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DELAYS INDUCED IN POPULATION DYNAMICS

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Abstract. This paper provides an introduction to delay differential equations together with a short survey on state-dependent delay differential equations arising in population dynamics. Our main goal is to examine how the delays emerge from inner mechanisms in the model, how they induce oscillations and stability switches in the system and how the qualitative behaviour of a biological model depends on the form of the delay.

1. Introduction. The goal of this work is to provide an introduction to delay differential equations considered in the context of ecology and to discuss some of the mathematical issues arising in their treatment. We remind the reader that delay differential equations are in some sense associated with the early development of mathematical ecology through the predator-prey models proposed in the twenties by V. Volterra ([42]). The subject has grown since, it has been extended in various ways, for example, to partial differential equations with functional delay terms ([12], [20], [21]). For these presentations, we chose to restrict our considerations to equations involving only time and possibly some structure variable, not space, involving only zeroth and first order terms, not second order terms (except possibly in the time variable). We decided to focus our presentation on stability and oscillations. There have been a lot of speculations in the seventies and eighties about the role of the delay in the occurrence of oscillations in real systems: it has been hypothesized that increasing delays in a system would result in an increase of oscillatory

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properties of the system and would finally drive the system towards oscillating stable states. This idea has been introduced in the context of blood production by L. Glass and M. Mackey ([35]) and has progressively invaded other domains, with nuances which for example led to the study of systems where stability and instability alternate when the delay is increased. Our personal inclination in the modeling of real systems is not to introduce delays in order to produce such or such a phenomenon, but rather let the delay emerge from some inner mechanisms of the model. One important class of models where delays emerge are those describing the dynamics of a population, divided into several stages, when the passage from a stage to the next one requires that the individual has reached a threshold size. These are the models on which we will concentrate after some preliminaries where we will introduce some vocabulary and present basic ways of investigating stability and oscillations. A study of the ecological mechanisms to provide delay has been performed in the eighties by W. Gurney and R. Nisbet and coworkers ([27], [31]). They notably were concerned with determining rules about the way stability and oscillations can also emerge from such ecological considerations. We will present a classification of the mechanisms and some of their results. More recently, one of us has considered, in collaboration with several students and colleagues, models where delays arise from a size threshold to be reached. This leads to state-dependent delay differential equations. The work is in the context of fish populations. But, such equations can be met in various contexts: for example, J. Bélair and M. Mackey ([10]) consider a state-dependent delay equation modeling commodity price. These equations pose problems even with regards the resolution and uniqueness of solutions. In collaboration with A. Fathallah ([9]), a classification of such equations has been proposed as well as the study of local stability and the onset of oscillations. In joint works of O. Arino with K. Hadeler, M. Hbid ([4]) and P. Magal ([36]), global results have been obtained for a subclass of such equations, namely, we proved the existence of a global branch of non-trivial slowly oscillating periodic solutions, thus extending to those equations results previously obtained for delay differential equations in the seventies and the eighties. These global aspects prolong naturally the local work near equilibriums. For the sake of focusing, we will not deal with such aspects and refer the interested reader to the above mentioned publications. In summary, the following subjects will be addressed, in the given order:

1. Preliminaries on delay differential equations.
2. Instability and oscillations induced by delays: local analysis using the characteristic equation.
3. State-dependent delay differential equations.

We will leave untouched most of the subject of delay differential equations: from the theoretical viewpoint, the past twenty years have been marked by the burgeoning of new approaches, using integrated semigroups or the so-called sun star machinery, which have shed a new light on such equations; the theory of dynamical systems associated with delay equations has also been spectacularly boosted starting at the beginning of the eighties: the most recent results give a full description of the attractor set of a class of delay differential equations. Such results have been reported in books, notably the latest edition of [28] by J. K. Hale and S. M. Verduyn Lunel, updating two previous editions by J. K. Hale, also the book [19] as well as a number of monographs of the A.M.S. or others and articles in various journals, by H. O. Walther, J. Mallet-Paret and coworkers. Delay functionals have also been introduced in a variety of ways and have led to as many types of equations which require specific treatment, not covered here: neutral equations, infinite delay equations, equations with piecewise constant delayed arguments, impulsive delay equations, partial differential equations with delays, stochastic delay equations.

2. Preliminaries on delay differential equations

2.1. *First examples and problems set.* Historically, the very first model of mathematical ecology is a predator-prey system of equations introduced by V. Volterra in the twenties ([42]). The system reads as:

$$\begin{cases} N_1'(t) = [b_1 - a_1 N_2(t)]N_1(t), \\ N_2'(t) = \left[-b_2 + a_2 N_1(t) + \displaystyle\int_{-r}^{0} k(s)N_1(t+s)ds\right] N_2(t) \end{cases}$$

where N_1 and N_2 are the densities of prey and predators respectively. A distributed delay in the second equation represents retarded growth of the predator ensuing prey consumption.

Since the seminal work by Volterra, delays have been considered in many situations. In the third section, we will present a general framework for delay in ecological models. Let us here focus our attention on a model simple enough to pose the main problems: the logistic equation. The logistic equation is an equation of the type

$$x'(t) = rx(t)\left[1 - \frac{x(t)}{K}\right]$$

in which $r > 0$ would be the growth rate of the population in the case of low abundance (supposedly here optimal for growth), while $K > 0$ would be the maximal population biomass that the system is able to sustain (the *carrying capacity*). Non zero solutions of that equation converge monotically towards the steady-state $x^* = K$. The introduction of a delay in the logistic equation is motivated by repeated observations made for several animal populations about oscillations of the abundance with, in some cases, bursts of populations followed by quasi-extinctions. One of the explanations would be that the system is not immediately responsive, there is some inertia or some delay between the environmental changes and the adaptation of the population. A very simple way to account for this leads to

$$x'(t) = rx(t)\left[1 - \frac{x(t-\tau)}{K}\right]$$

in which the number $\tau > 0$ is the delay, the quantity $1 - \frac{x(t-\tau)}{K}$ represents a modulation of the growth rate r in terms of the abundance of the population at a previous time. One can immediately see that such a term gives the possibility for oscillations about the value K. Oscillations may be of different natures: slow or fast, damped or sustained, and there is even the possibility of periodic oscillations. This equation has attracted a lot of interest in the seventies around a number of issues which constitute the main problems associated with such equations, especially in the context of ecology: existence of steady states, periodic solutions; stability, instability of steady states, bifurcation of new steady states, periodic solutions or more complicated invariant manifolds and the transitions from an equilibrium to another one or to an attracting set; parameter sensitivity, notably, the role of the delay in the dynamical features. So, the main problems are of a qualitative nature, as opposed to quantitative issues which would be connected to predictive models. In order to investigate such problems, it was necessary to develop a machinery analog to what is available for the study of dynamical systems associated with ordinary equations: this includes a linear theory of delay differential equations as well as a theory of nonlinear perturbations of such equations.

2.2. *Definition, existence, uniqueness, linear theory, semi-linear theory.* One of the simplest examples of a delay differential equation is

$$x'(t) = ax(t-1) \tag{1}$$

in which $x(t)$ denotes a real-valued function of time t, a is a parameter. In this formulation, one sees that the derivative of the unknown function $x(t)$ is, at time t, a function of the value of x at time $t-1$. We will also deal with the inhomogeneous equation

$$x'(t) = ax(t-1) + f(t) \tag{2}$$

in which it will be assumed that f is locally integrable. There are indeed several ways in which a solution may be defined. One can consider, as a solution, a function defined on the whole of $\mathbf{R}$, satisfying the above formula at every point. Assuming x to be continuous, the equation yields the same property for x'. The formula also shows that such a solution does not grow faster than linear when t is increased. On the other hand, no such limitation prevails when t is moved to the left. And in fact, there are such solutions defined on the whole of $\mathbf{R}$ and whose behavior at $-\infty$ is faster than any given exponential. As a consequence it is not in general feasible (or, say, not practical) to transform the equation via a Fourier transform. But, under the assumptions made on x, one can compute the Laplace transform for the restrictrion to any interval of the form $[t_0, +\infty[$. Let us compute it for example in the case $t_0 = 0$ and consider the homogeneous equation (1) for a moment. We denote

$$\widehat{x}(s) := \int_0^{+\infty} \exp(-st)x(t)\,dt$$

and we assume the reader is familiar with the basics on the Laplace transform. We obtain

$$s\widehat{x}(s) - x(0) = a\int_0^{+\infty} \exp(-st)x(t-1)\,dt$$

which, by an obvious change of variables in the integral, leads to

$$s\widehat{x}(s) - x(0) = a\int_{-1}^{0} \exp(-s(t+1))x(t)\,dt + a\widehat{x}(s)\exp(-s)$$

from which we get

$$\widehat{x}(s) = (s - a\exp(-s))^{-1}x(0) + a\exp(-s)(s - a\exp(-s))^{-1}\int_{-1}^{0} \exp(-st))x(t)\,dt. \tag{3}$$

The formula expresses $\widehat{x}(s)$, therefore using the inverse Laplace transform, $x(t)$, as a function of a quantity computed in terms of the restriction of $x(t)$ to the interval $[-1, 0]$.

