Hunting French Ducks in Population Dynamics

Ferdinand Verhulst

Abstract Equations with periodic coefficients for singularly perturbed growth can be analysed by using fast and slow timescales in the framework of Fenichel geometric singular perturbation theory and its extensions. The analysis is restricted to one-dimensional time-periodic ordinary differential equations and shows the presence of slow manifolds, canards and the dynamical exchanges between several slow manifolds. There exist permanent (or periodic) canards and periodic solutions containing canards.

1 Introduction

In this note we consider systems with slow-fast motion in a singularly perturbed setting; the slow motion is characterised by the exponential closeness of solutions to slow manifolds. In the case that the solution moves along a stable slow invariant manifold and at some point the slow manifold becomes unstable, we have the possibility of 'exponential sticking' or canard (French duck) behaviour. In this case, the solution continues for an $O(1)$ time along the slow invariant manifold that has become unstable and jumps after that away, for instance, to the neighbourhood of another invariant set. Following Pontrjagin (see [10]), one also calls this 'delay of stability loss'.

This delay or sticking process is closely connected to the so-called *canard* phenomenon for differential equations that can be described as follows: *Canard solutions are bounded solutions of a singularly perturbed system that, starting near an normally hyperbolic attracting slow manifold, cross a singularity of the system of differential equations and follow for an* $O(1)$ *time a normally hyperbolic repelling slow manifold.*

F. Verhulst (✉)
Mathematisch Instituut, University of Utrecht, PO Box 80.010,
3508 TA Utrecht, The Netherlands
e-mail: f.verhulst@uu.nl

J. Awrejcewicz (ed.), *Applied Non-Linear Dynamical Systems*, Springer Proceedings in Mathematics & Statistics 93, DOI 10.1007/978-3-319-08266-0_23

The canard behaviour will depend on the dimension of the problem and the nature of the singularity. An example of canard behaviour was found by the Strassbourg group working in non-standard analysis for a perturbed van der Pol equation; see [2] for details and references. In this example, the singularity crossed is a fold point. The analysis of this problem is quite technical.

Canards arising at transcritical bifurcations have been described in [6] and [9]. The purpose of the present note is to study such phenomena in growth equations that can be handled explicitly, both analytically and numerically; this may increase our understanding. In Sects. 2.4 and 4, we consider simple illustrations of exchange of stability between slow manifolds. The equations in Sect. 5 model growth phenomena with daily or seasonal fluctuations as appear in models of mathematical biology and economics. They are a natural extension of the logistic model introduced in [19].

We shall also meet *permanent canards*, solutions that are attracted to a slow manifold, travel across a singularity resulting in instability of the slow manifold, but are remaining near the slow manifold without leaving the unstable part.

The numerics which we used to obtain illustrations is based on the package CONTENT; see [8].

2 Fenichel Theory

In the period 1950–1960, many results were obtained for the asymptotic analysis of singularly perturbed ordinary differential equations; see for instance [15]. Later, these results were supplemented by essential qualitative insight based on developments of invariant manifold theory. This slow manifold analysis, as it is usually called, is often named after one of its main inventors, N. Fenichel. The canard aspects are an extension of the theory. We will summarise some important aspects.

2.1 The Slow Manifold: Fenichel's Results

Approximation theorems like Tikhonov's theorem ([15]) are concerned with the attraction, at least for some time, to the regular expansion that corresponds with a stable critical point of a boundary layer equation. The theory is quite general and deals with non-autonomous equations.

In many problems, it is possible to associate with the regular expansion a manifold in phase or solution space and to consider the attraction properties of the flow near this manifold. This raises the question of whether these manifolds really exist or whether they are just a phantom phenomenon. Such questions were addressed and answered in a number of papers by Fenichel (1971–1979) and other authors; for references and extensive introductions the reader is referred to the survey papers [3, 9] and [5]; see also [16].

Consider for $t \geq 0$ the $(n+m)$-dimensional non-autonomous system:

$$\dot{x} = f(x, y, t) + \varepsilon \cdots, \quad x \in D \subset \mathbb{R}^n,$$
$$\varepsilon \dot{y} = g(x, y, t) + \varepsilon \cdots, \quad y \in G \subset \mathbb{R}^m.$$

A corresponding theory can be developed for the system:

$$x' = \varepsilon f(x, y, \varepsilon t) + \varepsilon^2 \cdots, \quad y' = g(x, y, \varepsilon t) + \varepsilon \cdots,$$

where the prime denotes differentiation with respect to $\tau = t/\varepsilon$.

We will call y the fast variable and x the slow variable. The zero set of $g(x, y, t)$ is given by $y = \phi(x, t)$, which represents a first-order approximation M_0 of the slow manifold M_ε. The flow on M_ε is to a first approximation described by $\dot{x} = f(x, \phi(x, t), t)$.

In the Fenichel theory we assume

$$\text{ReSp} \;\; g_y(x, \phi(x, t)) \neq 0, x \in D.$$

That is, all the eigenvalues of the linearised flow near M_0, derived from the equation for y, have nonzero real parts.

A manifold is called hyperbolic if the local linearisation is structurally stable (real parts of eigenvalues all nonzero), and it is normally hyperbolic if in addition the expansion or contraction near the manifold in the transversal direction is larger than in the tangential direction (the slow drift along the slow manifold).

Note that this perspective on dynamics allows for interesting phenomena. One might approach M_ε for instance by a stable branch, stay for some time near M_ε, and then leave again a neighbourhood of the slow manifold by an unstable branch. This produces solutions indicated as 'pulse-like', 'multibump solutions', etc. This type of exchanges of the flow near M_ε is what one often looks for in geometric singular perturbation theory.

