation of the perturbed slow manifold $\mathcal{M}_\varepsilon^1$

358 For $\varepsilon = 0$ the limit (16b) prescribes the singular slow flow on \mathcal{M}_0^1 with $\tilde{x}_2 = q_0(\tilde{x}_1)$
 359 given by (32)

$$\frac{d\tilde{x}_1}{dt} = \tilde{x}_1 \left(1 - x_1 - \frac{a_1 q_0(\tilde{x}_1)}{1 + b_1 \tilde{x}_1} \right). \quad (36)$$

360 For sufficiently small non-zero $\varepsilon \ll 1$ the flow on the perturbed slow manifold $\mathcal{M}_\varepsilon^1$ can be
 361 approximated by inserting $\tilde{x}_2 = q(\tilde{x}_1, \varepsilon)$ with $q(\tilde{x}_1, \varepsilon)$ given by (29). In order to simulate
 362 the model we solve

$$\frac{d\tilde{x}_1}{dt} = \tilde{x}_1 \left(1 - \tilde{x}_1 - \frac{a_1 q(\tilde{x}_1, \varepsilon)}{1 + b_1 \tilde{x}_1} \right), \quad (37)$$

363 with properly chosen the initial values.

364 The results are shown in Fig. 6 for $b_1 = 3$, where the equilibrium E_2 is stable. They
 365 show that in this case the solution of the original model on $\mathcal{M}_\varepsilon^1$ is already well approximated
 by the second order approximation when $\varepsilon = 0.1$.

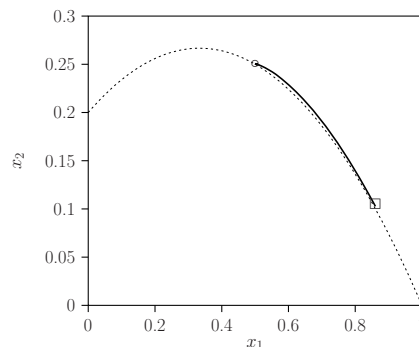


Figure 6: Results for the original system (2) (solid) describing the RM-model (29) with $b_1 = 3$ where $a_1 = 5/3 b_1$ and initial conditions $x_1 = 0.86038$ and $x_2(0) = 0.102646$.

366

367 In Fig. 7a and Fig. 7b the graph of the function $q(x_1, \varepsilon)$ is shown for $b_1 = 3$ and $b_1 = 8$,
 368 respectively. These results show that the asymptotic expansion for $\varepsilon > 0$ is only locally a
 369 good approximation for $\mathcal{M}_\varepsilon^1$ but fails at the top of the parabola point T .

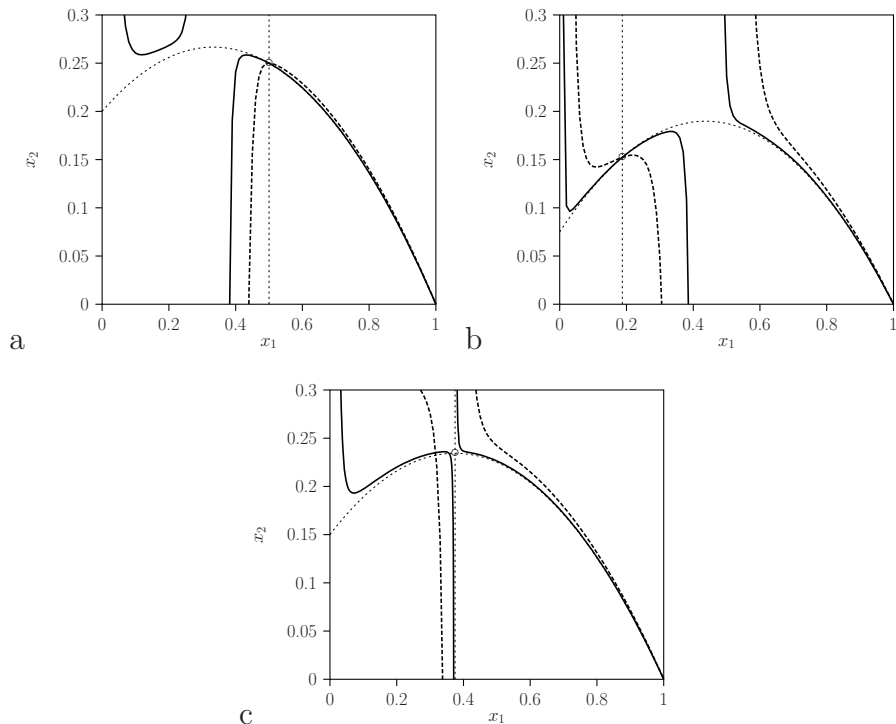


Figure 7: Second-order approximation of $\mathcal{M}_\varepsilon^1$ results with (a): $b_1 = 3$ (b): $b_1 = 8$ and (c): $b_1 = 4$ where $a_1 = 5/3 b_1$ for the RM-model (29). Solid: with $\varepsilon = 0.01$. Dotted with $\varepsilon = 0.1$.

370 **At the Hopf bifurcation** In Fig. 7c the graph of the function $q(x_1, \varepsilon)$ is shown for
 371 $b_1 = 4$. While the solution converges to the neutral stable equilibrium E_2 where the
 372 rate of convergence becomes slower when approaching the non-hyperbolic point (see also
 373 Fig. 4b,c) the asymptotic expansion approximation explodes and there is discontinuity at
 374 $x_1 = x_1^* = \bar{x}_1$:

$$\lim_{x_1 \downarrow \bar{x}_1} q(x_1, \varepsilon) = \infty \quad \text{and} \quad \lim_{x_1 \uparrow \bar{x}_1} q(x_1, \varepsilon) = -\infty. \quad (38)$$

375 In the next section we extend the asymptotic expansion in ε by varying parameter b_1
 376 in addition to ε in order to repair this unwanted property.

377 3.3 Canard explosion

378 In this section we analyse the Canard dynamics that occurs for b_1 values just above the
 379 Hopf bifurcation at $b_1 = 4$ similar to the analysis performed in [2]. Other papers on canards
 380 are [10, 6, 8, 11, 2]. We will expand the asymptotic expansion discussed in the previous
 381 section where the equilibrium point is unstable and the system itself shows oscillatory
 382 behaviour, a stable limit cycle.

383 We start with an exploration of this oscillatory behaviour for b_1 values just above the
 384 Hopf bifurcation by simulation of the full model in time for small ε values. In order to
 385 study the dynamics for small ε in more detail we re-analyse the continuation as in Fig. 1
 386 where $\varepsilon = 1$ in the region close to the Hopf bifurcation at $b_1 = 4$. The results are shown
 387 for $\varepsilon = 0.01$ in Fig. 8.

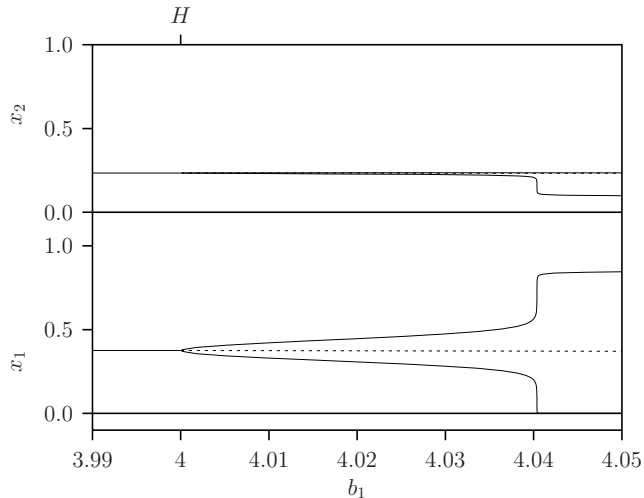


Figure 8: One-parameter bifurcation diagram for b_1 and $a_1 = 5/3 b_1$ of the RM-system (1) with $\varepsilon = 0.01$.

388 Unexpectedly the amplitude of the limit cycle increases sharply when b_1 passes a value
 389 just above $b_1 = 4.04$. In Fig. 9 parameter ε is varied continuously for a number values of
 390 b_1 just above the Hopf bifurcation point. Using (8) these results support the analytical
 391 expression for the amplitude of the unique stable limit cycles emerging from the Hopf
 392 bifurcation for small ε values being: $\sqrt{\mu(b_1)/\omega(b_1)}$.