So, in order to be able to compute $x(t)$ on the right of $t = 0$, it is first of all necessary to assume it known on the interval $[-1, 0]$ and, in fact, if x_1 and x_2 are two solutions equal on $[-1, 0]$, then

$$\widehat{x}_1(s) = \widehat{x}_2(s),$$

which allows us to extend the equality to the right of 0. Similarly, if we want to solve the equation to the right of a time t_0 it is necessary to assume it known on the interval $[t_0 - 1, t_0]$ and, from the value on that interval, there is only one possible extension to the right of t_0. So, the equation determines a family of maps from the space $\mathcal{C}([-1, 0])$ into the space $\mathcal{C}([t_0 - 1, t_0])$, $\forall t_0 \geq 0$, which can be viewed as a one-parameter family of maps on the same space by shifting the functions defined on $[t_0 - 1, t_0]$ over the fixed interval $[-1, 0]$, using the phase shift

$$\forall \theta \in [-1, 0], \qquad x_t(\theta) := x(t + \theta). \tag{4}$$

Existence may be proved in at least two ways. The most elementary way is to integrate equation (1) stepwise. From an initial value given on the interval $[-1, 0]$, one can compute the solution on the next interval $[0, 1]$ by a direct quadrature formula

$$x(t) = \varphi(0) + a \int_{-1}^{t-1} \varphi(s)\, ds.$$

Then $x(t)$ can be shifted back to $[-1, 0]$ and provides a new initial datum from which the same computation as above can be repeated, infinitely many times. The function obtained this way is continuous on $[-1, +\infty[$, it is differentiable on $[0, +\infty[$, it is twice differentiable on $[1, +\infty[$, three times differentiable on $[1, +\infty[$, etc.

The other way starts from (3) and uses the inverse Laplace transform of $\widehat{x}$ given by (3). Note $\mathcal{R}(t)$ the inverse transform of the function $(s - a\exp(-s))^{-1}$. The second term in the right hand side of (3) can be written in the form

$$a(s - a\exp(-s))^{-1} \int_0^1 \exp(-st))x(t-1)\, dt$$

which appears as the product of the Laplace transforms of $a\mathcal{R}(t)$ and the function $\chi_{[0,1]}(t)x(t-1)$. This leads to the following expression for the solution:

$$x = \mathcal{R}\varphi(0) + a\mathcal{R} * \chi_{[0,1]}(\cdot)\varphi(\cdot - 1)$$

where $*$ denotes the convolution in the set $\mathbf{R}_+$. This formula makes sense even for the case when φ is a step function, equal to zero for $\theta \in [-1, 0[$ and some value ξ at $\theta = 0$. In this case, the solution reduces to

$$x(t) = \mathcal{R}(t)\xi.$$

Indeed, $\mathcal{R}(t)$ can be interpreted as the solution of equation (1) starting from the initial data X_0 defined by

$$\forall \theta < 0, \qquad X_0(\theta) = 0, \qquad X_0(0) = 1.$$

We now introduce the shift operator along the solutions, namely a one-parameter family of linear maps $\{T(t)\}_{t \geq 0}$, defined as follows:

$$T(t) : \mathcal{C}([-1, 0]) \to \mathcal{C}([-1, 0]), \qquad \varphi \mapsto T(t)\varphi := x_t,$$

where x_t is defined in (4). It is immediate to see that

$$T(0) = Id, \qquad T(t)T(s) = T(t+s), \qquad \text{for all } t, s \geq 0$$

which gives the family the basic properties of a semigroup of operators. Moreover, the implication (*continuity on closed bounded intervals* $\Rightarrow$ *uniform continuity*) entails the continuity of the map $t \mapsto x_t$, that is to say, for each $\varphi \in \mathcal{C}([-1,0])$, the map $t \mapsto T(t)\varphi$ is continuous. This property is named in the literature *strong continuity*: $\{T(t)\}_{t\geq 0}$ is a strongly continuous semigroup of operators, also called a C_0-semigroup of operators. Using the expression of $T(t)\varphi$ in terms of the solution x, one can observe an important property, typical for semigroups associated with delay equations, namely that $(T(t)\varphi)(\theta)$ depends only on $t+\theta$, in particular

$$(T(t)\varphi)(\theta) = \begin{cases} (T(t+\theta)\varphi)(0) & \text{if } t+\theta \geq 0, \\ \varphi(t+\theta) & \text{if } t+\theta < 0. \end{cases}$$

A semigroup enjoying such a property is called a *translation semigroup*. Since the semigroup is defined on a space of functions $\mathcal{F}(J, X)$, where J is an interval and X is a Banach space, it is possible to associate with each solution a function $x(t)$ with values in X such that

$$T(t)\varphi = x_t.$$

2.2.1. *Extension of the concept of solution to discontinuous functions.* For each $t \geq 0$, $\theta \in [-1, 0]$, the map

$$\varphi \mapsto (T(t)\varphi)(\theta)$$

is linear, continuous, from the space $\mathcal{C}([-1,0])$ into $\mathbf{R}$, so it determines a Radon measure which can be extended to a larger set of functions, notably to Borel measurable ones. The extension is unique, and satisfies the semigroup properties as well as the shift property. However, it is not in general strongly continuous. We will keep the same notation $T(t)$ for the extension. In terms of the extension, we can notably express $\mathcal{R}(t)$ as

$$\mathcal{R}(t) = (T(t)X_0)(0).$$

2.2.2. *Solution of the inhomogeneous equation (variation of constants formula).* Assuming that f has a Laplace transform, equation (2) can be transformed into

$$(s - a\exp(-s))\widehat{x}(s) = x(0) + a\exp(-s)\int_{-1}^{0} \exp(-st))x(t)\,dt + \widehat{f}(s)$$

which leads to

$$x = \mathcal{R}\varphi(0) + a\mathcal{R} * \chi_{[0,1]}(\cdot)\varphi(\cdot - 1) + \mathcal{R} * f.$$

In terms of the semigroup $T(t)$ and its extension, the above expression reads

$$x(t) = (T(t)\varphi)(0) + \int_0^t (T(t-s)X_0)(0)f(s)\,ds$$

or

$$x_t = T(t)\varphi + \int_0^t T(t-s)X_0 f(s)\,ds. \tag{5}$$

2.2.3. *Generalization.* The following is a more general linear delay differential equation, the most frequently used in the literature

$$x'(t) = L(x_t) \tag{6}$$

or its inhomogeneous expression

$$x'(t) = L(x_t) + f(t) \tag{7}$$

in which x takes its values in X, X being $\mathbf{R}^n$ or an infinite dimensional Banach space, L is a bounded linear operator from the space $\mathcal{C}([-r, 0], X)$, $(r > 0)$, into X. In finite dimensions, L is just a vector valued Radon measure and can be represented (in the canonical basis) as the measure associated with a matrix valued function with bounded variations

$$L(\varphi) = \int_{-r}^{0} d\eta(\theta)\varphi(\theta).$$

Let us define

$$\Delta(s) := sId - L(\exp(s\cdot)). \tag{8}$$

As in the example, the Laplace transform inverse of $\Delta(s)$ determines a matrix valued function $\mathcal{R}(t)$, defined for $t \geq 0$, which is the *fundamental solution* of the equation, from which it is possible to calculate solutions in terms of the initial value or the inhomogeneous forcing. When there is a risk of confusion we will use the notation $\mathcal{R}_L$ for the fundamental solution associated with the operator L.

2.2.4. *Semigroup theory.* A delay differential equation may be regarded in two ways: it describes the temporal variations of some numerical indicators of a real system, at a given time t, but the variations are determined in terms of past values of these indicators. One can focus on the values at each given time and treat the past values as a forcing term or a parameter function, it is the way it is done when using the Laplace transform method. Or, one may prefer to work in a phase space context, and consider the solution operator as a shift along the initial values. This view is more suited to the study of dynamical features of the equation. The phase space in this case is $\mathcal{C}([-r, 0], X)$, where X may be a general Banach space or just $\mathbf{R}^n$. This view is in the line of ordinary differential equations or evolution equations associated with PDE's. For ODE's, the shift $T(t)$ expresses itself as $\exp(tA)$ where A is the linear map defining the equation

$$x'(t) = Ax(t).$$

For evolution equations, the operator is most of the time an unbounded operator defined on part of the phase space and $T(t)$ although being tightly related to A is not expressible as an exponential. There are several advantages in taking the view of a generalized ODE: the reduction of the equations to invariant subspaces determined solely in terms of the operator A, the description of spectral properties of $T(t)$ in terms of those of A, valid when the semigroup has some additional properties, for example, if it is a compact operator or an eventually compact operator. For instance, if $X = \mathbf{R}^n$, the following property can be shown (see [28]):

PROPOSITION 1. *The semigroup $\{T(t)\}_{t\geq 0}$ associated with equation* (6) *is compact for $t \geq r$.*

The operator A, which is called the *infinitesimal generator* of the semigroup, is calculated from $T(t)$ by the formula:

$$A\varphi := \lim_{h\to 0_+} \frac{T(t)\varphi - \varphi}{t} \quad \text{(convergence in } X\text{)}$$

and the domain of A, $D(A)$, is the set of $\varphi \in X$ for which the limit exists.