2.2 Existence of the Slow Manifold

The question of whether the slow manifold M_ε, approximated by $y = \phi(x, t)$, persists for $\varepsilon > 0$ was answered by Fenichel. The main result is as follows. If M_0 is a compact manifold that is normally hyperbolic, it persists for $\varepsilon > 0$ (i.e., there exists for sufficiently small, positive ε a smooth manifold M_ε close to M_0). Corresponding with the signs of the real parts of the eigenvalues, there exist stable and unstable manifolds of M_ε, smooth continuations of the corresponding manifolds of M_0, on which the flow is fast.

There are some differences between the cases where M_0 has a boundary or not. For details, see [3, 4] and the original papers by Fenichel.

2.3 The Compactness Property

Note that the assumption of compactness of D and G is essential for the uniqueness of the slow manifold. In many examples and applications, M_0, the approximation of the slow manifold obtained from the fast equation, is not bounded. This can be remedied, admittedly in an artificial way, by applying a suitable cutoff of the vector field far away from the domain of interest. In this way, compact domains arise that coincide locally with D and G. However, this may cause some problems with the uniqueness of the slow manifold. Consider for instance the following example from [16]:

Example. Consider the system

$$\begin{cases} \dot{x} &= 1, x(0) = x_0 > 0, \\ \varepsilon \dot{y} &= -\frac{y}{x^2}, y(0) = y_0 \geq 0. \end{cases} \tag{1}$$

Putting $\varepsilon = 0$ produces $y = 0$, which corresponds with M_0. We can obtain a compact domain for x by putting $x_0 \leq x \leq L$ with x_0 and L positive constants independent of ε. However, the limiting behaviour of the solutions depends on the initial condition and L. Integration of the equations yields

$$y(x) = y_0 \exp\left(\frac{1}{\varepsilon}(\frac{1}{t + x_0} - \frac{1}{x_0})\right).$$

As t tends to infinity, the solution for $y(t)$ tends to

$$y_0 \exp\left(-\frac{1}{\varepsilon x_0}\right),$$

so the solutions are, after an initial fast transition, all exponentially close to $y = 0$. However, there are an infinite number of slow manifolds dependent on x_0 and L, all tunnelling into an exponentially small neighbourhood of M_0 given by $y = 0$; see Fig. 1.

It is easy to modify the example to keep the variables on a compact domain; the slow manifold will then be unique. Consider for instance:

Example.

$$\begin{cases} \dot{x} &= \cos t, x(0) = x_0 > 1, \\ \varepsilon \dot{y} &= -\frac{y}{x^2}, y(0) = y_0 \geq 0. \end{cases} \tag{2}$$

We have $x(t) = x_0 + \sin t$ and $(x_0 - 1)^2 \leq x^2(t) \leq (x_0 + 1)^2$. It is easy to see that we have the estimate:

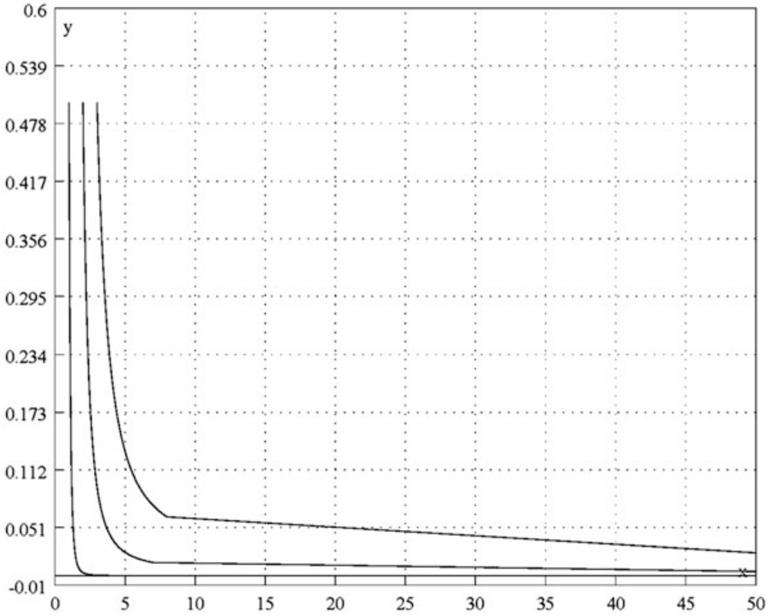

Fig. 1 Slow manifold behaviour of system (1) with initial conditions $x_0 = 1, 2, 3$, $y_0 = 0.5, \varepsilon = 0.1$. The limiting behaviour depends on the initial condition and the time interval

$$y_0 e^{-\frac{1}{\varepsilon}\frac{t}{(x_0-1)^2}} \leq y(t) \leq y_0 e^{-\frac{1}{\varepsilon}\frac{t}{(x_0+1)^2}}.$$

The solutions decrease towards $y = 0$.

One might wonder about the practical use of exponential closeness as such solutions are difficult to distinguish numerically. The phenomenon is important and of practical use when there is a change of stability, a bifurcation of the slow manifold. As we will see in a number of examples, exponentially close orbits may trigger different canard phenomena.

2.4 Permanent or Periodic Canards

Consider an example discussed in [16] (example 8.13):

$$\varepsilon \dot{y} = -x(t)y(1-y), \;\; y(0) = y_0, \;\; 0 \leq y_0 \leq 1.$$

The continuous function $x(t)$ may be explicitly given or can be derived from a coupled oscillator equation; ε is a small positive parameter. The slow manifolds are $y = 0$ and $y = 1$; one expects that if $x(t)$ changes sign periodically, the solutions will move very fast and periodically from one slow manifold to the other. This turns out not to be the case.