393 The continuation of the curves calculated with AUTO [7] failed for small ε . This is due
 394 to the part of the cycle close to the vertical axis where x_1 is small, see Fig. 3bd. In order
 395 to avoid this dynamics we study now an augmented system

$$\frac{dx_1}{dt} = \delta + f(x_1, x_2, \varepsilon) = \delta + x_1 \left(1 - x_1 - \frac{a_1 x_2}{1 + b_1 x_1} \right), \quad (39a)$$

$$\frac{dx_2}{dt} = \varepsilon g(x_1, x_2, \varepsilon) = \varepsilon x_2 \left(\frac{a_1 x_1}{1 + b_1 x_1} - 1 \right), \quad (39b)$$

396 where δ is a small allochthonous input rate of the prey population. Addition of this extra
 397 term removes the transcritical bifurcation at $x_2 = 1/a_1$ because it is structurally unstable
 398 with respect to such a perturbation. Fig. 10 is a similar diagram as Fig. 9 where $\delta = 0.0001$
 399 instead of $\delta = 0$. Note that the Hopf bifurcation occurs at values slightly different from
 400 $b_1 = 4$, namely at $b_1 = 4.000711364$ and this is taken into account in what follows. The

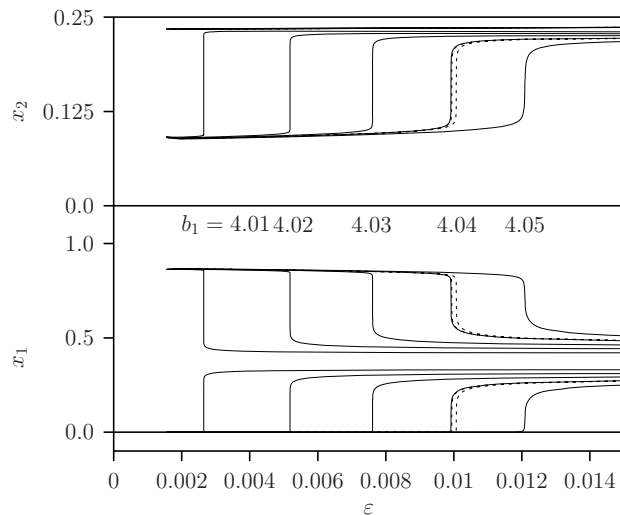


Figure 9: One-parameter bifurcation diagram for ε with various $b_1 = 4.01, 4.02, 4.03, 4.04, 4.0401, 4.0407, 4.05$ values where $a_1 = 5/3 b_1$ of the RM-system (1). For $b_1 > 4$ the minimum and maximum populations values during the stable limit cycle are shown. Also the two dashed curves are shown for $b_1 = 4.0409$ and 4.04061 . Between these two values the explosion occurs at $\varepsilon = 0.01$ see also Fig. 8. The curves terminate for low ε values. This is due to numerical problems of the parameter continuation for these low values. Theory predicts that these curves of maximums and minimums are continuing almost horizontally.

401 results in Fig. 10 imply that continuation is possible toward very low ε values. The results
 402 show that the canard is a robust and smooth phenomenon that occurs for stable limit
 403 cycles. When $\varepsilon \downarrow 0$ the canard explosion point converges to the point T .

404 In Fig. 11 the shape of the limit cycles is shown for two values of b_1 just below and above
 405 the sudden changes: $b_1 = 4.04019$ and $b_1 = 4.04061$ where $\varepsilon = 0.01$. These results show
 406 how the unique stable limit cycle changes shape very abruptly at $b_1 \approx 4.0403$ where b_1 is
 407 varied keeping ε fixed: the canard explosion. In Fig. 12 the shape of the limit cycles is shown
 408 for four values: $\varepsilon = 0.008, 0.009$, big stable limit cycles and $\varepsilon = 0.01, 0.011$, small stable
 409 limit cycles with fixed $b_1 = 4.0403$, the value calculated with the extended asymptotic
 410 expansion technique. These results show the dynamics with ε values above the canard
 411 explosion at approximately $\varepsilon = 0.01$, are limit cycles with small amplitudes consisting of
 412 two concatenated slow (close to the critical manifold and just above the parabola) and fast
 413 (almost horizontal part of the trajectory below the parabola). Below the canard explosion
 414 the limit cycles with large amplitudes consist of four episodes, two slow (close to the
 415 critical manifold, one just above the parabola and one close to the vertical axis) and two
 416 fast (almost horizontal, one leaving close from point T and one leaving the vertical axis
 417 and landing close to the parabola).

418 Carefully examination indicates that there is one point where the trajectories for the
 419 four ε values intersect. Starting at that point and changing ε gives the unique stable limit

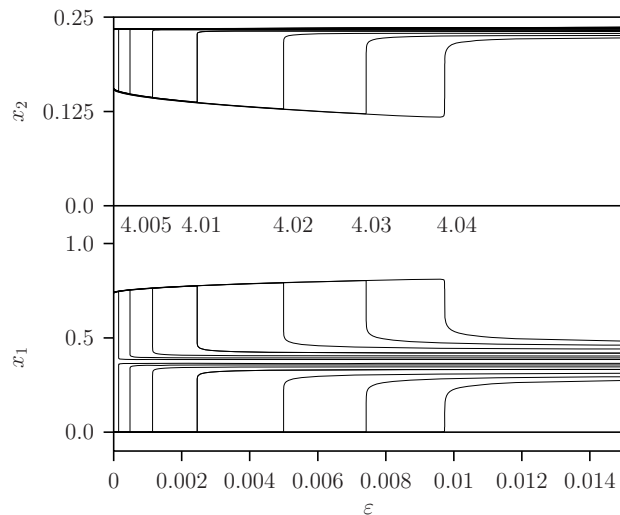


Figure 10: One-parameter bifurcation diagram for ε with various $b_1 = 4.00125, 4.0025, 4.005, 4.01, 4.02, 4.03, 4.04$ values where $a_1 = 5/3 b_1$ of system (39) with prey input rate $\delta = 0.0001$. The parameter continuation is here successful to very small values of ε .

420 cycles calculated and this shows that these curves change smoothly, only the sensitivity of
 421 the shape of the cycles is very large at the explosion point.

422 3.3.1 Asymptotic expansion and canard explosion

423 Following [13] we repeat the extended asymptotic expansion in ε technique introduced in
 424 (29) now near the Hopf bifurcation point. To that end the expansion is not only taken
 425 for the function $x_2 = q(x_1, \varepsilon)$ evaluated at $q_0(x_1)$ (see (32)) but also in the bifurcation
 426 parameter $b_1 = b_1(\varepsilon)$ and consequently $a_1(\varepsilon) = 5/3 b_1(\varepsilon)$ evaluated at the Hopf bifurcation
 427 point $b_{10} = 4$ with $a_{01} = 20/3$. This comes with more freedom which leads to an extra
 428 criterion: the singularity of the approximation at point T is removed. This function is now
 429 denoted as $r(x_1, \varepsilon)$ and the expansion is evaluated at $r(x_1 = \bar{x}_1, \varepsilon = 0)$. When $b_1 = b_{10}$ we
 430 have $r(\bar{x}_1, \varepsilon) = q(\bar{x}_1, \varepsilon)$.