For equation (6) the following characterization of the operator A can be shown:

$$A\varphi = \varphi',$$

$$D(A) = \{\varphi \in \mathcal{C}([-r,0],X);\ \varphi' \in \mathcal{C}([-r,0],X) \text{ and } \varphi'(0) = L(\varphi)\}.$$

In order to determine the spectrum of A, it is first advisable to compute the resolvent operator, that is to say, the operator

$$R(\lambda, A) := (\lambda I - A)^{-1}$$

obtained by solving for each $f \in \mathcal{C}([-r,0],X)$ given, the equation

$$\lambda\varphi - A\varphi = f.$$

This equation leads readily to the following expression:

$$\varphi(\theta) = \exp(\lambda\theta)\varphi(0) + \int_\theta^0 \exp\lambda(\theta - s) f(s)\,ds \tag{9}$$

to be completed by the condition $\varphi'(0) = L(\varphi)$ which leads to

$$\Delta(\lambda)\varphi(0) = f(0) + L\Big(\int_\cdot^0 \exp\lambda(\cdot - s) f(s)\,ds\Big) \tag{10}$$

where $\Delta(\lambda)$ is given by formula (8). It is easily seen that the right hand side of equation (10) has X for its range, both in finite and infinite dimensions. So, in order for equation (9) to have a solution for each f, it is necessary and sufficient that $\Delta(\lambda)$ be invertible.

We refer the reader to [28] for a wide development of this theory and to [6] and [7] for the infinite dimensional case.

In the following we restrict ourselves to the finite dimensional case. In this case, $[\Delta(\lambda)]^{-1}$ exists if and only if $\det\Delta(\lambda) \neq 0$. We will use the notation $p(\lambda)$ or $p_L(\lambda)$ for the characteristic equation of the delay equation, namely,

$$p(\lambda) := \det\Delta(\lambda) = 0. \tag{11}$$

Lemma 2. *Each root of $p(\lambda)$ has a finite multiplicity. The location of the roots is as follows: only a finite number of roots can be found on any right half-plane of the complex plane; only a finite number of roots can be found in any vertical band, with finite width, of the complex plane.*

Lemma 3. *Let λ be such that $p(\lambda) = 0$. Denote $m(\lambda)$ the multiplicity of λ as a root of p, and let $N(\lambda)$ be a vector subspace of $\mathcal{C}([-r,0],X)$, maximal (with respect to the inclusion) within the spaces invariant under A on which the operator $\lambda I - A$ is nilpotent. Then $N(\lambda)$ is unique and has dimension equal to $m(\lambda)$.*

Let us consider the following nonlinear delay differential equation

$$x'(t) = L(x_t) + f(x_t) \tag{12}$$

where L is linear and f is a nonlinear perturbation of L near 0, that is,

$$f(\varphi) = o(\varphi).$$

For our next purpose, it is sufficient that f be $\mathcal{C}^1$ and such that $f(0) = 0$ and $Df(0) = 0$. Equation (12) can be seen as an inhomogeneous equation of the type of equation (7) with $f(t) = f(x_t)$, thus, it is possible to write it in integral form, using the variation of constants formula for the linear part (5):

$$x_t = T(t)\varphi + \int_0^t T(t-s)X_0 f(x_s)\, ds.$$

Using the above formula, one can show that the nonlinear perturbation inherits the stability and instability properties of the linear equation, more precisely:

Proposition 4. *Consider equation* (12)*, with $f \in \mathcal{C}^1$ near* 0 *and such that $f(0) = 0$ and $Df(0) = 0$. Assume that* 0 *is a hyperbolic equilibrium of equation* (6)*, that is, the characteristic equation* (11) *has no root with zero real part. Then, both the linear and the nonlinear equations behave the same near* 0*, that is, they are both stable or unstable. Moreover, the stable (resp. unstable) manifold associated with the nonlinear equation is, near* 0*, homeomorphic to the corresponding linear manifold and tangent to it at* 0*.*

The treatment of the critical case, that is, when there is an imaginary root or 0 is a root, leads to bifurcation theory. For most of our purposes, the above result will be sufficient: it tells us that the study of stability of an equilibrium of a nonlinear delay differential equation reduces to the study of the characteristic equation associated with the linearization of the equation near that equilibrium.

3. Instability and oscillations induced by delays: local analysis using the characteristic equation. The intuition is that delays induce oscillations which drive the system to instability from which stability can only be regained near periodic orbits or more complicated invariant subsets. Although the intuition is right in a number of cases, for example for the logistic equation, it fails in many cases where increasing the delay may lead to a succession of unstable then stable situations. We briefly discuss examples illustrating the right and wrong intuition, before we present a theory elaborated in the beginning of the eighties by W. Gurney and R. Nisbet in which some distinctive features of oscillations are related to biological properties of the modeled population.

3.1. *Introductory examples*

3.1.1. *A first order equation with delay.* Consider the first order delayed differential equation

$$x'(t) = ax(t) + bx(t-\tau). \tag{13}$$

The characteristic equation of (13) is

$$\lambda - a - b\exp(-\lambda\tau) = 0.$$

in which we may eliminate one parameter, say τ, introducing $z := \lambda\tau$, $p := a\tau$, $q := b\tau$ and then,

$$pe^z + q - ze^z = 0. \tag{14}$$

THEOREM 5 (see [29]). *A necessary and sufficient condition for all the roots of equation* (14) *to have a negative real part is that*

1. $p < 1$ *and*
2. $p < -q < (\theta^2 + p^2)^{1/2}$, *where, for* $p \neq 0$, θ *is the only root of the equation*

$$\theta = p \tan\theta, \qquad 0 < \theta < \pi$$

or $\theta = \pi/2$ *for* $p = 0$.

A general consequence of Theorem 5 is that if equation (13) is stable for $\tau = 0$, then either it is stable for all $\tau \geq 0$, or there exists a value τ^* such that the equation is stable for $\tau < \tau^*$ and unstable for all $\tau > \tau^*$. In this situation, stability, once lost, cannot be recovered.

3.1.2. *The case of a second order equation with delay.* Consider the second order delayed differential equation

$$x''(t) + ax'(t) + bx(t) + cx(t - \tau) = 0 \tag{15}$$

whose characteristic equation is

$$p(\lambda) := \lambda^2 + a\lambda + b + ce^{-\tau\lambda} = 0. \tag{16}$$

In order to determine stability changes, one looks for imaginary roots and the sign of the derivative of the real part. We restrict the study to the case when the three parameters a, b and c are positive. If in addition we assume $b \leq c$, then there is a threshold value for τ beyond which the equation is unstable.

If, on the other hand, $b > c$, then one may have stability switches, that is to say, when τ is increased, one crosses intervals of values for which the equation is stable followed by intervals where it is unstable, then again stability, etc. Let us look at the situation more precisely. The equation for imaginary roots reads, substituting $i\omega$, $\omega \in \mathbf{R}$, for λ,

$$\begin{cases} \cos\tau\omega = \dfrac{\omega^2 - b}{c}, \\[2ex] \sin\tau\omega = \dfrac{aw}{c}, \end{cases} \tag{17}$$

which implies

$$\omega^4 + (a^2 - 2b)\omega^2 + (b^2 - c^2) = 0. \tag{18}$$

Equation (18) characterizes the possibility for the instability index of equation (15), that is, the number equal to the sum of multiplicities of the roots of equation (16) with a positive real part to increase when the delay increases. Equation (18) has 0, 1 or 2 real roots.

We examine the three cases:

• **Zero root.** This case corresponds to

$$(a^2 - 2b)^2 - 4(b^2 - c^2) < 0$$

which, after straightforward algebra, reduces to

$$4c^2 < a^2(4b - a^2).$$

In this case, the instability index is the same for non-negative τ. As a consequence, if the equation is stable for $\tau = 0$, it remains stable for all $\tau > 0$.

• **One root.** This case corresponds to

$$b^2 - c^2 < 0.$$

The equation

$$X^2 + (a^2 - 2b)X + (b^2 - c^2) = 0$$

has two real roots, one positive, the other negative. The positive root is

$$X = \frac{1}{2}[-(a^2 - 2b) + \sqrt{(a^2 - 2b)^2 - 4(b^2 - c^2)}]$$

which yields

$$\omega = \sqrt{\frac{1}{2}[-(a^2 - 2b) + \sqrt{(a^2 - 2b)^2 - 4(b^2 - c^2)}]}. \tag{19}$$

Let us now compute τ for (17) to hold. One has $\sin \tau\omega > 0$, while $\cos \tau\omega > 0$, $= 0$ or < 0 according to whether

$$a^2 b < c^2, \quad a^2 b = c^2 \quad \text{or} \quad a^2 b > c^2.$$

Let us only consider the case $a^2 b < c^2$. It can be shown that there is one and only one value τ_0 such that $0 < \tau_0 \omega < \frac{\pi}{2}$, which satisfies the two equations (17):

$$\tau_0 = \frac{1}{\omega} \sin^{-1}\left(\frac{a\omega}{c}\right)$$

and there are infinitely many other solutions, τ_n, $n \geq 1$,

$$\tau_n = \tau_0 + \frac{2n\pi}{\omega}.$$

For each value τ_n, $i\omega$ is a simple root of equation (16). In fact, we have,

$$\frac{\partial p}{\partial \lambda} = 2\lambda + a - c\tau e^{-\tau\lambda}$$

so that

$$\mathrm{Im}\left(\frac{\partial p}{\partial \lambda}\right)_{\lambda = i\omega} = 2\omega + c\tau \sin \tau\omega = 2\omega + a\omega\tau > 0.$$

As a consequence, the root $i\omega$ can be extended, in a neighborhood of each τ_n, as a root of the equation for values of τ close to τ_n. The extension leads to the definition, for each n, of a function $\lambda = \lambda_n(\tau)$, smooth enough.