Solving the initial value problem we find

$$y(t) = \frac{y_0 e^{-\frac{1}{\varepsilon}\int_0^t x(s)ds}}{1 - y_0 + y_0 e^{-\frac{1}{\varepsilon}\int_0^t x(s)ds}}.$$

The solutions $y = 0$ and $y = 1$ are the (exact) slow manifolds of the dynamical system. If $x(t) > 0$, $y = 0$ is stable, $y = 1$ unstable; if $x(t) < 0$, $y = 1$ is stable, $y = 0$ unstable.

Assume that $x(t)$ is T-periodic with alternating positive and negative values. We can express $x(t)$ as

$$x(t) = a + f(t),\ a = \frac{1}{T}\int_0^T x(t)dt,\ \int_0^T f(t)dt = 0.$$

The solution can then be written as

$$y(t) = \frac{y_0 e^{-\frac{a}{\varepsilon}t} E(t)}{1 - y_0 + y_0 e^{-\frac{a}{\varepsilon}t} E(t)},\ E(t) = e^{-\frac{1}{\varepsilon}\int_0^t f(s)ds}. \tag{3}$$

The function $E(t)$ is positive and bounded. We conclude:

1. The condition for periodicity $y(0) = y(T)$ applied to eq. (3) produces the requirement $a = 0$. If $a = 0$, all solutions with $0 < y_0 < 1$ are T-periodic.
2. If $a > 0$, $\lim_{t\to\infty} y(t) = 0$; although $x(t)$ takes alternating positive and negative values, the solution stays near $y = 0$; we have a permanent canard. See Fig. 2 where $x(t) = a + \sin t$. Increasing n does not change the picture qualitatively.

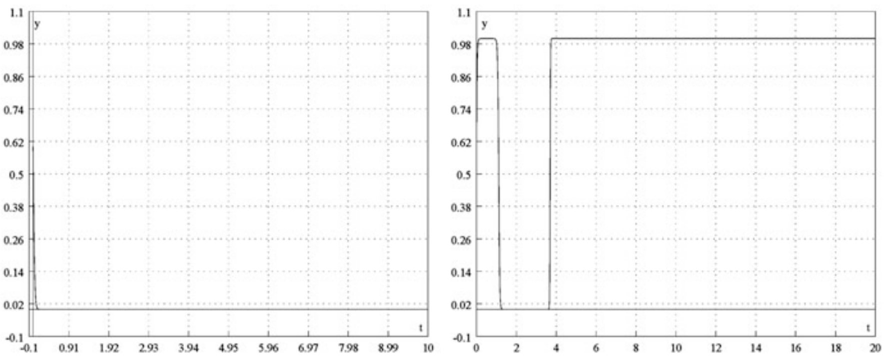

Fig. 2 Permanent canards resulting from the dynamics of $\varepsilon\dot{y} = -(a + \sin nt)y(1 - y)$, $y_0 = 0.6$, $\varepsilon = 0.01$. *Left* $a = 0.5$, $n = 1$, *right* $a = -0.5$, $n = 1$. Although the stability of the slow manifolds changes periodically, the solutions tend after transient behaviour to $y = 0$ and $y = 1$, respectively, to remain in their neighbourhood

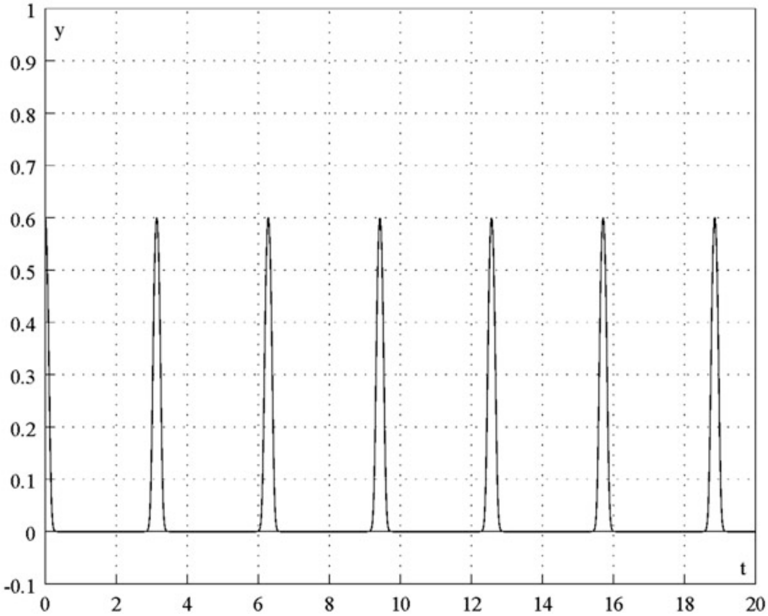

Fig. 3 Spike solutions from the equation $\varepsilon \dot{y} = -\sin(2t)y(1-y),\ y_0 = 0.6$

3. If $a < 0$, $\lim_{t\to\infty} y(t) = 1$; the slow manifold $y = 1$ shows permanent canard behaviour after a transient excursion to $y = 0$. See Fig. 2. Increasing n does not change the picture qualitatively.
4. If $a = 0$, we have even more interesting canard behaviour with the possibility of spikes for $y(t)$; see Fig. 3 where we have near-homoclinic behaviour in the sense that the spikes return periodically; between the spikes the solutions are exponentially close to the slow manifold $y = 0$. In the case of Fig. 3 we have

$$E(t) = e^{\frac{1}{2\varepsilon}(\cos 2t - 1)}.$$

The spikes arise whenever $\cos 2t - 1 = O(\varepsilon)$; the spike width in this case is $O(\sqrt{\varepsilon})$.

Increasing n for $x(t) = \sin nt$, the spikes diminish in height; this can also be directly concluded from eq. (3).

In [16] it is indicated that if $x(t)$ is derived from a chaotic oscillator, we may have chaotic jumping between the slow manifolds.