431 Similar to the invariance condition of the perturbed slow manifold $\mathcal{M}_\varepsilon^1$ we derive now
 432 the adapted equation that replaces (28) where we substitute $a_1(\varepsilon) = 5/3 b_1(\varepsilon)$:

$$\frac{\partial r}{\partial x_1} x_1 \left((1 - x_1)(1 + b_1(\varepsilon)x_1) - 5/3 b_1(\varepsilon)r(x_1, \varepsilon) \right) = \varepsilon r(x_1, \varepsilon) (2/3 x_1 b_1(\varepsilon) - 1). \quad (40)$$

433 The following extended asymptotic expansion in ε for $r(x_1, \varepsilon)$ is introduced as follows:

$$x_2 = r(x_1, \varepsilon) = r_0(x_1) + \varepsilon r_1(x_1) + \varepsilon^2 r_2(x_1) + \dots, \quad (41)$$

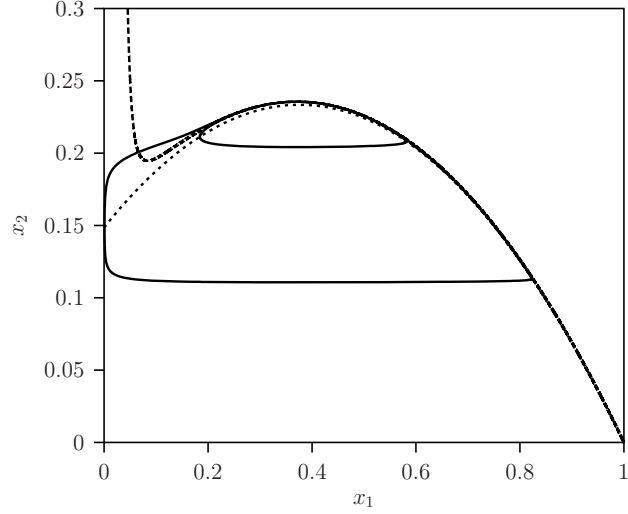


Figure 11: Phase-space diagram with $\varepsilon = 0.01$. Solid lines: stable limit cycle for two values of $b_1 = 4.04019$ (small cycle) and $b_1 = 4.04061$ (big cycle) while $a_1 = 5/3 b_1$ of the RM-system (1). Dashed line: extended asymptotic expansion $r(x_1, \varepsilon)$ of $\mathcal{M}_\varepsilon^1$ (41) where $b_1 = 4.0403$.

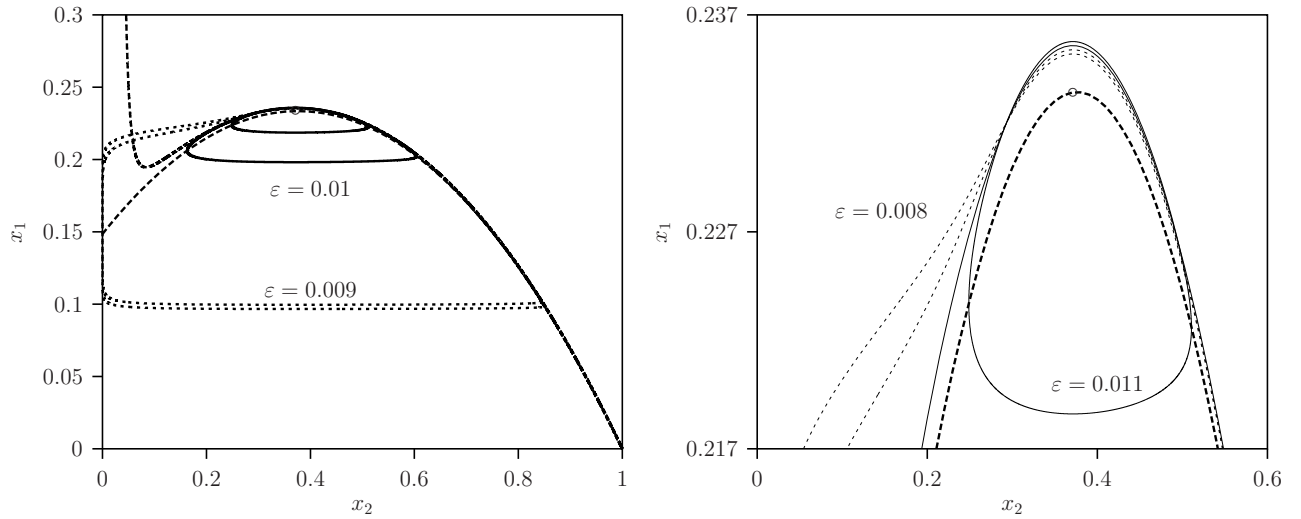


Figure 12: Phase-space diagram with $\varepsilon = 0.008, 0.009, 0.01, 0.011$. Solid lines: stable limit cycle for two values $\varepsilon = 0.008, 0.009$ (big cycle) and two values $\varepsilon = 0.01, 0.011$ (small cycle) of the RM-system (1). Dashed line: extended asymptotic expansion $r(x_1, \varepsilon)$ of $\mathcal{M}_\varepsilon^1$ (41) where $b_1 = 4.0403$.

434 and

$$\frac{\partial r}{\partial x_1} = \frac{dr_0}{dx_1} + \varepsilon \frac{dr_1}{dx_1} + \varepsilon^2 \frac{dr_2}{dx_1} + \dots, \quad (42)$$

435 whereby $b_1(\varepsilon)$ is given by

$$b_1(\varepsilon) = b_{10} + \varepsilon b_{11} + \varepsilon^2 b_{12} + \varepsilon^3 b_{13} + \varepsilon^4 b_{14} \dots, \quad (43)$$

436 where r_j and b_{1j} , $j = 1 \dots$ are independent of ε and are described by the invariance
437 condition (40) by equality order by order of powers of ε of this condition. Equating $\mathcal{O}(1)$
438 terms yields:

$$r_0 = \frac{(1 - x_1)(1 + b_{10}x_1)}{5/3 b_{10}}. \quad (44)$$

439 With $b_{10} = 4$ this gives the zero order approximation of $\mathcal{M}_\varepsilon^1$ equal to \mathcal{M}_0^1 . Using (44)
440 and substitution of (41), (42) and (43) in (40) and equating the resulting first order $\mathcal{O}(\varepsilon)$
441 terms, yields:

$$r_1(x_1) = \frac{3(1 - x_1)(1 - b_{10} + 2x_1 b_{10})b_{11}x_1 b_{10} - x_1 b_{10}^2 - 3b_{10} + 2x_1^2 b_{10}^3}{5b_{10}^2(1 + 2x_1 b_{10} - b_{10})x_1}. \quad (45)$$

442 It appears that the terms with b_{11} , namely $3x_1 b_{11}(b_{10} - 1 - 2x_1 b_{10}) = 0$, are already
443 eliminated when they are evaluated at the Hopf bifurcation support point with $b_{10} = 4$ and
444 $a_{10} = 20/3$ at the equilibrium E_2 with $x_1 = \bar{x}_1 = x_1^* = 1/(a_{10} - b_{10})$. At that point both
445 the numerator and the denominator are zero but $\lim_{x_1 \downarrow \bar{x}_1} r_1(x_1) = \lim_{x_1 \uparrow \bar{x}_1} r_1(x_1)$ and this
446 shows that function $r_1(x_1)$ is continuous for all b_{11} .

447 From this point a recursive procedure can be followed. One by one, r_i , $i \geq 2$ is
448 determined by taking the i^{th} order term in the invariance condition (40) equal to zero and
449 thereafter the term $b_{1(i-1)}^{\text{th}}$ by the condition that this term is continuous at $x_1 = \bar{x}_1 =$
450 $(b_{10} - 1)/(2b_{10})$. This means that the free parameter is chosen such that the singularity is
451 removed. The requirement that the sum of second order terms is zero gives

$$r_2 = (1 - x_1) \frac{(-288x_1^4 + 108x_1^3)b_{12} + (72x_1^4 - 27x_1^3)b_{11}^2 + (96x_1^3 + 84x_1^2)b_{11} + 256x_1^3 - 128x_1^2 - 112x_1 - 16}{960x_1^3(8x_1 - 3)}. \quad (46)$$

452 At the support point T being the Hopf bifurcation point with $b_{10} = 4$ and $x_1 = \bar{x}_1$ given by
453 (14) we have $(-288x_1^4 + 108x_1^3)b_{12} = 0$. Furthermore the denominator is zero $b_{10} = 4$. The

454 expression for b_{11} is then obtained by setting also the numerator equal to zero in order to
 455 remove the singularity at that support point.

456 This is related to the case analysed in the previous section for the asymptotic expansion
 457 $x_2 = q(x_1, \varepsilon)$ at $q(\bar{x}_1, \varepsilon)$ for coefficient q_1 given in (34) where this expression was also
 458 unbounded. Now, because we have more freedom we can take b_{11} so that the expression
 459 stays bounded at this point. The expression $b_{11} = 100/27$ is obtained by substitution of
 460 the equilibrium value for $x_1 = \bar{x}_1 = 3/8$ given by (14) into (45).