Let us determine the sign of $\mathrm{Re}\left(\frac{d\lambda_n(\tau)}{d\tau}\right)$ near $\tau = \tau_n$. Differentiating formula (16) we have

$$\frac{d\lambda}{d\tau} = \frac{c\lambda e^{-\lambda\tau}}{2\lambda + a - c\tau e^{-\lambda\tau}}.$$

At $\lambda = i\omega$, we obtain the following expression:

$$\frac{d\lambda}{d\tau} = \frac{c\omega \sin \omega\tau + ic\omega \cos \omega\tau}{(a - c\tau \cos \omega\tau) + i(2\omega + c\tau \sin \omega\tau)},$$

which leads to

$$\begin{aligned} \mathrm{sign}\left(\mathrm{Re}\, \frac{d\lambda}{d\tau}\right) &= \mathrm{sign}[(c\omega \sin \omega\tau)(a - c\tau \cos \omega\tau) + (c\omega \cos \omega\tau)(2\omega + c\tau \sin \omega\tau)] \\ &= \mathrm{sign}[a \sin \omega\tau + 2\omega \cos \omega\tau] = \mathrm{sign}[a^2 - 2b + 2\omega^2]. \end{aligned}$$

In view of (19), one deduces that

$$\operatorname{sign}\left(\operatorname{Re}\frac{d\lambda}{d\tau}\right)(\tau_n) > 0.$$

In conclusion, at each value τ_n, the instability index gains two units, due to two new branches of roots of the characteristic equation crossing the imaginary axis. So, increasing the delay increases the instability and one could also see that the oscillations associated with this instability are becoming more and more rapid.

• **Two roots.** Note that equation (18) has $\omega = 0$ as a root if $b^2 - c^2 = 0$ and it is indeed the only root if in addition we have $a^2 - 2b = 0$. However, equation (16) has 0 as a root only if $b + c = 0$, which is precluded here by the assumption $b > 0$ and $c > 0$. Conditions for the existence of two distinct roots of (18) > 0 are

$$a^2 - 2b < 0, \qquad b^2 - c^2 > 0 \quad \text{and} \quad (a^2 - 2b)^2 - 4(b^2 - c^2) > 0.$$

We assume these conditions hold. Then, one has two roots, ω_+ and ω_-,

$$\omega_\pm = \sqrt{\frac{1}{2}[-(a^2 - 2b) \pm \sqrt{(a^2 - 2b)^2 - 4(b^2 - c^2)}]}.$$

Assuming in addition $a^2 b - c^2 < 0$, one has $\omega_-^2 < b < \omega_+^2$ from which we obtain

$$\begin{cases} \cos\tau\omega_- < 0, \\ \sin\tau\omega_- > 0, \end{cases} \quad \text{and} \quad \begin{cases} \cos\tau\omega_+ > 0, \\ \sin\tau\omega_+ > 0. \end{cases}$$

To each root, a family of delays is associated, $\tau_{+,n}$, $\tau_{-,n}$, each of them being computed according to the same formula as previously seen:

$$\tau_{+,n} = \tau_{+,0} + \frac{2n\pi}{\omega_+}, \qquad 0 < \tau_{+,0} < \frac{\pi}{2}$$

and

$$\tau_{-,n} = \tau_{-,0} + \frac{2n\pi}{\omega_-}, \qquad \frac{\pi}{2} < \tau_{-,0} < \pi.$$

By construction, one has

$$\tau_{+,0} < \tau_{-,0}.$$

On the other hand, one can compute the sign of the real part of the root, as has been done previously,

$$\pm\operatorname{sign}\left(\operatorname{Re}\frac{d\lambda}{d\tau}\right)(\tau_{\pm,n}) > 0.$$

This implies that the instability index gains 2 at each $\tau_{+,n}$, and loses 2 at $\tau_{-,n}$. Moreover, $\dfrac{2\pi}{\omega_-} > \dfrac{2\pi}{\omega_+}$. Therefore, even if returns to stability are feasible, there are only a finite number of them, and the equation is eventually unstable.

3.2. *A population growth equation ([17]).* In this section we consider the equation

$$P'(t) + d(P(t))P(t) = \int_{-\infty}^{t} g(t-s)m(P(s))P(s)\,ds \tag{20}$$

which models the growth of a population, with $P(t)$ denoting the biomass at time t. The coefficient $d(P)$ is the *mortality rate* per unit of time and unit of population biomass,

$m(P)$ is the *maternity function*, equal to the mass of eggs produced per unit of time and unit of population biomass and g is a distribution density which we assume to be supported by the half-line $[0, +\infty[$, so that,

$$\int_0^{+\infty} g(s)ds = 1.$$

For each $s > 0$, $g(s) \geq 0$ is the density of probability for eggs produced at some moment of time to reach maturity at age s. In [17], J. Cushing considers a number of models of the distribution g. Specifically, he studies the following family of distributions,

$$g_n(s) = \frac{1}{n!} T^{-n-1} s^n \exp(-s/T), \qquad n = 0, 1, \dots \tag{21}$$

where T is a fixed parameter. For $n = 0$, it is the expectation of the Poisson law

$$g_0(s) = \frac{1}{T} \exp(-s/T).$$

For all n, the quantity

$$\int_0^{+\infty} s g_n(s)\, ds = (n+1)T := \tau_n$$

represents the average time from hatching to maturity, and it can also be interpreted as a delay to reproduction.

3.2.1. *Equilibrium points.* Apart from $P = 0$, equilibrium points are the solutions of the equation

$$d(P_0) = m(P_0).$$

A usual scheme is that the function $d(P)$ is increasing and $m(P)$ decreases, therefore a solution P_0 exists and is unique.

3.2.2. *Linearization near P_0.* To construct a linearized system near P_0, we express the solution in the form

$$P(t) = P_0 + y(t)$$

and we expand all the terms of equation (20) in powers of y. Retaining the first order terms in y and dropping the higher order terms, this leads to

$$y'(t) + [d(P_0) + P_0 d'(P_0)]y(t) = [m(P_0) + P_0 m'(P_0)] \int_{-\infty}^{t} g(t-s)y(s)\, ds. \tag{22}$$

Note that in order for the equation to make sense, it is necessary that the integral exists. It is also important to check that $\int_{-\infty}^{0} g(t-s)y(s)ds \to 0$ as t tends to $+\infty$: this is a *fading memory* effect. It holds for example with $g(s) = e^{-\alpha s}$ for some $\alpha > 0$, if the function y is just bounded on $]-\infty, 0]$.

Equation (22) can be written in the form

$$y'(t) + ay(t) = b \int_{-\infty}^{t} g(t-s)y(s)\, ds$$

where a, b are some constants.

Stability of zero as a solution of that equation is equivalent to that of the null solution of the Volterra equation

$$y'(t) + ay(t) = b\int_0^t g(t-s)y(s)\,ds.$$

If $\widehat{y}(z)$ (resp. $\widehat{g}(z)$), denotes the Laplace transform of y (resp. g), the transformed equation reads

$$(z + a - b\widehat{g}(z))\widehat{y}(z) = y(0).$$

Each solution is determined by its value at $t = 0$ and solutions are just multiples of one another. Let us assume for example that $y(0) = 1$, that is,

$$\widehat{y}(z) = \frac{1}{(z + a - b\widehat{g}(z))}.$$

Stability of equation (22) is entailed by the sign of the real part of the root with the greatest real part of the equation

$$z + a - b\widehat{g}(z) = 0. \tag{23}$$

Let us now restrict our attention to the family g_n defined by (21), starting with $n = 0$. In this case, we have

$$\widehat{g}_0(z) = \frac{1}{1 + zT}.$$

Substituting in equation (23), the following polynomial equation is obtained:

$$Tz^2 + (aT + 1)z + (a - b) = 0$$

where the expressions of the coefficients a and b in terms of the parameters of the original equation are:

$$a = d(P_0) + P_0 d'(P_0), \qquad b = m(P_0) + P_0 m'(P_0).$$

Under the assumptions $d'(P_0) > 0 > m'(P_0)$, one concludes that

$$a - b = P_0(d'(P_0) - m'(P_0)) > 0 \quad \text{and} \quad a > 0.$$

It implies that both the roots of the polynomial equation have a negative real part, that is to say, stability holds independent on the delay T.

We now turn to the case $n = 1$ in (21). This gives

$$\widehat{g}_1(z) = \frac{1}{(1 + zT)^2}.$$

Substituting in equation (23), we obtain the following polynomial equation:

$$T^2z^3 + (2T + aT^2)z^2 + (1 + 2aT)z + (a - b) = 0. \tag{24}$$

In the case when $a > b$, one can have either each of the three roots with a negative real part, or a negative real root and two roots with a positive real part. This time, stability depends on T.