3 Periodic Solutions

In a slow-fast system of the form

$$\dot{x} = f(x, y, t), \ \ \varepsilon\dot{y} = g(x, y, t),$$

with a normally hyperbolic slow manifold (so without critical points), periodic solutions can be found by localising to the slow manifold and applying standard theory for periodic solutions. The idea is based on the rigorous theory of slow manifolds. This is not the main subject of this note but see for instance [17].

Transcritical bifurcations play a part in [6] and [12]. In the last reference a prey-predator system is analysed with a Holling II interaction term. This produces the intersection of two slow manifolds with a periodic solution involving a canard when the intersection is crossed. In the case of a constant carrying capacity, this model is also considered in [18]. As we shall see, a modified logistic equation can be considered as a standard form for this behaviour; an additional advantage of the one-dimensional equations is that often they can be analysed in more analytic detail.

Although we can solve a number of equations explicitly, it is convenient to have general theorems. From [11] we have the one-dimensional equation:

$$\dot{x} = f(x, t), \tag{4}$$

with $f(x, t)$ defined for $x \in \mathbb{R}$ and $t \in [0, \infty)$, continuous and satisfying the uniqueness condition; $f(x, t)$ is T-periodic in t.

- The solutions $x(t)$ of the eq. (4) are either periodic or monotonic in the sense that $x(0) < x(T) < x(2T) < \ldots < x(nT) < \ldots$ (or $x(0) > x(T) > \ldots$ etc.); see Theorem 9.1 in [11].
- If an isolated periodic solution of eq. (4) is Lyapunov-stable, then it is asymptotically stable; see Theorem 9.2 in [11].

4 A Modified Logistic Equation

Consider the non-autonomous equation for $y \geq 0$:

$$\varepsilon\dot{y} = x(t)y - y^2, \tag{5}$$

in which the growth rate $x(t)$ is sufficiently smooth and can take positive and negative values. Values of t for which $x(t)$ vanishes correspond with a transcritical bifurcation. The equation can model daily or seasonal changes of the growth rate. We solve the equation for general continuous $x(t)$ and $y(0) = y_0 > 0$. Putting

$$\Phi(t) = \int_0^t x(s)ds,$$

we find for the solution of eq. (5):

$$y(t) = \frac{e^{\frac{1}{\varepsilon}\Phi(t)}}{\frac{1}{y_0} + \frac{1}{\varepsilon}\int_0^t e^{\frac{1}{\varepsilon}\Phi(s)}ds}. \quad (6)$$

If $x(t)$ is T-periodic, we can write

$$x(t) = a + f(t)$$

and

$$\Phi(t) = at + F(t),\ F(t) = \int_0^t f(s)ds, \quad (7)$$

with a a real constant and $f(t)$ a zero average T-periodic function; $F(t)$ is bounded and $F(T) = 0$. In the cases that $x(t)$ is quasi- or almost-periodic, we can write similar expressions; see for an example Fig. 4.

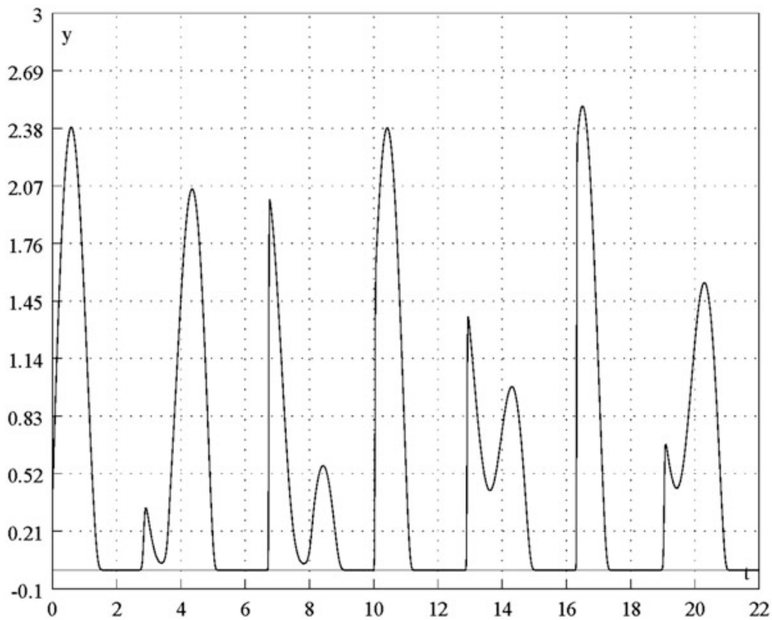

Fig. 4 Solutions from eq. (5) with almost-periodic growth rate $\varepsilon\dot{y} = (0.5 + \sin 2t + \sin \pi t)y - y^2,\ y_0 = 0.4,\ \varepsilon = 0.01$; see Sect. 4

From now on, we assume that $x(t)$ is continuous and T-periodic and δ is a small positive constant, but independent of ε; we have the following cases:

1. If the growth rate is negative, $a + f(t) \leq -\delta < 0$ for $0 \leq t \leq T$, we state that $\lim_{t\to\infty} y(t) = 0$. This can be deduced from the equation with a simple estimate from $\varepsilon\dot{y} \leq -\delta < 0$ for all time, but also from the explicit solution (6). Clearly $a < 0$ and the proof is simple: multiplying with $\exp(-at/\varepsilon)$ produces a bounded numerator and a monotonically increasing denominator. There is no periodic solution with $y_0 > 0$.
2. Less trivial is the case $a = 0$. In this case $\Phi(t)$ is bounded. The solution $y(t)$, given by expression (6), decreases to zero as $t \to \infty$ as the integral takes over a positive function. Again, there is no periodic solution with $y_0 > 0$. In Fig. 5 we choose $x(t) = \sin t$ for an illustration; $y = 0$ is associated with a permanent canard.
3. $a > 0$ with $a + \min_{0\leq t\leq T} f(t) < -\delta < 0$. In this case a periodic solution exists. Several proofs are possible, but a simple one runs as follows:

   Assuming the periodicity condition $y(0) = y(T) = y_0(> 0)$, we obtain from the solution (6) the expression

$$y_0 = \frac{e^{\frac{aT}{\varepsilon}} - 1}{\frac{1}{\varepsilon}\int_0^T e^{\frac{1}{\varepsilon}\Phi(s)} ds}.$$

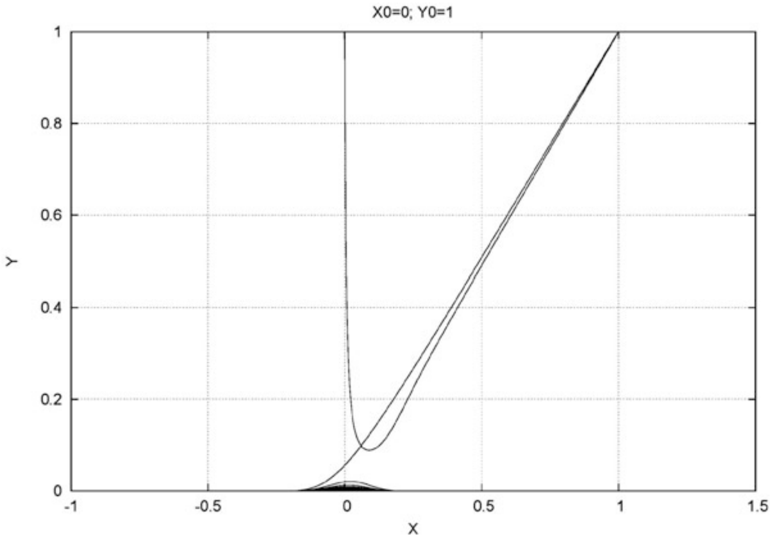

Fig. 5 Solution approaching the periodic solution in $y = 0$ of the modified logistic equation (5) with $x(t) = \sin t, x(0) = 0, y(0) = 1, \varepsilon = 0.01$. To the right of the y-axis, $y = 0$ corresponds with an unstable slow manifold

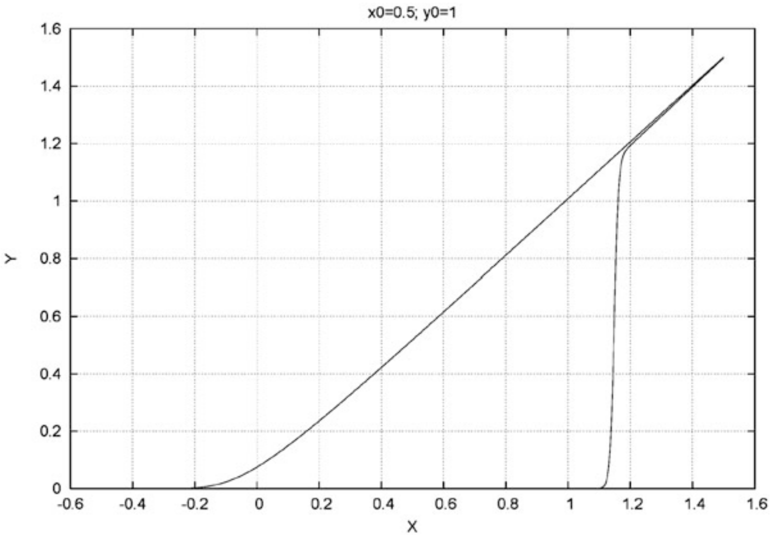

Fig. 6 Canard-like periodic solution of the modified logistic equation (5) with $x(t) = 0.5 + \sin t$, $\varepsilon = 0.01$. To the right of the y-axis, $y = 0$ is an unstable slow manifold; $x = 0$ corresponds with a transcritical bifurcation

With the right-hand side being positive, we have constructed a positive solution for y_0 and so a positive periodic solution.

For more explicit choices of $x(t)$ we can show that y_0 can both be exponentially small and can be $O(1)$. See Fig. 6. The periodic solution follows closely the slow manifold $y = 0$, produces a canard and increases quickly at a positive value of $x(t)$; this value depends on a (in this case 0.5) and the shape of $x(t)$ as it depends on the time interval of exponential attraction during the stable slow manifold phase. For instance, taking for simplicity the non-periodic transition $x(t) = -a + bt$, $a, b > 0$, we have $\Phi(t) = -at + \frac{1}{2}bt^2$. It is easy to show that at the time of transition of the y-axis, $t = a/b$, we have $y(a/b) = O(exp.(-a^2/(2b\varepsilon)$. For $t > a/b$ the solution remains exponentially close to $y = 0$ (canard) until the solution in an $O(\varepsilon)$-neighbourhood of $t = 2a/b$ jumps off to the slow manifold $y = x(t)$. In the case of the example displayed in Fig. 6, this jump off (end of the canard) is delayed somewhat by the shape of $\Phi(t) = 0.5t + 1 - \cos t$ in this example.

The transcritical bifurcation takes place also periodically by the descent of $x(t)$ following the slow manifold $y = x(t)$. Starting in an $O(\varepsilon)$-neighbourhood of the periodic solution on the slow manifold at $x = y = 1$ and choosing for the transition the simple example $x(t) = 1 - bt$, $b > 0$, we find

$$y(\frac{1}{b}) = \frac{e^{\frac{1}{\varepsilon 2b}}}{1 + \frac{1}{\varepsilon}\int_0^{\frac{1}{b}} e^{\frac{1}{\varepsilon}(t - \frac{1}{2}bt^2)} ds} = O(\sqrt{\varepsilon}).$$

Assuming that we can non-trivially linearise the slow manifold and the solutions on it near the transcritical bifurcation, this estimate is typical.