461 Further recursion gives higher order approximations, again first r_n with b_{n-1} then r_{n+1}
 462 with b_n and so on. We calculated the following fourth order approximation

$$\begin{aligned}
 b_1(\varepsilon) &= b_{10} + \varepsilon b_{11} + \varepsilon^2 b_{12} + \dots, \\
 b_1(\varepsilon) &= 4 + \varepsilon \frac{100}{27} + \varepsilon^2 \frac{58700}{2187} + \varepsilon^3 \frac{80536900}{177147} + \varepsilon^4 \frac{171270040300}{14348907}.
 \end{aligned}
 \tag{47}$$

463 In Fig. 11 besides the shape of the limit cycles for two values $b_1 = 4.04019$ (small
 464 limit cycle) and $b_1 = 4.04061$ (big limit cycle) also the result of the extended asymptotic
 465 expansion $r(x_1, \varepsilon)$, where $\varepsilon = 0.01$, (41) with $b_1 = 4.0403$ is shown. The approximation
 466 for $\mathcal{M}_\varepsilon^1$ follows the limit cycle closely up-to a separation point where the small limit cycle
 467 bends toward the nullcline which is crossed where the rate of x_1 changes sign and the rate
 468 becomes fast. This occurs for the smallest $b_1 = 4.04019$ -value. For the big limit cycle at
 469 $b_1 = 4.04061$, from the separation point the trajectory along the cycle continuous to move
 470 toward the vertical axis. The asymptotic expansion for $\mathcal{M}_\varepsilon^1$ with $b_1 \approx 4.0403$ continuous
 471 after the separation point between the two limit cycles before the approximation becomes
 472 unbounded.

473 These results show how the unique stable limit cycle changes its shape very abruptly
 474 when $b_1 \approx 4.0403$ is varied keeping ε fixed, here in our example 0.01: the canard explo-
 475 sion. That the iteration process converges to this bifurcation parameter value where the
 476 approximation of the asymptotic expansion $r(x_1, \varepsilon)$ works for the limit cycle with the small
 477 amplitude that intersect with the parabolic f-nullcline vertically at the minimum predator
 478 size during the limit cycle. This makes in plausible that the iteration procedure yields
 479 indeed the canard point.

480 However, the extended asymptotic expansion $r(x_1, \varepsilon)$ (41) is divergent as shown in
 481 Fig. 13 where the coefficients b_{1i} as function of i is depicted.

482 It was shown in [39, 38] and reference therein, that the summation up to the smallest
 483 term gives an optimal (and very accurate) approximation in the case of the van der Pol
 484 system. In Fig. 14, again with allochthonous prey input where $\delta = 0.0001$, the parameter
 485 value where the explosion occurs is plotted. This b_1 parameter value is taken from Fig. 10.
 486 Fortunately, the result presented are in agreement.

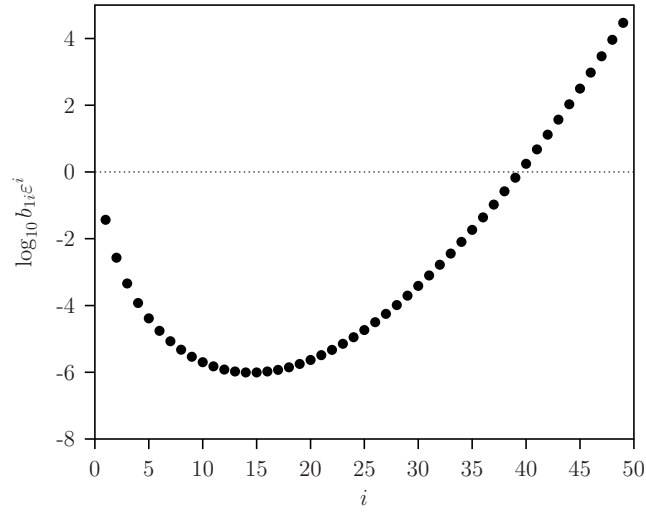


Figure 13: Coefficients b_{1i} as function of i given by (47) with $\varepsilon = 0.01$.

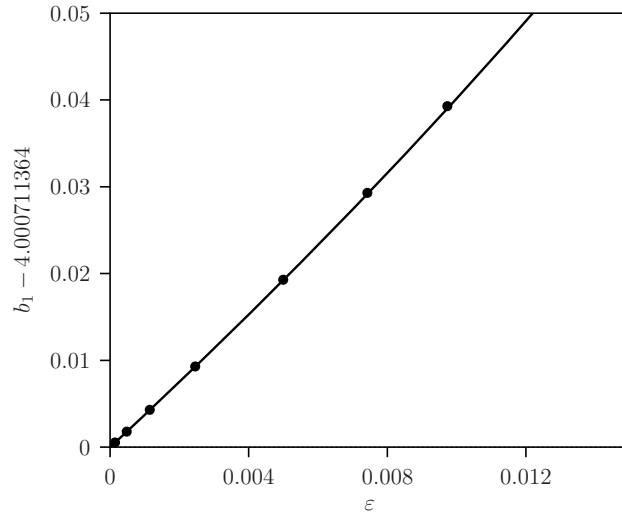


Figure 14: Distance from parameter value b_1 where canard explosion occurs from $b_1 = 4.000711364$ where the Hopf bifurcation occurs with allochthonous prey input $\delta = 0.0001$ as function of ε . Solid line is graph of the truncated expression (43) and the dots taken from Fig. 10.

4 The MB bitrophic food chain model

This section presents the Monod chemostat model [34, 45, 24, 26]. In this model the nutrients consumed by the prey are modelled explicitly instead of using a logistic growth model for the growth of the prey in absence of the predator. Let $x_0(t)$ denote the density of the nutrient, and $x_i(t) \in \mathbb{R}_+$, $t \geq 0$, $i = 1, 2$ the biomass densities of prey and predator, respectively. The scaled version of the Monod model reads

$$\frac{dx_0}{dt} = (x_r - x_0)D_1 - a_0x_0x_1, \quad (48a)$$

$$\frac{dx_1}{dt} = a_0x_0x_1 - D_1x_1 - \frac{a_1x_1x_2}{1 + b_1x_1}, \quad (48b)$$

$$\frac{dx_2}{dt} = e_1 \frac{a_1x_1x_2}{1 + b_1x_1} - D_1x_2. \quad (48c)$$

where x_r is the concentration of nutrient in the reservoir and D_1 the dilution rate, the rate at which the nutrient enters and all trophic levels are exported from the chemostat reactor. The second term of (48a) and the first term of (48b) model the Lotka-Volterra functional response at the prey-nutrient level. The first term of (48c) and the last term on the right-hand sides of (48b) represent the Holling type II functional response. The efficiency e_1 is the ratio of these two terms. For simplicity we assume $e_1 = 1$ and $a_0 = 1$.