Let us first look at the asymptotic situation, that is, when T approaches $+\infty$. We define $t = 1/T$ and divide by T^2 in (24) arriving at

$$z^3 + (2t + a)z^2 + (t^2 + 2at)z + (a - b)t^2 = 0.$$

We then perform the study in terms of t, starting from $t = 0$. For $t = 0$, the equation reduces to

$$z^3 + az^2 = 0$$

whose roots are: $z = -a$ and $z = 0$ (double). For $t > 0$ small enough, the root $z = -a$ extends to a real root close to $-a$, while the double root splits into two roots of the order t, $z = t\varsigma$. The equation in ς reads

$$t\varsigma^3 + (2t + a)\varsigma^2 + (t + 2a)\varsigma + (a - b) = 0.$$

For $t = 0$, the equation reduces to

$$a\varsigma^2 + 2a\varsigma + (a - b) = 0$$

which, if $a > b > 0$, has two real negative roots

$$\varsigma = -1 \pm \sqrt{\frac{b}{a}}$$

or two conjugate complex roots with real part equal to -1, if we have $b < 0$.

So, the equation is stable for T large enough. Let us study whether it can become unstable for lower values of T. If so, it can only be done by the onset of imaginary roots for some T. Therefore, we look for roots of equation (24) of the form $z = i\alpha$ with $\alpha > 0$, which leads to the following system of equations:

$$\begin{cases} -(2T + aT^2)\alpha^2 + (a - b) = 0, \\ \qquad -T^2\alpha^3 + (1 + 2aT)\alpha = 0, \end{cases}$$

from which we can compute a single value for α,

$$\alpha = \sqrt{\frac{a - b}{2T + aT^2}}$$

and the following formula relating a, b and T (eliminating α between the above two equations):

$$2a^2T^2 + (4a + b)T + 2 = 0. \tag{25}$$

If we assume $b < -8a$, then equation (25) has two positive roots T_1 and T_2, $T_1 < T_2$. Differentiating equation (24) with respect to T, at a root z, yields the following expression at $z = i\alpha$ and T_j, $j = 1, 2$,

$$\text{sign}\left(\text{Re}\,\frac{\partial z}{\partial T}\right) = (2 + 2aT_j)[(1 + 2aT_j) - 3T_j^2\alpha^2] + (2T_j\alpha^2 - 2a)2(2T_j + aT_j^2).$$

One can check that the sign is negative at T_1 and positive at T_2.

As a conclusion of this example, when the delay increases from the value 0, the equation is stable at first, then it loses stability at T_1 and remains unstable up to the value T_2. It then recovers stability again and remains so for all $T > T_2$. The same result holds for higher values of n, however with an increasing number of switches when n increases.

3.3. *Slow and fast oscillations induced in population dynamics.* In [27], W. Gurney and R. Nisbet introduce a variety of models of population dynamics, differing by the point in the life cycle where a limiting resource acts on the growth rate or simply by the way it acts. In [31], a classification of these models is proposed, according to the value of the period/delay ratio: some of the control mechanisms are connected to long cycle duration (with a period/delay ratio larger than 2), while the others correspond to short cycle, with a period falling inside the interval $[1, 2]$. We first briefly recall the models presented in [27]: the first two belong to the long cycle category, the last two to the short cycle. We illustrate in two examples the intuitive idea according to which the proposed classification can be interpreted by the nature of the feedback: long cycle would correspond to negative feedback, short cycle to positive feedback. Note that the classification is of local nature: it is expected to reflect the behavior in the vicinity of an equilibrium, and is established by inspection of the characteristic equation.

3.3.1. *Long cycle and short cycle models.* Let us consider models for insect populations with two stages: larva and adult. The delay is the duration of the larval stage which depends on the relationship between the total population and the environment.

In these models, the following variables are considered, either all of them, or, more frequently, some of them:

$$\begin{cases} \tau(t) = \text{duration of the larval stage for larvae becoming adults at time } t \\ L(t) = \text{total number of larvae at time } t \\ \Delta(t) = \text{mortality rate/larva/unit of time, at time } t \\ P(t) = \text{proportion of larvae born at } t-\tau(t) \text{ becoming adults at time } t \\ \alpha(t) = \text{probability of success of the maturation at time } t \\ R(t) = \text{recruitment rate in the adult stage at time } t \\ A(t) = \text{total number of adults at time } t \\ B(t) = \text{rate of production of viable eggs at time } t \\ \delta(t) = \text{adult mortality rate/adult/unit of time, at time } t \end{cases}$$

Some of these variables can be expressed in terms of the others, for example

$$\begin{cases} P(t) = \exp(-\int_{t-\tau(t)}^{t} \Delta(x)\,dx), \\ R(t) = B(t-\tau(t))(1-\tau'(t))P(t)\alpha(t). \end{cases} \tag{26}$$

The following four types of competition can be considered:

Model 1. Density dependence of the larval mortality rate. In this case, the larval mortality rate increases with the density of larvae $L(t)$ and tends to infinity as L tends to a threshold value. An example of such models can be:

$$\begin{cases} L'(t) = B(t) - B(t-\tau)P(t) - \Delta(t)L(t), \\ A'(t) = R(t) - \delta A(t), \\ P'(t) = P(t)[\Delta(t-\tau) - \Delta(t)], \end{cases} \tag{27}$$

where

$$\Delta(t) = \begin{cases} \dfrac{c_1 + L(t)}{c_2 - L(t)} & \text{if } L(t) < c_2, \\ +\infty & \text{otherwise,} \end{cases}$$

for some values of the positive constants c_1, c_2.

Model 2. Density dependence in the duration of the larval stage. Transition from larva to adult depends on a size threshold. Growth slowed down implies the maturation slowed down and then the survival from egg to adult decreases.

Let $W(t, t_0)$ be the individual weight at time t, of the larvae of the cohort born at t_0. Then:

$$W(t, t_0) = W_0 + \int_{t_0}^{t} g(x)\, dx$$

where $g(x)$ is the individual larval growth rate. It is a function of the total number of larvae at time t. Under the simplifying assumption of the ideal free distribution of food, larvae going to the adult stage at time t are those whose weight reaches a threshold value W^* at that time.

The birth date t_0 or, equivalently, the duration of the larval stage $\tau(t) = t - t_0$ is determined by solving the equation

$$W(t, t_0) = W^*.$$

The formula (26) for P shows that an increase in $\tau(t)$ results in a decrease in the larval survival.

Model 3. Metamorphosis at a fixed age with success depending on weight. The duration of the larval stage is a constant τ for all the individuals but the transition to adult stage depends on weight. The weight at metamorphosis is

$$W(t) = \int_{t-\tau}^{t} g(x)\, dx$$

where

$$g(t) = \begin{cases} \dfrac{g_m}{1 + L(t)/L_0} - \Gamma & \text{if } L(t) < L_0\left(\dfrac{g_m}{\Gamma} - 1\right), \\ 0 & \text{otherwise,} \end{cases}$$

and g_m, Γ, L_0 are positive constants.

In this model it is accepted that the rate of success of metamorphosis for the larvae aged τ at time t is given by

$$\alpha(t) = \begin{cases} \dfrac{W(t) - W_1}{K_W + W(t) - W_1} & \text{if } W(t) > W_1, \\ 0 & \text{otherwise.} \end{cases}$$

Furthermore, under the hypotheses:

$$\begin{cases} \Delta(t) = 0 & \text{(no larvae mortality)}, \\ \delta(t) = \delta & \text{(mortality of adults constant)}, \\ B(t) = eA(t), \end{cases}$$

we arrive at the following system of retarded differential equations:

$$\begin{cases} L'(t) = B(t) - B(t-\tau), \\ A'(t) = B(t-\tau)\alpha(t) - \delta A(t), \\ W'(t) = g(t) - g(t-\tau). \end{cases} \tag{28}$$

While in the preceding model, larvae reach maturity at a fixed weight, in this one, weight is distributed. We observe that this model does not give any information about the weight of adults and, in particular, the model does not establish any relationship between the weight of adults and the number of descendents or their initial weight. It would be logical to suppose the existence of such relationship in the form of $e = e(W(t))$ and this is the hypothesis we make in the following competition model.

Let us notice that in fact the system (28) is not equivalent to the model: indeed, the model assumes

$$L(t) = \int_{t-\tau}^{t} B(s)\,ds, \qquad W(t) = \int_{t-\tau}^{t} g(s)\,ds, \tag{29}$$

which is only one out of all the expressions (up to the addition of two arbitrary constants) obtained by integrating the first and third equations of system (28). This difference is essential in the study of steady-state solutions: there are an infinity of such solutions for the system (28), but only one non-trivial if the integral formulation (29) is considered.

Model 4. Density dependence on adult fertility. If the adults do not eat or the females get their protein needs from the food eaten during the larval stage, and if the transition into the adult stage is subject to an age threshold, then a slower larval growth will result in less fecund adults.

Supposing that $\tau(t) = \tau$ (constant), $\Delta(t) = 0$, $\delta(t) = \delta$ (constant), $\alpha(t) = 1$ and the following equation for the newborns:

$$B'(t) = qR(t)W(t) - \delta B(t)$$

in which $q > 0$ is a proportionality constant between the fecundity and the weight at metamorphosis, the model reads:

$$\begin{cases} L'(t) = B(t) - B(t-\tau), \\ A'(t) = B(t-\tau) - \delta A(t), \\ W'(t) = g(t) - g(t-\tau), \\ B'(t) = qB(t-\tau)W(t) - \delta B(t). \end{cases}$$

Models 1 and 2 are *short cycle* models, in which the period of oscillations is less than two times the maximum delay. Models 3 and 4 are *long cycle* models, with oscillations whose period exceeds two times the maximum delay. Roughly speaking, the first two classes of models would correspond to *positive feedback*, while the last two present some similarity with the delayed logistic equation, thus, corresponds to *negative feedback*.