Solutions near the slow manifold $y = 0$ correspond with near-extinction, followed by a sudden explosive increase of the y-variable. The stability question is more delicate in this case; we will consider this in Sect. 5.

4. If $a < 0$, we find a negative expression for y_0 and no periodic solution, but a permanent canard associated with $y = 0$.
5. If the growth rate is periodic but always positive, $a + f(t) \geq \delta > 0$, we find a periodic solution in an ε-neighbourhood of the slow manifold $y = x(t)$. This is an example of the theory mentioned earlier; see [17].

5 The Periodic P.F. Verhulst Model

Consider the classical logistic equation of [19], but now with periodically varying growth rate $r(t)$ and carrying capacity $K(t)$, period T. In standard notation for the population size $N(t)$ with *positive growth rate* $r(t)$, the equation is

$$\varepsilon \dot{N} = r(t)N\left(1 - \frac{N}{K(t)}\right), \; N(0) = N_0 > 0. \tag{8}$$

We have $K(t) > m > 0$. Without the fast growth perspective, the equation was studied in [1, 14] and [13].

It is a natural assumption, at least for limited intervals of time, that $r(t)$ can take negative values. For such cases we modify the logistic equation to

$$\varepsilon \dot{N} = r(t)N - \frac{N^2}{R(t)}, \; N(0) = N_0 > 0 \tag{9}$$

with $R(t) > 0$ and T-periodic. Without this modification, a negative growth rate would be accompanied by a positive nonlinear term; there is no rationale for this.

Equations (8) and (9) describe the dynamics if interaction with other populations is negligible.

5.1 Positive Growth Rate

The slow manifolds that exist for eq. (8) are approximated by the limit cases $N(t) = 0$ and $N(t) = K(t)$. Consider the stability of the slow manifolds. The 'eigenvalues' are respectively $r(t)$ and $-r(t)$ so that the slow manifold $N(t) = K(t)$ is stable if $r(t) > \delta > 0$. Replacing $x(t)$ by $r(t)$ we can repeat the calculation of Sect. 4 to obtain

$$N(t) = \frac{e^{\frac{1}{\varepsilon}\Phi(t)}}{\frac{1}{N_0} + \frac{1}{\varepsilon}\int_0^t \frac{r(s)}{K(s)} e^{\frac{1}{\varepsilon}\Phi(s)} ds}. \tag{10}$$

As before, we put $r(t) = a + f(t)$ with a a constant and $f(t)$ a T-periodic function with average zero. From eq. (10) we find with the periodicity condition $N_0 = N(T) > 0$:

$$N_0 = \frac{e^{\frac{aT}{\varepsilon}} - 1}{\frac{1}{\varepsilon}\int_0^T \frac{r(s)}{K(s)} e^{\frac{1}{\varepsilon}\Phi(s)} ds}. \tag{11}$$

As $a > 0$, a periodic solution exists. We conclude: Assume that the growth rate is T-periodic with $r(t) \geq \delta$ with $\delta > 0$, $0 \leq t \leq T$, so we have stability of the slow manifold $N(t) = K(t)$; N_0 from eq. (11) is positive. For the periodic solution, we have $N(t) = K(t) + O(\varepsilon)$ for all time. This is not immediately clear from the exact solution (10).

5.2 *Positive and/or Negative Growth Rate*

The solution of eq. (9) is easy to find:

$$N(t) = \frac{e^{\frac{1}{\varepsilon}\Phi(t)}}{\frac{1}{N_0} + \frac{1}{\varepsilon}\int_0^t \frac{1}{R(s)} e^{\frac{1}{\varepsilon}\Phi(s)} ds}. \tag{12}$$

For intervals of time when $r(t) \geq \delta > 0$, a slow manifold is given by $N(t) = r(t)R(t)$. On such intervals, this slow manifold is stable. When $r(t) \neq 0$, $N(t) = 0$ is a slow manifold.

For a periodic solution to exist we apply the periodicity condition $N(T) = N_0$. This produces

$$N_0 = \frac{e^{\frac{aT}{\varepsilon}} - 1}{\frac{1}{\varepsilon}\int_0^T \frac{1}{R(s)} e^{\frac{1}{\varepsilon}\Phi(s)} ds}. \tag{13}$$

As $r(t)$ changes sign during a period, we have the possibility of periodic transitions between the approximate slow manifold $N(t) = r(t)R(t)$ for $r(t) > 0$ and a neighbourhood of the slow manifold $N(t) = 0$ if $r(t) < 0$ We draw a number of conclusions:

1. Assume stability of the trivial solution ($r(t) \leq -\delta < 0$ for $0 \leq t \leq T$). As expected, it follows from solution (12) that $N(t) \to 0$ for $t \to \infty$, so the population will become extinct. No periodic solution exists.