It can be shown that all solutions system (48) starting in the non-negative cone eventually lie in the set

$$\Omega = \{x = (x_0, x_1, x_2) \in \mathbb{R}_+^3 : x_0 + x_1 + x_2 \leq x_r\}. \quad (49)$$

So, the asymptotic behavior of system (48) is bounded by x_r . It is possible to decouple this system by the introduction of the function

$$H(t) = x_0(t) + x_1(t) + x_2(t) - x_r, \quad t \geq 0. \quad (50)$$

This gives

$$\frac{dH}{dt} = -D_1H, \quad (51a)$$

$$\frac{dx_1}{dt} = (H + x_r - x_1 - x_2)x_1 - D_1x_1 + D_1\left(\frac{a_1x_1x_2}{1 + b_1x_1}\right), \quad (51b)$$

$$\frac{dx_2}{dt} = D_1x_2\left(\frac{a_1x_1}{1 + b_1x_1} - 1\right). \quad (51c)$$

When furthermore $H = 0$ for the asymptotic dynamics we can study the two dimensional predator-prey system

$$\frac{dx_1}{dt} = x_1 \left(x_r - x_1 - x_2 - D_1 - D_1 \frac{a_1 x_2}{1 + b_1 x_1} \right), \quad (52)$$

$$\frac{dx_2}{dt} = D_1 x_2 \left(\frac{a_1 x_1}{1 + b_1 x_1} - 1 \right). \quad (53)$$

506 In order to be able to make a clear comparison with the RM-model formulations possible
 507 we use $x_r = 1 + D_1$. This gives with $D_1 = \varepsilon$

$$\frac{dx_1}{dt} = x_1 \left(1 - x_1 - x_2 - \varepsilon \frac{a_1 x_2}{1 + b_1 x_1} \right), \quad (54a)$$

$$\frac{dx_2}{dt} = \varepsilon x_2 \left(\frac{a_1 x_1}{1 + b_1 x_1} - 1 \right). \quad (54b)$$

508 We call this the MB-model. One main difference with the RM-model is that the last term
 509 of (54a) is proportional to ε and consequently the efficiency, is constant. Another difference
 510 with the RM-model is that the logistic prey growth equation $x_1(1 - x_1)$ is replaced by the
 511 expression $x_1(1 - x_1 - x_2)$ with one extra term namely that of the predator biomass, x_2 .
 512 In absence of the predator, $x_2 = 0$, both expressions for the prey growth are the same.
 513 For the three trophic system including the nutrients, which is used with the derivation of
 514 the MB-model, the biomass allocated in the predator gives a feed-back mechanism so that
 515 there is less nutrient available for the prey. In the food chain the predator has two adverse
 516 effects on the growth of prey population. Firstly the prey is consumed by the predator and
 517 they consume building-block material not only for themselves but also for their predators
 518 population that can only exists when the prey exists in the absence of inter-guild predation.

519 The biological interpretation of the $-D_1 H = -\varepsilon H$ term in (51a) is the difference
 520 between the influx rate and the out-flux rate of the total biomass expressed in the biomass
 521 of the predator. In [45] (50) is used to show that Monod's model is dissipative and that the
 522 system converges asymptotically to the manifold $H = 0$ where the influx rate and out-flux
 523 rate of the total biomass are the same. Observe that where $H = 0$ there is with respect to
 524 the RM-model a new x_2 term in the expression for the prey growth rate.

525 4.1 Existence and stability analysis of equilibria and limit cycles

526 For the analysis of model in the chemostat environment we refer to [45]. The three relevant
 527 equilibria are summarized in Table 2. In Table 3 the bifurcation analysis results are given.
 528 Important difference of these results with those for the RM-model is that while the expres-
 529 sions for the TC bifurcation are the same those for the Hopf H bifurcation still depends
 530 on ε .

531 Firstly we calculate by continuation of the parameter b_1 the bifurcation diagram shown
 532 in Fig. 15. This diagram looks very much the same as Fig. 1 for the RM model. The main
 533 difference is that the Hopf bifurcation occurs at a somewhat higher b_1 value.

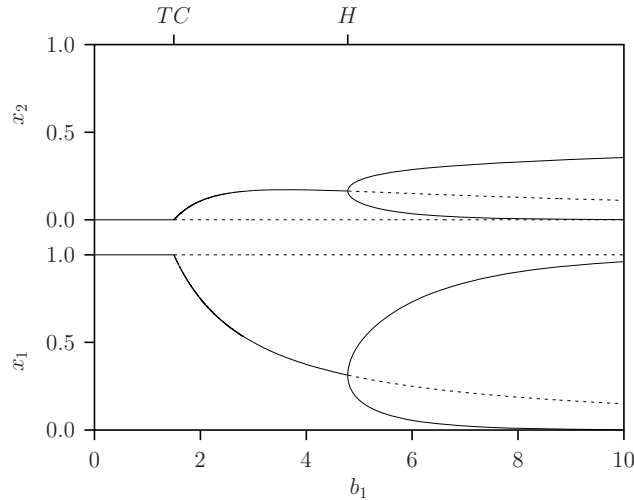


Figure 15: One-parameter bifurcation diagram for b_1 and $a_1 = 5/3 b_1$ of the MB-system (54) with $\varepsilon = 1$.

534 4.2 Phase-space analysis

535 Figure 16 displays the simulation results for the MB-model for three values of ε where
 536 $b_1 = 3$. There is convergence to a stable equilibrium, similar as we found for the RM-
 537 model in Fig. 3a,c.

538 For $b_1 = 8$ the results are shown in Fig. 17. These results differ much from the RM-
 539 model in Fig. 3b,d case where the equilibrium E_2 was unstable. Here this holds true for
 540 $\varepsilon = 1$ (Fig. 17a) but for smaller values the equilibrium becomes stable (Fig. 17b,c).

541 4.3 The degenerate phase point

542 With $\varepsilon = 0$ substituted in the MB-model (54) there is no input of nutrients (54a) and also
 543 no export of the abiotic and biotic elements from the reactor environment. The prey grows
 544 logistically to the equilibrium $x_0(0) + x_1(0)$ and the predator population remains constant
 545 $x_2(0)$. Hence, the equilibrium E_2 is neutral stable. The degenerate phase curve is just this
 546 point which is an equilibrium point x_1 together with the initial predator size $x_2(0)$.

547 This degenerate phase curve differs completely from that of the RM-model. This is a
 548 consequence of the fact that in the MB-model the second term of (54a) is proportional to
 549 ε and therefore the ratio of this and the first term of (54b), the efficiency, is constant.

550 4.4 Bifurcation analysis of MB-model

551 In order to find-out why this happens we calculated a two-parameter bifurcation diagram
 552 shown in Fig. 18 where besides b_1 (whereby $a_1 = 5/3 b_1$), parameter ε is the second variable.

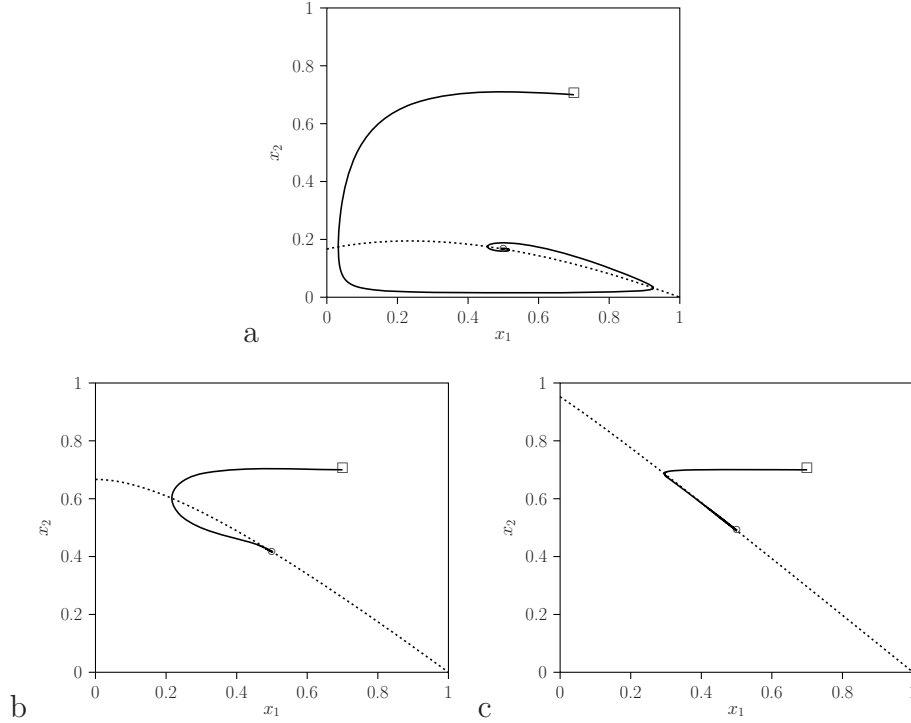


Figure 16: Phase-space analysis for system (54) describing the MB-model with $a_1 = 5/3 b_1$, $b_1 = 3$, for three different values of ε : $\varepsilon = 1$, $\varepsilon = 0.1$ and $\varepsilon = 0.01$.

553 In this diagram the transcritical bifurcation TC , and the Hopf bifurcation H , curves are
 554 drawn (see Table 3 for the expressions that describe the curves).