Positive feedback. Let us for example consider system (27), assuming, to make it easier, that: $B(t) = eA(t)$, where e is a constant, and $\alpha(t) = 1$. The relationship between Δ and L may be given a more general expression than the one given in the example, namely,

$$\Delta = \Phi \circ L$$

where the function Φ is assumed to be increasing, and such that $\Phi(x) = +\infty$ for $x > \overline{L}$. From the equation satisfied by P we obtain

$$P(t) = \exp\Big(-\int_{t-\tau}^{t} \Delta(s)\,ds\Big).$$

Introducing the variables

$$a(t) = \exp\left(\int_0^t \Delta(s)\, ds\right) A(t), \qquad l(t) = \exp\left(\int_0^t \Delta(s)\, ds\right) L(t)$$

we arrive at the following system:

$$\begin{cases} a'(t) = (\Delta(t) - \delta)a(t) + ea(t-\tau), \\ l'(t) \ = e(a(t) - a(t-\tau)). \end{cases}$$

From the latter equation, we deduce

$$l(t) = e \int_{t-\tau}^{t} a(u)\, du.$$

Plugging the expression of Δ in terms of L in the equation for l, we have

$$l(t) = \exp\left(\int_0^t \Phi(L(s))\, ds\right) L(t)$$

from which one can extract L in terms of l

$$L = \Lambda(l).$$

(L may be obtained as a solution of the Volterra equation $L = l \exp(-\int_0^{\cdot} \Phi(L(s))\, ds)$. It is not difficult to see that the operator Λ is non-decreasing.) Combining this relationship and the expression of l in terms of a, we arrive at

$$L = \Lambda\left(e \int_{\cdot-\tau}^{\cdot} a(u)\, du\right).$$

Thus, the whole system may be reduced to a differential equation to be satisfied by the function a

$$a'(t) = \left(\Phi\left(\left[\Lambda(e\int_{\cdot-\tau}^{\cdot} a(u) du)\right](t)\right) - \delta\right) a(t) + ea(t-\tau).$$

Clearly, the right hand side of the above equation is non-decreasing with respect to a, which corresponds to positive feedback.

Negative feedback. We can find this type of feedback in system (28). Since $\alpha(t)$ is increasing in W, W can be expressed in terms of g through the integral formula (29),

$$g(t) = \min\left(\frac{g_m}{1 + L(t)/L_0} - \Gamma, 0\right)$$

which in turn allows us to express g in terms of L, and finally using the fact that $B = eA$, we obtain for A an equation of the form

$$A'(t) = eA(t-\tau)\mathcal{F}(A_t) - \delta A(t)$$

where $\mathcal{F}$ is a non-increasing operator. Under further assumptions, the map $\varphi \mapsto \varphi(-\tau)\mathcal{F}(\varphi)$ will also be non-increasing, so that the last equation is similar to a delayed logistic equation.

3.3.2. *Relationship between slow and fast oscillations and the characteristic equation.* We have just seen that the classes of delay differential systems considered by W. Gurney and R. Nisbet ([27]) can be divided into systems with positive feedback and systems with negative feedback. W. Gurney, R. Nisbet and coworkers ([31]) have shown that the feedback type can be associated with the ratio period/delay of the periodic oscillations arising in the vicinity of an unstable equilibrium. Their results are local, they are based on the study of the characteristic equation associated with the linearization of the equation near an equilibrium. Before going through these results, we give a brief historical perspective about the study of the comparison of the delay and the period. For scalar delay differential equations of logistic type, which were introduced in ecology by G. E. Hutchinson ([30]), J. A. Yorke ([44]) was the first to observe that a large class of such equations (with odd non-linearity) have periodic solutions of period 4 times the delay. On the other hand, in the case of positive feedback and delay differential equations of monotone type (non-decreasing in the sense of the usual order in the state space), it has been shown that periodic solutions are never stable and the period in this case is less than 2 times the delay. Indeed, for *slowly oscillating* periodic solutions typical of negative feedback, two times the delay seems to be a lower bound, while it is an upper bound for equations with positive feedback. Incidentally, it was also J. A. Yorke who observed that scalar delay differential equations with a single delay

$$x'(t) = f(x(t), x(t-\tau))$$

cannot have non-trivial periodic solutions of period 2τ, a result that was partially extended by S. N. Chow and J. Mallet-Paret ([14]). It is a little of a happy surprise to see that such a separation can be traced in the class of systems considered by W. Gurney and R. Nisbet, even though the results in this case are only local. A related result due to J. Mahaffy ([37]) for delay differential equations with a characteristic equation of the type

$$F(\lambda) - G(\lambda)e^{-\lambda\tau} = 0 \tag{30}$$

where $F(\lambda)$ and $G(\lambda)$ are some particular polynomials, shows that the period/delay ratio is greater than 2 when the values of parameters are taken in the boundary of stability.

In the sequel we present similar results in a more general setting than polynomials. The parameter values in the boundary of stability (i.e. the values of parameters in which the solutions become unstable) are characterized by purely imaginary roots in equation (30). Suppose that F, G satisfy for all $\omega \in \mathbf{R}$:

$$F(i\omega) = \overline{F(-i\omega)}, \qquad G(i\omega) = \overline{G(-i\omega)}$$

and let us denote

$$\begin{aligned} P(z) &:= \mathrm{Re}(F(z)), \qquad & Q(z) &:= \mathrm{Im}(F(z)),\\ A(z) &:= \mathrm{Re}(G(z)), \qquad & B(z) &:= \mathrm{Im}(G(z)). \end{aligned}$$

A root $i\omega$ with $\omega > 0$ of equation (30) should satisfy the system

$$\begin{cases} A(i\omega)\cos\omega\tau + B(i\omega)\sin\omega\tau = P(i\omega),\\ B(i\omega)\cos\omega\tau - A(i\omega)\sin\omega\tau = Q(i\omega), \end{cases} \tag{31}$$

from which we obtain

$$\cos\omega\tau = \frac{[X(\omega)]^2 - 1}{[X(\omega)]^2 + 1}, \qquad \sin\omega\tau = \frac{2X(\omega)}{[X(\omega)]^2 + 1} \tag{32}$$

where $X(\omega)$ is a rational function of A, B, P, Q.

If a root $i\omega$ ($\omega > 0$) of (31) exists, the following condition should be satisfied:

$$[A(i\omega)]^2 + [B(i\omega)]^2 = [P(i\omega)]^2 + [Q(i\omega)]^2. \tag{33}$$

In this case, there exists $\theta > 0$ such that the system (31) is satisfied with θ instead of $\omega\tau$. To obtain a root $i\omega$ of equation (30) it is enough to choose $\tau = \theta/\omega$.

A simple calculation shows that

$$\omega\tau = \begin{cases} 2m\pi - \alpha & \text{if } X(\omega) < 0, \\ 2(m-1)\pi + \alpha & \text{if } X(\omega) > 0, \end{cases}$$

where

$$\cos\alpha = \frac{[X(\omega)]^2 - 1}{[X(\omega)]^2 + 1}.$$

From this, we obtain the following relationship between the period T and the delay τ:

$$\frac{T}{\tau} = \begin{cases} \dfrac{1}{m - (\alpha/2\pi)} & \text{if } X(\omega) < 0, \\ \dfrac{1}{m - 1 + (\alpha/2\pi)} & \text{if } X(\omega) > 0. \end{cases}$$

This formula allows us to conclude that the appearance of new purely imaginary roots of equation (30) leads to a decreasing ratio T/τ.

We are now developing a model for larval competition presented in [31] which is an interesting example of a state-dependent delay differential equation. In this model, the authors find the ratio T/τ to lie in the interval $[1, 2]$, which corresponds to a *short cycle* model similar to model 2 we presented before.

Keeping the above notations, the model reads

$$\begin{cases} L'(t) = eA(t) - M(t) - \delta L(t), \\ A'(t) = M(t) - A(t), \end{cases} \tag{34}$$

where $M(t)$ is the rate of exit from the larval stage per unit of time. This rate is modeled in the following way:

$$M(t) = eA(t - \tau(t))e^{-\delta\tau(t)} \frac{g(t)}{g(t - \tau(t))}. \tag{35}$$

In this formula, $g(t)$ is the rate of larvae growth per unit of time. Let us suppose that this rate is inversely proportional to the density of larvae,

$$g(t) = \frac{1}{1 + L(t)}.$$

The growth is expressed in units of time, hence $g(t)$ can be understood as the progression rate in the larval stage per unit of time and per individual. This progression is fastest in absence of competition, i.e. if $L(t) = 0$. In this case, the duration of the larval stage, τ_m, is the same as the larva age at metamorphosis.

In the general case, the progression through the larval stage is slower than chronological time. For a larva which becomes adult at time t, if $\tau(t)$ is the duration of the larval stage,

$$\tau_m = \int_{t-\tau(t)}^{t} g(s)\, ds. \tag{36}$$

Differentiating this formula with respect to t we get

$$1-\tau'(t)=\frac{g(t)}{g(t-\tau(t))} \tag{37}$$

which is an ordinary differential equation for $\tau(t)$, supposing that the function $g(t)$ is known. Since $g(t)$ is a function of $L(t)$, the delay $\tau(t)$ depends in fact on the state variables.