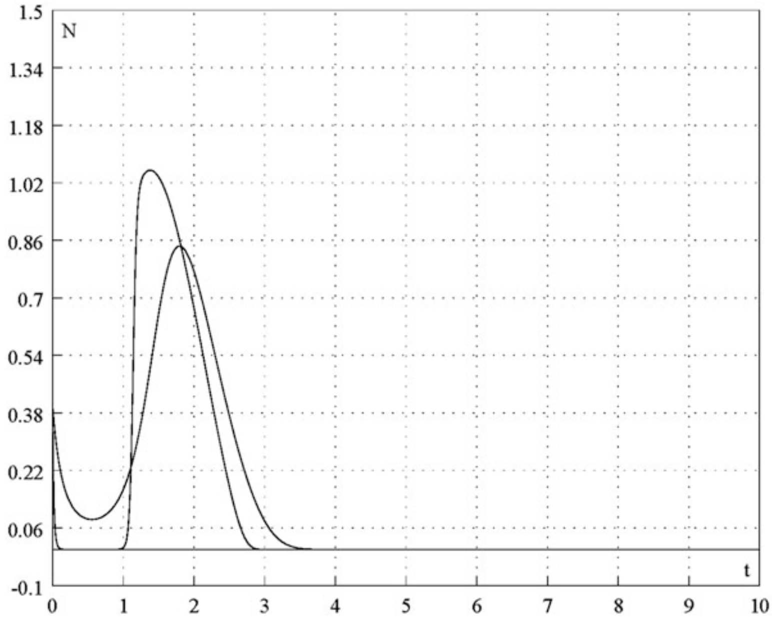

Fig. 7 The case of eq. (9) with sign changing $r(t) = -0.5 + \sin t$, $R(t) = 2 + \cos t$, $N_0 = 0.4$. The first interval where $r(t) > 0$ is $\pi/6 < t < 5\pi/6(\pi/6 = 0.52\ldots, 5\pi/6 = 2.62\ldots)$. At $t = 5\pi/6$, the trivial solution becomes stable; at $t = 13\pi/6 = 6.80\ldots$, the trivial solution becomes unstable again. If $\varepsilon = 0.1$, a canard develops after $r(t)$ becomes negative (at $t = 2.62\ldots$) that puts the stable slow manifold $N = r(t)R(t)$ that exists for positive values of $r(t)$ outside of reach. If $\varepsilon = 0.01$, a canard develops earlier, at $t = 0.52\ldots$, the transient maximum is larger, a permanent canard develops near $t = 2.62\ldots$

2. Assume that $r(t)$ changes sign with $a < 0$ (or $\int_0^T r(t)dt < 0$). In the periodicity condition (13), the numerator is negative and the denominator is positive, so no periodic solution exists. All solutions of eq. (9) are monotonic. This can also be seen as follows. The integral in the denominator of solution (12) is positive, so we have the estimate:

$$N(t) \leq N_0 e^{\frac{1}{\varepsilon}(at+F(t))}.$$

In the case $a < 0$, this is a strong estimate of exponential decay, but how do we conciliate this with the stability of the slow manifold $N = r(t)R(t)$ for intervals of time when $r(t) > 0$? In Fig. 7 we have $r(t) = -0.5 + \sin t$ so we start with negative values of $r(t)$ for $0 \leq t < \pi/6 = 0.52\ldots$; $r(t)$ is positive for $\pi/6 < t < 5\pi/6 = 2.62\ldots$. After $t = 13\pi/6 = 6.80\ldots$, a canard develops that keeps the solution close to the trivial solution $N(t) = 0$. The solution cannot make the jump transition back to the slow manifold $N = r(t)R(t)$. Taking $\varepsilon = 0.01$, a

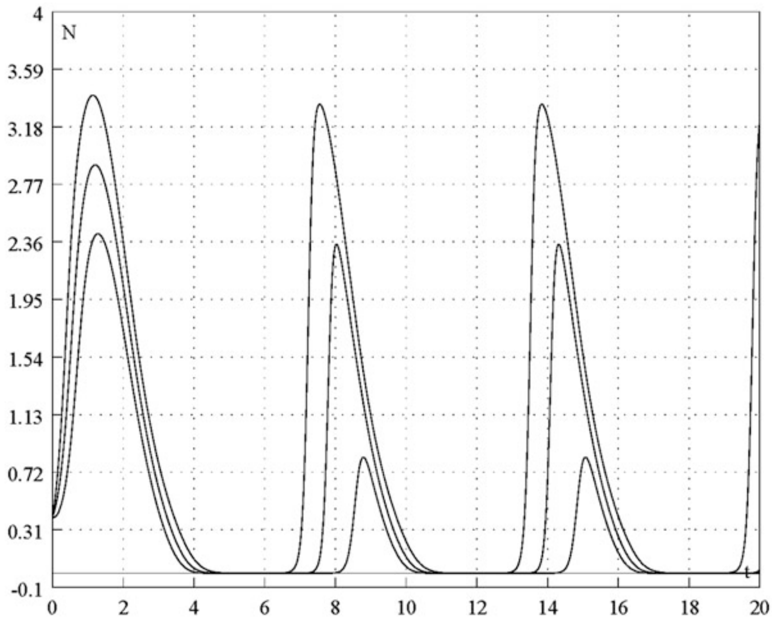

Fig. 8 Three solutions of eq. (9) approaching periodic solutions in the cases $r(t) = a + \sin t$, $R(t) = 2 + \cos t$ with $a = 0.5$ (largest amplitude), $a = 0.3, 0.1$; $N(0) = 0.4, \varepsilon = 0.1$. Canards develop at the transitions from positive to negative values of $r(t)$

canard develops earlier, between $t = \pi/6 = 0.52$ and 1; but near $t = 1$, the solution grows again after which a permanent canard emerges near $t = 2.62$.

3. Assume that $r(t)$ changes sign with $a > 0$ (or $\int_0^T r(t)dt > 0$). In the periodicity condition (13), the numerator is positive, so a unique periodic solution exists. In Fig. 8 we present three solutions approaching periodic solutions if $r(t) = a + \sin t$ with $a = 0.5, 0.3, 0.1$; $R(t) = 2 + \cos t$. Canards develop at the sign transitions of $r(t)$. For instance, if $a = 0.5$, the first transition is at $t = 7\pi/6 = 3.67\ldots$, but the canard delays the transition until a little above $t = 4$. If $a > 0$ is diminished, the corresponding canard increases in size, as expected. In all cases, each cycle faces the possibility of near-extinction.
4. Assume that we have the boundary case when $r(t)$ changes sign with $a = 0$ or $\int_0^T r(t)dt = 0$. In this case the periodicity condition (13) cannot be satisfied. In solution (12), the numerator varies periodically; the integral in the denominator produces a positive, constant contribution at each cycle. The maximum population density will decrease algebraically with time; see Fig. 9.