555 The transcritical bifurcation TC , is the same for all models. This is obviously due to
 556 the fact that the model for the dynamics of the predator is the same for all models and
 557 furthermore that for the prey-only ($x_2 = 0$) equilibrium E_1 is also the same. For the MB-
 558 model the Hopf bifurcation H terminates at the origin where $b_1 \rightarrow \infty$ and $\varepsilon \rightarrow 0$. There
 559 is a stable equilibrium E_2 in almost the whole $b_1 > 4$ range up to $\lim b_1 \uparrow \infty$ while in the
 560 RM-model there is a stable limit cycle L_2 .

561 From this we conclude that in the case of the MB-model the parameter ε can not to
 562 be used as a single perturbation parameter. We conclude that the complete model has
 563 to be analysed using a straight-forward phase-space and bifurcation analysis of the local
 564 bifurcations H and TC .

565 5 Discussion and conclusions

566 The use of time-scale separation technique has a long tradition in ecology and biochemistry,
 567 starting with the quasi-steady-state approximation (QSSA) used to derive the Holling types
 568 functional response [17] and Michaelis-Menten kinetics.

569 In this paper we compared two fast-slow versions of predator-prey models: the RM-

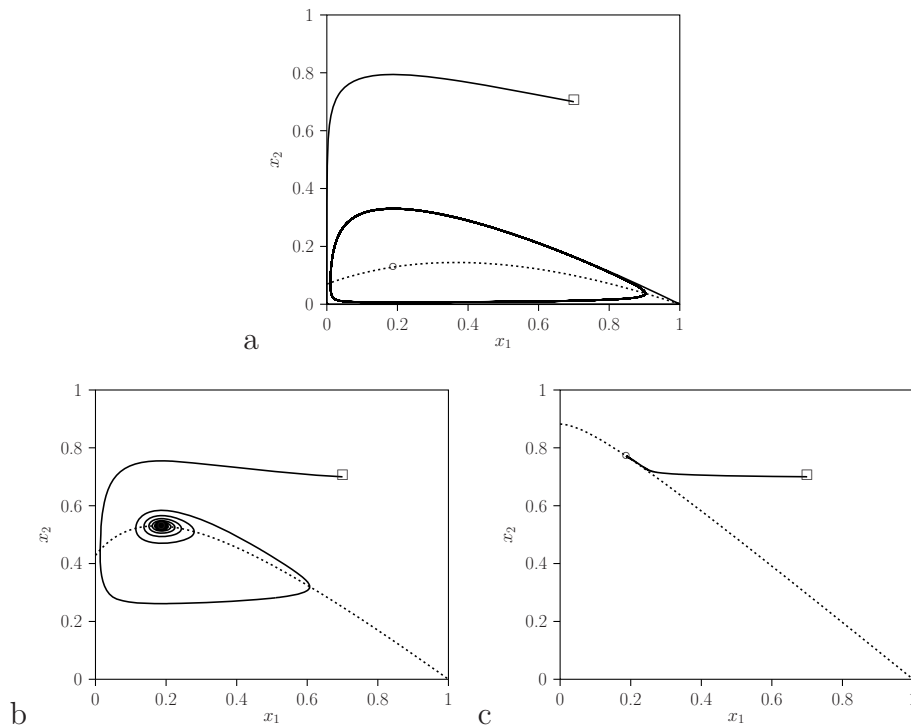


Figure 17: Phase-space analysis for system (54) describing the MB-model with $a_1 = 5/3 b_1$, and $b_1 = 8$, that is at the Hopf bifurcation point for three different values of ε : $\varepsilon = 1$, $\varepsilon = 0.1$ and $\varepsilon = 0.01$.

570 model and MB-model. In the classical RM-model the small perturbation parameter is
 571 proportional to the efficiency of the predator-prey trophic interaction and the predator
 572 death rate. In a series of papers [35, 42, 41] the dynamics of this bitrophic systems has
 573 been studied intensively.

574 In [11] this subject was also studied focusing on the dynamics close to the critical
 575 manifold \mathcal{M}_0^0 (Fig. 5) (part of the vertical axis where the prey is absent) and related to
 576 a delayed (transcritical) bifurcation phenomenon. Recently in [16] the analysis technique
 577 based on the geometric singular perturbation theory was applied. This theory can also be
 578 used where the interior equilibrium is unstable and relaxation dynamics occurs.

579 We used the invariant manifold criterion together with an extended asymptotic expansion
 580 with respect to both, the perturbation parameter and the free bifurcation parameter.
 581 This gives an iteration process that approximates the $\mathcal{M}_\varepsilon^1$ slow manifold close to the
 582 parabolic critical manifold \mathcal{M}_0^1 in the neighbourhood of its top. In the parameter range
 583 just above the Hopf bifurcation where stable limit cycles exist, this process converges to
 584 the point where the canard explosion occurs. In [2] a similar method has been used: here
 585 the advantage is that all calculations are done in Maple, [32] with rational numbers.

586 Direct application, however, showed that the delayed transcritical bifurcation dynamics
 587 close to the critical manifold \mathcal{M}_0^0 leads to an disturbing effect because the prey population

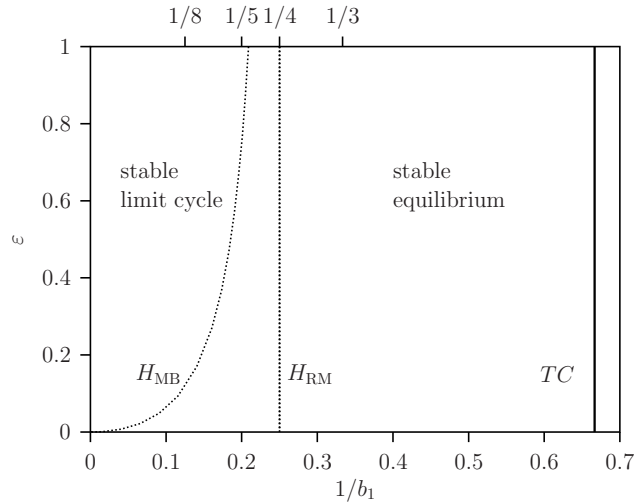


Figure 18: Two-parameter bifurcation diagram with ε and $1/b_1$ as free parameters. The expressions are given in Table 3. The transcritical bifurcation curve TC is for both models RM-model and MB-model the same. For $\varepsilon = 1$ the point of the Hopf bifurcations differ slightly but for $\lim \varepsilon \downarrow 1$ they differ essentially. In the MB-model there is a stable equilibrium E_2 in almost the whole $b_1 > 4$ range up to $\lim b_1 \uparrow \infty$ while there is a stable limit cycle L_2 in the RM-model.

588 becomes very low. Therefore we introduced a small allochthonous input of prey in which
 589 case the non-generic transcritical bifurcation disappears. In [46] the uniqueness of the limit
 590 cycles in the RM-model with prey immigration is shown that supports the applicability of
 591 this additionally introduced mechanism.

592 The canard phenomenon found can be described as follows. Also for small perturba-
 593 tion parameter values the trajectories follow the stable limit cycles like in the case where
 594 no time scale differences occur $\varepsilon = 1$. However, just above the Hopf bifurcation point
 595 depending also on the perturbation parameter the stable limit cycle with small amplitude
 596 consists of two concatenated slow and fast episodes. In the phase space, the top part is
 597 just above the parabolic stable and unstable critical manifold and the bottom just below
 598 the horizontal line connecting the two points where the limit cycle intersects with the f-
 599 nullcline vertically. At the canard point of the bifurcation parameter, the dynamics tends
 600 abruptly toward the relaxation dynamics. This transition point resembles what happens
 601 due to the delayed bifurcation effect where the trajectory leaves the vertical axis below the
 602 transcritical bifurcation TC in Fig. 5. For higher bifurcation parameters values the limit
 603 cycle with large amplitude changes smoothly and approaches the degenerated phase curves
 604 consisting of a concatenation of two slow and two fast episodes (Fig. 5).

605 Despite the approximate series expansion diverges, we found accurate approximations
 606 for small ε of the part the limit cycles originating from the Hopf bifurcation point. Further-
 607 more, the numerical approximate asymptotic iterative scheme, gives very good approxima-
 608 tions of the bifurcation parameter b_1 and perturbation parameter ε values where a canard
 609 explosion occurs (see Fig. 11).