Substituting the left side of (37) for the ratio $g(t)/g(t-\tau(t))$ in (35) yields

$$M(t)=eA(t-\tau(t))(1-\tau'(t))e^{-\delta\tau(t)}.$$

Omitting natural mortality, the density of larvae at instant t can be represented in terms of those who where produced by adults and who have not yet metamorphosized:

$$L(t)=\int_{t-\tau(t)}^{t} eA(s)\,ds.$$

Differentiating in this formula with respect to time, we obtain a state-dependent delayed differential equation.

If we take into account natural mortality of larvae, the formula is

$$L(t)=\int_{t-\tau(t)}^{t} eA(s)e^{-\delta(t-s)}\,ds \tag{38}$$

which gives the first equation of system (34) by differentiation with respect to t.

We focus our attention to the steady-state solutions of system (34). Setting in this system $L'(t)=A'(t)=0$, it is evident that $A=L=0$ is such a solution. In general, there is an additional one, under the assumption $\log e>\delta\tau_m$, which is

$$L^*=\frac{\tau^*}{\tau_m}-1,\qquad A^*=\frac{\delta}{e-1}L^*,\qquad \tau^*=\frac{\log e}{\delta}.$$

The linearized equation about this point is obtained by writing the variational equations and keeping only the first order terms:

$$L(t)=L^*+u(t),\qquad A(t)=A^*+v(t),\qquad \tau(t)=\tau^*+w(t).$$

We calculate, for example, the first order variation of the expression $g(t)/g(t-\tau(t))$ which appears in the calculations for M and $\tau'(t)$. Since

$$\frac{g(t)}{g(t-\tau(t))}=\frac{1+L(t-\tau(t))}{1+L(t)}$$

we have, bearing in mind that $\Delta[L(t)]=u(t)$, $\Delta[L(t-\tau(t))]=u(t-\tau(t))$,

$$\Delta\left(\frac{g(t)}{g(t-\tau(t))}\right)=\frac{(1+L^*)\Delta[L(t-\tau(t))]-(1+L^*)\Delta[L(t)]}{(1+L^*)^2}=\frac{u(t-\tau^*)-u(t)}{1+L^*}.$$

Hence, the variational equation for M is

$$\begin{aligned}\Delta M(t)&=e\Delta[A(t-\tau(t))e^{-\delta\tau(t)}]+eA^*e^{-\delta\tau^*}\Delta\left[\frac{g(t)}{g(t-\tau(t))}\right]\\ &= e[v(t-\tau^*)e^{-\delta\tau^*}-A^*\delta e^{-\delta\tau^*}w(t)]+eA^*e^{-\delta\tau^*}\left[\frac{u(t-\tau^*)-u(t)}{1+L^*}\right].\end{aligned}$$

Therefore, the linearized system of (34) about the non-trivial steady-state is

$$\text{(39)}\qquad \begin{cases} u'(t) = ev(t) - \delta u(t) - e[v(t-\tau^*)e^{-\delta\tau^*} - A^*\delta e^{-\delta\tau^*}w(t)] \\ \qquad\qquad -eA^*e^{-\delta\tau^*}\left[\dfrac{u(t-\tau^*)-u(t)}{1+L^*}\right], \\ v'(t) = \ -v(t) + e[v(t-\tau^*)e^{-\delta\tau^*} - A^*\delta e^{-\delta\tau^*}w(t)] \\ \qquad\qquad +eA^*e^{-\delta\tau^*}\left[\dfrac{u(t-\tau^*)-u(t)}{1+L^*}\right], \\ w'(t) = \dfrac{u(t)-u(t-\tau^*)}{1+L^*}. \end{cases}$$

The characteristic equation for (39) is derived by looking for a non-trivial solution of the form

$$u(t) = e^{\lambda t}U, \qquad v(t) = e^{\lambda t}V, \qquad w(t) = e^{\lambda t}W$$

which leads to

$$\det \begin{bmatrix} \lambda + \delta + (A^*/(1+L^*))(e^{-\lambda\tau^*}-1) & e^{-\lambda\tau^*} - e & -\delta A^* \\ -(A^*/(1+L^*))(e^{-\lambda\tau^*}-1) & 1+\lambda - e^{-\lambda\tau^*} & \delta A^* \\ (1/(1+L^*))(e^{-\lambda\tau^*}-1) & 0 & \lambda \end{bmatrix} = 0,$$

that is,

$$(\lambda+\delta)\left[\lambda(1-e^{-\lambda\tau^*}+\lambda) - \frac{A^*}{1+L^*}(1-e+\lambda)(1-e^{-\lambda\tau^*})\right] = 0.$$

This equation has the root $\lambda = 0$, which is not an eigenvalue for the integral formulation (38). Putting aside the root $\lambda = -\delta$, the equation can be written as

$$\text{(40)}\qquad F(\lambda) - G(\lambda)e^{-\lambda\tau^*} = 0$$

with

$$\begin{cases} F(\lambda) = \ \lambda^2 + \left[1 - \dfrac{\tau^*-\tau_m}{\tau^{*2}} \times \dfrac{\log e}{e-1}\right]\lambda + \dfrac{(\tau^*-\tau_m)\log e}{\tau^{*2}}, \\ G(\lambda) = \left[1 - \dfrac{\tau^*-\tau_m}{\tau^{*2}} \times \dfrac{\log e}{e-1}\right]\lambda + \dfrac{(\tau^*-\tau_m)\log e}{\tau^{*2}}. \end{cases}$$

Remark 1. Since $F(0) = G(0)$, $\lambda = 0$ is a root of the characteristic equation and $F'(0) = G'(0)$, $\tau^* G'(0) \neq 0$ in the general case, 0 is a simple root. Nevertheless, $\lambda = 0$ is not an eigenvalue for the model formulated in its integral form (38). Let us notice that the linearization (39) has been calculated for the differential system.

The linearization of the integral equation (38) gives

$$u(t) = eA^*e^{-\delta\tau^*}w(t) + e\int_{t-\tau^*}^{t} v(s)e^{-\delta(t-s)}\,ds$$

where

$$\text{(41)}\qquad w(t) = \frac{1}{1+L^*}\int_{t-\tau^*}^{t} u(s)\,ds$$

is the linearization of equation (36). A simple calculation shows that the eigenvectors associated to $\lambda = 0$ in system (39) satisfy

$$U = \frac{e-1}{\delta}V, \qquad W = 0.$$

Substituting these values in (41) we obtain

$$W = \frac{1}{1+L^*}\tau^* U$$

which implies $U = 0$ and then $V = 0$. Therefore, $\lambda = 0$ cannot be an eigenvalue except in the case $e = 1$.

A feature added by the state-dependent delay to the characteristic equation is the following: the coefficients of F and G depend on the delay τ^*. This is in sharp contrast with the ordinary delay case in which τ^* appears only in the exponent.

With the aim to study the existence of purely imaginary roots $\lambda = i\omega$ of equation (40), we proceed as in (30), decomposing functions F and G into real and imaginary parts. We obtain the system (31) and equation (33), but in all these equations the corresponding functions A, B, P, Q and X depend on the parameters τ^* and τ_m.

Let us notice that as τ^* approaches infinity, F and G tend to the functions

$$F_\infty(\lambda) = \lambda^2 + \lambda, \qquad G_\infty(\lambda) = \lambda$$

which are independent of the parameters and the same is true for the corresponding limit functions A_∞, B_∞, P_∞, Q_∞ and X_∞. Then we can assure the existence of a solution $\omega = \omega_\infty \geq 0$ of (40).

By a standard application of the implicit function theorem, we can determine a branch of solutions of (40) $\omega = \omega(\tau^*)$ defined for τ^* big enough, with ω_∞ as a limit as τ^* approaches infinity. Going back to the equations (32), we observe that the point $(\cos(\tau^*\omega(\tau^*)), \sin(\tau^*\omega(\tau^*)))$ goes around infinitely many times the unit circumference as τ^* tends to infinity, while $X(\omega(\tau^*))$ tends to a constant, $X(\omega_\infty)$, so that the point defined by the right member of (32) goes around the unit circumference at most a finite number of times. Applying an *intermediate value theorem* type of argument, we can assure the existence of infinitely many purely imaginary roots of the characteristic equation (40).

In our model,

$$P_\infty(i\omega) = -\omega^2, \qquad Q_\infty(i\omega) = \omega, \qquad A_\infty(i\omega) = 0, \qquad B_\infty(i\omega) = \omega$$

and equation (33) is $\omega^4 + \omega^2 = \omega^2$, which leads to the solution $\omega_\infty = 0$.