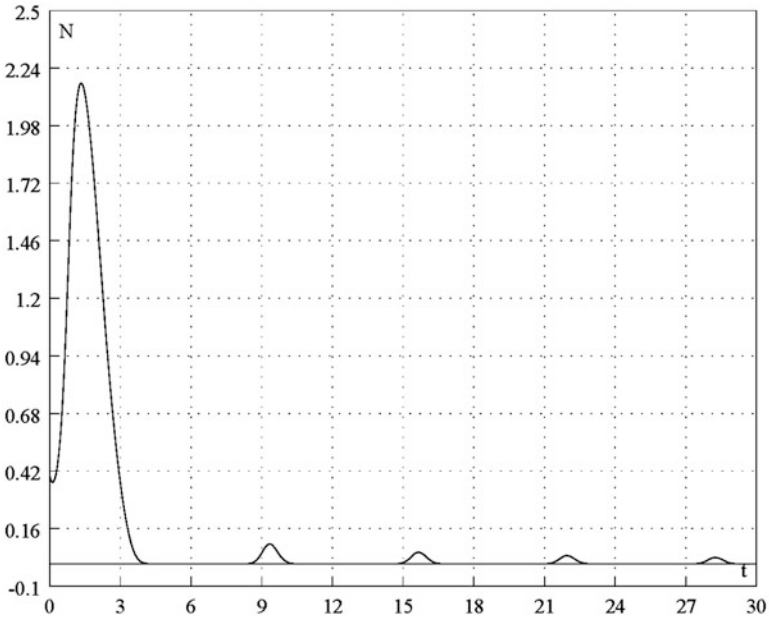

Fig. 9 Solution of eq. (9) in the case $r(t) = \sin t$, $R(t) = 2 + \cos t$, $N(0) = 0.4, \varepsilon = 0.1$. The solution decreases as predicted; for smaller values of ε the decrease is faster

6 Conclusion

It is remarkable that we can analyse the dynamics of a number of one-dimensional growth models in some analytic detail. The analysis may serve as an inspiration for problems with more complicated exchange of stability of slow manifolds.

Our models can be extended to involve one or more predators and to involve spatial diffusion. This will be a subject of a forthcoming paper.

Acknowledgements Taoufik Bakri kindly introduced me to the use of CONTENT. Comments by Odo Diekmann on the interpretation of the time-varying P.F. Verhulst model are gratefully acknowledged.

References

1. Bernadete, D.M., Noonburg, V.W., Pollina, B.: Qualitative tools for studying periodic solutions and bifurcations as applied to the periodically harvested logistic equation. MAA Monthly **115**, 202–219 (2008)
2. Eckhaus, W.: Relaxation oscillations including a standard chase on French ducks. Asymptotic Analysis II. Lect. Notes Math.**985**, 449–494 (1983)

3. Jones, C.K.R.T.: Geometric singular perturbation theory. Dynamical Systems, Lect. Notes Math. Montecatini Terme **1609**, 44–118 (1994)
4. Kaper, T.J.: An introduction to geometric methods and dynamical systems theory for singular perturbation problems. Proc. Symp. Appl. Math. **56** (1999)
5. Kaper, T.J., Jones, C.K.R.T.: A primer on the exchange lemma for fast-slow systems. IMA Vols. Math. Appl. **122** 65–88 (2000)
6. Krupa, M., Szmolyan, P.: Extending slow manifolds near transcritical and pitchfork singularities. Nonlinearity **14**, 1473–1491 (2001a)
7. Krupa, M., Szmolyan, P.: Relaxation oscillation and canard explosion. J. Diff. Equat.**174**, 312–368 (2001b)
8. Kuznetsov, Y.A., Levitin, V.V.: A multiplatform environment for analysing dynamical systems. Dynamical Systems Laboratory, Centrum voor Wiskunde en Informatica, Amsterdam, (1997) (http://www.math.uu.nl/people/kuznet/)
9. Kuznetsov, Y.A., Muratori, S., Rinaldi, S.: Homoclinic bifurcations in slow-fast second order systems. Nonlinear Anal. Theory, Methods Appl. **25**, 747–762 (1995)
10. Neihstadt, A.I.: Asymptotic investigation of the loss of stability by an equilibrium as a pair of imaginary eigenvalues slowly cross the imaginary axis. Usp. Mat. Nauk **40**, 190–191 (1985)
11. Pliss, V.A. Nonlocal problems of the theory of oscillations. Academic Press, NewYork (1966)
12. Rinaldi, S., Muratori, S., Kuznetsov, Y.A.: Multiple attractors, catastrophes and chaos in seasonally perturbed predator-prey communities. Bull. Math. Biol. **55**, 15–35 (1993)
13. Rogovchenko, S.P., Rogovchenko, Y.V.: Effect of periodic environmental fluctuations on the Pearl-Verhulst model. Chaos, Sol. Fract. **39**, 1169–1181 (2009)
14. Sonneveld, P., van Kan, J.: On a conjecture about the periodic solution of the logistic equation. J. Math. Biol. **8**, 285–289 (1979)
15. Tikhonov, A.N.: Systems of differential equations containing a small parameter multiplying the derivative. Mat. Sb. **31**(73), 575–586 (1952)
16. Verhulst, F.: Methods and Applications of Singular Perturbations. Springer, NewYork (2005)
17. Verhulst, F.: Periodic solutions and slow manifolds. Int. J. Bifur. Chaos. **17**(8) 2533–2540 (2007)
18. Verhulst, F., Bakri, T.: The dynamics of slow manifolds. J. Indones. Math. Soc. (MIHMI) **13**, 73–90 (2007)
19. Verhulst, P.F.: Notice sur la loi que la population poursuit dans son accroissement. Correspondance Mathématique et Physique **10**, 113–121 (1838)