610 An other mathematical method to analyse a canard explosion is the blow-up technique
611 [8, 9, 29, 30]. This technique can be used to study the unfolding of the degenerated Hopf
612 bifurcation where $\lim \varepsilon \rightarrow 0$. This will be the subject of a forthcoming paper.

613 In [35, 42, 41, 20, 16, 11] the RM-model predator-prey slow-fast model showed complex
614 relaxation oscillation dynamics, however, no canard explosion was observed.

615 In [26, 1, 23] food chain systems were already studied where the small parameter, mea-
616 suring the timescale disparity between the rate of changes in the prey (fast) and predator
617 (slow), in the MB-model was introduced. Then the fast subsystem converges to a criti-
618 cal manifold of stable equilibria which yields an algebraic relationship between the state
619 variable leading to a reduced (aggregated) lower dimensional (DAE) system. Predator prey
620 systems with fast oscillating migrations were studied in [36] and with slow migrations in
621 [33] wherein reduction methods were proposed. In those papers, relaxation oscillations
622 were not discussed.

623 In the MB-model, conservation of mass is obeyed and therefore it is more realistic than
624 the RM-model where nutrients are not modelled explicitly. An open chemostat environment
625 is assumed with inflowing nutrients and the outflow of all abiotic and biotic components.
626 Under specific situations the logistic growth rate of the prey is replaced by a prey growth
627 model whereby nutrients are not only used for its own growth but also for its predator.
628 This is a bottom-up effect in addition to the top-down effect of the prey consumption by
629 the predator. The consumption occurs with a constant efficiency like in the alternative
630 fast-slow version of the RM-model introduced in [16, Example 2.2]. The introduction of
631 this constant efficiency in the fast-slow RM-model, however, leads to unrealistic equilibrium
632 population sizes when ε becomes small. In the MB-model (54) these sizes remain realistic.
633 A constant efficiency, instead of the less realistic variable efficiency, was earlier used in [26]
634 in the fast-slow version of the RM-model and described by (2) [16, Example 2.1].

635 The dynamics of the MB-model was analysed using a classical phase-space and bifurca-
636 tion analysis approach where only equilibria and limit cycles occur in the whole parameter
637 space. Calculations showed that in this more realistically and mechanistically underpinned
638 model the complex fast-slow canard explosion does not occur.

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744 A Derivation of the dimensionless RM-model

From [48] we recall (after some adjustments of the notation), that the classical RM-model is given as

$$\frac{dX_1}{dT} = RX_1(1 - X_1/K) - AF(X_1)X_2, \quad (55a)$$

$$\frac{dX_2}{dT} = (CAF(X_1) - M)X_2, \quad (55b)$$

745 where $F(X_1) = X_1(1 + AkX_1)^{-1}$ is the well-known Holling type II functional response,
746 with X_j the state variables, k handling time, A the attack rate, C a conversion efficiency,
747 M the predator removal rate (mortality, maintenance, and harvesting), and T is time. A
748 list of symbols is given in Table 4.

749 This model can be rescaled by using $t = TR$, $x_1 = X_1/K$, and $x_2 = X_2/K$. Note that
750 in the last transformation for the predator biomass differs from [48] to let the efficiency C
751 not disappear in the dimensionless formulation and to be able to deal with the time-scale
752 difference in the fast-slow system the subject here.

Table 4: List of symbols used for RM-model with dimension with their meaning. the biomass of both populations have the same dimension.

Symbol	Meaning
T	Dimensional time
t	Dimensionless time
X_j	Dimensional state variable, indicated by j
x_j	Dimensionless state variable, indicated by j
R	Intra-specific growth rate
A	Attack rate
$F(X_1)$	Functional response, non-dimensional
C	Efficiency, conversion yield, non-dimensional
M	Mortality rate per unit of time
k	Handling time

753 The non-dimensional model then reads

$$\frac{dx_1}{dt} = x_1(1 - x_1) - \frac{a_1 x_1}{1 + b_1 x_1} x_2, \quad (56a)$$

$$\frac{dx_2}{dt} = x_2 \left(\frac{c_1 a_1 x_1}{1 + b_1 x_1} - d_1 \right), \quad (56b)$$

754 where $a_1 = AK/R$, $b_1 = kAK$, $c_1 = C$ and $d_1 = M/R$.

755 **B The slow dynamics on the parabola part of the f -** 756 **nullcline**

757 We give the results for the slow dynamics in the degenerated case $\varepsilon = 0$ where the dynamics
758 is on a part of the f -nullclines critical manifolds.

759 The slow dynamics on the vertical axis is described again by the system (12). We will
760 now focus on the slow dynamics on the parabola shown in Fig. 19 where the dynamics
761 of the reduced system (21) is solved numerically, yielding the prey population size $x_1(\tau)$
762 while (20) is used to get the associated predator population size $x_2(\tau)$. Figure 19a gives
763 the results for the stable equilibrium E_2 , $b_1 = 3$ where $a_1 = 5/3$ $b_1 = 5$ case with initial
764 condition $x_2(0) = 0.225$. This value is below point T , where $x_2 = 0.25$. In this case there
765 are two valid initial points given by (19). Starting at the largest x_1 prey value on the
766 right-hand parabolic branch there is convergence toward the equilibrium E_2 . But at the
767 lowest prey value on the left-hand branch there is convergence to the trivial zero-solution
768 where $x_1 = 0$ and $x_2 = 0$.

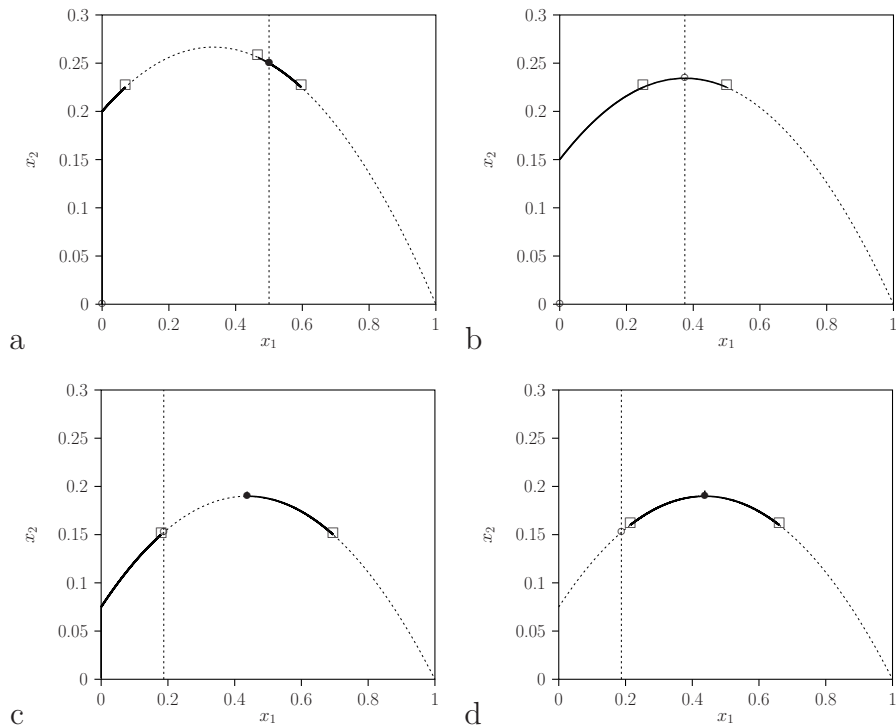


Figure 19: Phase-space analysis for slow system (19) of the RM-model. (a): At the top-panel left $b_1 = 3$ and $a_1 = 5/3 b_1$, with initial values $x_2 = 0.225$ and $x_2 = 0.256$. The equilibrium E_2 is stable and the right-branch of the parabola is the basin of attraction. On the other hand the left-branch of the parabola is in the attraction basin of the zero solution. (b): At the top-panel right $b_1 = 4$ and $a_1 = 5/3 b_1$, with initial values $x_2 = 0.225$. The equilibrium E_2 is unstable. (c) and (d): The lower panel with $b_1 = 8$ and $a_1 = 5/3 b_1$ the two initial values $x_2 = 0.15$ and $x_2 = 0.16$. The associated initial value of the $x_1(0)$ is for $x_2 = 0.15$ below the unstable equilibrium E_2 value. For $x_2 = 0.16$ the associated initial value of the $x_1(0)$ is above the unstable equilibrium E_2 value.

769 Hence, the right-hand branch of the parabola is in the basin of attraction of the stable
770 equilibrium of the reduced system equal to that of the original system E_2 . On the other
771 hand for the left-hand branch it is in the basin of attraction of the zero solution.

772 Figure 19c,d were calculated with parameter values $b_1 = 8$ and $a_1 = 5/3 b_1 = 40/3$ where
773 the equilibrium E_2 of the original system is unstable. In Fig. 19c starting at the lowest
774 prey value and $x_2(0) = 0.15$, the results are similar to that in the above discussed case.
775 However, starting with the largest prey value on the critical manifold there is convergence
776 to the limit point T for the reduced system, and not to the unstable equilibrium E_2 of the
777 full model. Note that the vector field is not defined at the top T . In Fig. 19d the initial
778 value is $x_2(0) = 0.16$ where both simulations terminate at a limit point T of the reduced
779 system. Hence, the unstable equilibrium E_2 of the full system is a separatrix between the
780 two equilibrium points of the reduced system, being limit point T in (13) and the zero
781 point $E_0(x_1, x_2) = (0, 0)$.

782 For the special case $b_1 = 4$ at the Hopf bifurcation the results are shown in Fig. 19b.
 783 The equilibrium E_2 of the full system (2) at point T in (14) is now for the reduced system
 784 restricted to the critical manifold not an equilibrium of the reduced system and there is no
 785 convergence to that point. Starting for $x_2(0) = 0.225$ there is always convergence to the
 786 trivial zero solution E_0 which is here a global stable equilibrium of the reduced system.

787 In order to study the dynamics at the critical manifold (the parabola) further we plot
 dx_1/dt versus $x_1(t)$ in Fig 20 in addition to $x_2(t)$ versus $x_1(t)$ in the phase space. For the

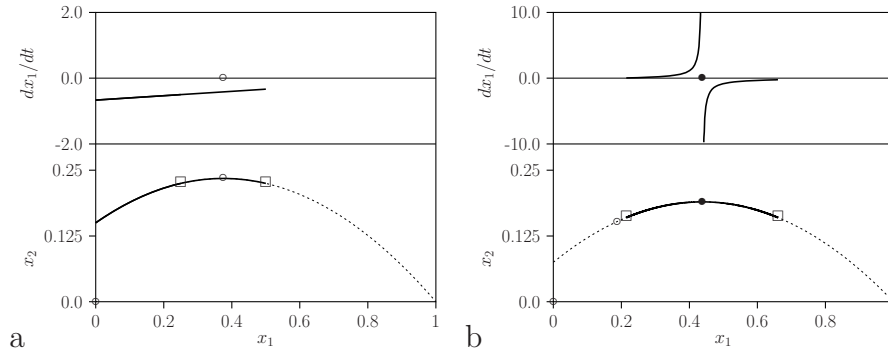


Figure 20: Phase-space analysis for slow system (19) of the RM-model. In the top-subpanels the rate dx_1/dt versus $x_1(t)$ while in the bottom-subpanel the dynamics $x_2(t)$ versus $x_1(t)$ on the critical manifold (see also Fig 19). (a): The left-panel $b_1 = 4$ and $a_1 = 5/3 b_1$, with initial value $x_2 = 0.225$ where the equilibrium E_2 is stable. (b): The right-panel with $b_1 = 8$ and $a_1 = 5/3 b_1$ the initial value is $x_2 = 0.16$ whereby the associated initial value of the $x_1(0)$ is above the unstable equilibrium value.

788 Hopf bifurcation value $b_1 = 4$ the rate dx_1/dt given in (21) is always negative and hence
 789 there is convergence always to the global stable zero solution. Note that the numerator in
 790 (21) is zero and this does not hold when $b_1 \neq 4$. However, for $b_1 = 8$ where the equilibrium
 791 is unstable the situation differs. Now when starting on the left side of point T the rate
 792 dx_1/dt is positive and there is convergence toward the limit point T given in (13). Similarly
 793 starting on the right-side the rate dx_1/dt is negative and there is also convergence toward
 794 T . Now, the plot shows a vertical asymptote. Thus the rate is discontinuous at point T
 795 and this is due to the fact that dq/dx_1 (20) is zero at T . Calculations showed that the
 796 equilibrium point of the reduced system is reached in finite time. This is proved in the
 797 Appendix B.

799 In summary, the computational results show that point T is in the case of the reduced
 800 system not a simple tangent bifurcation. When the parameter equals the Hopf bifurcation
 801 value it is not even an equilibrium. Otherwise it is a limit point reached in finite time.

802 To support this the dynamics of the RM-model (2) on the parabola, the \mathcal{M}_0^1 part of
 803 the f -nullcline (22b) is studied. From equations (20) and (21), one has

$$\frac{dx_1}{d\tau} = \frac{(1-x_1)((a_1-b_1)x_1-1)}{b_1-2b_1x_1-1}. \quad (57)$$

804 Since we have :

$$\frac{-2b_1x_1 + b_1 - 1}{(1 - x_1)((a_1 - b_1)x_1 - 1)} = \frac{b_1 + 1}{b_1 + 1 - a_1} \frac{1}{1 - x_1} + \frac{b_1^2 + b_1 - a_1b_1 + a_1}{b_1 + 1 - a_1} \frac{1}{(a_1 - b_1)x_1 - 1}, \quad (58)$$

805 it follows that equation (57) is equivalent to

$$\frac{b_1 + 1}{1 - x_1} + \frac{b_1^2 + b_1 - a_1b_1 + a_1}{(a_1 - b_1)x_1 - 1} dx_1 = (b_1 + 1 - a_1) d\tau, \quad (59)$$

806 thus

$$\int_{x_1(0)}^{x_1(T)} \left(\frac{b_1 + 1}{1 - x_1} + \frac{b_1^2 + b_1 - a_1b_1 + a_1}{(a_1 - b_1)x_1 - 1} \right) dx_1 = \int_0^T (b_1 + 1 - a_1) d\tau, \quad (60)$$

807 where $x_1(T)$ is the coordinate of the top of the parabola: $x_1(T) = \bar{x}_1 = \frac{b_1 - 1}{2b_1}$.

808 If we consider that the equilibrium point ($x_1^* = \frac{1}{a_1 - b_1}$) is at point T , that is at the
809 Hopf bifurcation point when $b_1 = 4$, it follows that: $b_1^2 + b_1 - a_1b_1 + a_1 = 0$.

810 We can then express the time t_T needed for starting from $x_1(0)$ to reach the equilibrium
811 E_2 at point T

$$t_T = \frac{1}{a_1 - b_1 - 1} \left((1 + b_1) \ln \left(\frac{(1 + b_1)/(2b_1)}{1 - x_1(0)} \right) \right). \quad (61)$$

812 But in this case point T is not an equilibrium. If one assumes that the equilibrium is on
813 the right of point T , that is $b_1 < 4$, see Fig. 3a, (60) shows that the equilibrium is not
814 reach in a finite time.

815 Finally, if we assume that the equilibrium x_1^* is on the left of point T that is $b_1 > 4$
816 and if we consider an initial condition between x_1^* and 1, see Fig. 3d, point T attracts the
817 trajectory. It is, however, not an equilibrium in the usual sense because equation (57) does
818 not vanish, it is actually not well defined. Nevertheless this point is reached in a finite
819 time according to (60), and the time needed to reach this point t_T^* is

$$t_T^* = \frac{1}{a_1 - b_1 - 1} \left((1 + b_1) \ln \left(\frac{(1 + b_1)/(2b_1)}{1 - x_1(0)} \right) + \frac{A}{a_1 - b_1} \ln \left(\frac{A/(2b_1)}{(a_1 - b_1)x_1(0) - 1} \right) \right), \quad (62)$$

820 where $A = a_1b_1 - a_1 - b_1^2 - b_1 > 0$ under the above mentioned conditions.