3.3.3. *Study of the period/delay ratio.* Bearing in mind that $T/\tau = 2\pi/(\omega\tau)$, we can estimate an asymptotic expression for the ratio near $\tau^* = +\infty$. To this end, we introduce $s := 1/\tau^*$ and define

$$a(s) := 1 - (s - s^2\tau_m)\frac{\log e}{e-1}, \qquad b(s) := (s - s^2\tau_m)\log e.$$

Then

$$\begin{aligned} A(i\omega, s) &= b(s), \qquad & B(i\omega, s) &= \omega a(s), \\ P(i\omega, s) &= -\omega^2 + b(s), \qquad & Q(i\omega, s) &= \omega a(s). \end{aligned}$$

Equation (33) can be written as

$$b^2(s) + \omega^2 a^2(s) = \omega^4 + \omega^2[a^2(s) - 2b(s)] + b^2(s) \ \Rightarrow\ \omega^2[\omega^2 - 2b(s)] = 0$$

which should be coupled with the formulae

$$\cos\omega\tau^* = \frac{b^2(s) + \omega^2[a^2(s) - b^2(s)]}{\omega^2 a^2(s) + b^2(s)}, \qquad \sin\omega\tau^* = \frac{-\omega^3 a(s)}{\omega^2 a^2(s) + b^2(s)}.$$

Putting $\omega^2 = 2b(s)$ in these expressions we have:

$$\begin{cases} \cos\omega\tau^* = \dfrac{b(s) + 2[a^2(s) - b^2(s)]}{2a^2(s) + b(s)} := \gamma(s), \\ \sin\omega\tau^* = \dfrac{-2\sqrt{2b(s)}a(s)}{2a^2(s) + b(s)} := \sigma(s), \end{cases} \tag{42}$$

where

$$\lim_{s\to 0}\gamma(s) = 1, \qquad \lim_{s\to 0}\sigma(s) = 0, \qquad \sigma(s) < 0.$$

On the other hand,

$$\omega\tau^* = \frac{\sqrt{2b(s)}}{s} \sim \frac{\sqrt{2\log e}}{\sqrt{s}} \ (s \to 0).$$

Therefore, the system (42) has infinitely many solutions which determine a sequence $\{s_n\}$ going to zero and such that

$$\frac{1}{\sqrt{s_{n+1}}} - \frac{1}{\sqrt{s_n}} \sim \frac{2\pi}{\sqrt{2\log e}} \ (n \to \infty).$$

To each solution corresponds a pair of values τ_n^*, ω_n,

$$\tau_n^* = \frac{1}{s_n}, \qquad \omega_n = \sqrt{2b(1/\tau_n{}^*)}, \qquad \omega_n\tau_n^* \in \left(\frac{3\pi}{2}, 2\pi\right) \pmod{2\pi}.$$

The largest value of the ratio T/τ is $4/3$, which is actually achieved.

We then conclude that the model has only *short cycle* oscillations.

4. State-dependent delay differential equations. State-dependent delay differential equations have already appeared in the previous section. We have seen that, in the scenarios considered by W. Gurney and R. Nisbet, the time to maturity or the weight at maturity are often expressed as a function of the population or part of the population. We will return to this later on when discussing some specific models of stage-structured population. Here we want to provide a quick review of what has been done in terms of mathematical issues. As far as we know, one of the earliest studies of a state-dependent delay equation was undertaken in the sixties by K. Cooke ([15]) who considered an equation of the type

$$x'(t) = -ax(t - r|x(t)|)$$

in which the delay at time t is

$$\tau(t) = r|x(t)|.$$

Clearly, it is a function of the solution. K. Cooke was interested in proving an asymptotic result, for solutions going to zero at infinity. In this case, the delay is also going to zero, and the equation is asymptotically close to

$$y'(t) = -ay(t).$$

So, the question was: can we compare the solutions of both equations? that is, can we recover asymptotically the same result for the state-dependent equation as for its limit equation, namely that solutions approach zero as a multiple of $\exp(-at)$? This is indeed one of the results obtained by K. Cooke in his work. In the mid-seventies, R. Nussbaum ([41]) considered a logistic like state-dependent delay equation of the type

$$x'(t) = -f(x(t - r(x(t))) \tag{43}$$

in which the delay is a function $r(x)$, and showed, as a consequence of a general index theory, the existence of slowly oscillating periodic solutions to the above equation. At the end of the seventies and beginning of the eighties, W. Alt ([3]) considered a broad class of such equations, including the equation that had been studied by R. Nussbaum, and proved a result of existence of slowly oscillating periodic solutions. One of the successful efforts made by W. Alt was to give a sort of direct proof of the result, avoiding the recurse to the somewhat involved treatment presented by R. Nussbaum. From the theoretical viewpoint, no significant achievement seems to have been done during the eighties, and in some sense the subject fell into *dormancy* as far as the theory is concerned. Next, we will discuss the progress in the modeling. To end with the theory, the subject regained interest by the beginning of the nineties. In 1993, two concurrent papers appeared: one by Y. Kuang and H. L. Smith ([34]), the other by J. Mallet-Paret and R. Nussbaum ([39]). The paper by J. Mallet-Paret and R. Nussbaum introduces a functional analysis framework for the treatment of such equations and proves the existence of periodic slowly oscillating solutions for an equation which again is very close to the logistic delay. On the other hand, it seems that Y. Kuang and H. L. Smith had been the first to notice a crucial property, also essentially valid in the case of state-dependent logistic-like equations, namely that if $x(t)$ is a solution of equation (43), then for each point t_0 where $x'(t_0) = 0$, we have

$$\forall t \geq t_0, \qquad t - r(x(t)) \geq t_0 - r(x(t_0))$$

and

$$\forall t < t_0, \qquad t - r(x(t)) < t_0 - r(x(t_0)).$$

So, this means that the past to be considered to solve the equation from t_0 onwards does not go earlier than $t_0 - r(x(t_0))$. If we take the view of $r(x)$ being the duration of the juvenile stage of an individual and $t - r(x(t))$ is the birth date of individuals becoming mature at time t, we can say that there is no overlap of generations between those born before t_0 and those born after t_0. This property allowed the authors to derive the existence of slowly oscillating periodic solutions using a straight extension of the method previously used for the delay logistic equation. Concerning periodic solutions of equations with state-dependent delay, the paper [40] should be cited. More recently, O. Arino, K. P. Hadeler and M. L. Hbid ([4]), then P. Magal and O. Arino ([36]) have proved existence of slowly oscillating periodic solutions for a class of equations completely different from the one studied by the above-mentioned authors.

We will now briefly discuss modeling issues. Models involving state-dependent delays can be found in various contexts: in economy ([10]), in [25] a structured model of blood cell production is considered by A. Grabosch and H.J.A.M. Heijmans. The model is initially a system of PDE of the first order, which, by solving along the characteristic lines, is turned into a state-dependent delay. Closely related to it is a model derived recently by J. Mahaffy, J. Bélair and M. Mackey ([38]). The model is a system of equations

$$\begin{cases} M'(t) = \exp(\beta\mu_1)S_0(E(t-T)) - \gamma M(t) - Q, \\ E'(t) = f(M(t)) - kE(t), \\ v_F'(t) = 1 - \dfrac{Q\exp(-\beta\mu_1 + v_F(t))}{S_0(E(t-T-v_F(t))}. \end{cases}$$

Note that in that model, the state-dependence is not on the delay, which is constant, but on the coefficients of the ordinary differential equation satisfied by v_F.

An important class of state-dependent delays corresponds to threshold models, in which a change of stage is subject to a functional of the state reaching a prescribed level. Here is a simple example of such a threshold model ([5]).

4.1. *Population divided into two stages with stage change subject to reaching a threshold size.* Consider a population divided into two stages, the juveniles and the adults, each one being structured by the age in the stage. Denote by $j(a,t)$ (resp. $m(a,t)$) the density (in biomass per unit of age) of juveniles (resp. adults) of age a. μ_j (resp. μ_m) is the mortality rate of juveniles (resp. adults). We have the following equations:

$$\begin{cases} \dfrac{\partial j}{\partial a} + \dfrac{\partial j}{\partial t} = -\mu_j(a)j(a,t), \\ \dfrac{\partial m}{\partial a} + \dfrac{\partial m}{\partial t} = -\mu_m(a)m(a,t). \end{cases} \tag{44}$$

We point out the fact that the variable a represents the age of the juveniles in the function $j(a,t)$ while it is the age of the adults in the function $m(a,t)$. The above two equations have to be supplemented by boundary conditions and initial values. For the juvenile, we have

$$j(0,t) = B(t), \qquad j(a,0) = 0$$

where $B(t)$ represents the time density of newborns, and the condition $j(a,0) = 0$ expresses the fact that no juvenile is supposed to exist at the time $t = 0$ (or, no one is able to survive beyond a certain time period). We define $J(t)$ to be the biomass of juveniles at time t,

$$J(t) = \int_0^T j(a,t)\,da,$$

T being the maximum age of juveniles at time t. The passage from the juvenile to the adult stage is described in terms of the weight function of the juvenile, namely, we assume that

$$\frac{\partial w}{\partial a} + \frac{\partial w}{\partial t} = \frac{K}{J(t)+C}$$

where $w(a,t)$ is the quantity of food eaten until time t by an individual entered in the juvenile stage a time units ago. Assuming that $w(0,t) = 0$ and $w(a,0) = 0$ (which corresponds to the absence of juveniles at time $t = 0$), we arrive at

$$w(a,t) = \int_{t-a}^{t} \frac{K}{J(s)+C}\,ds.$$

We now introduce a threshold condition: we assume that juveniles turn adult when the food index reaches a prescribed value w^*, that is, at each time t,

$$w(a,t) = w^*.$$

We define $a(t)$ to be the root of the above equation: it is unique if it exists, that is, for t large enough. Assuming t chosen so that $a(t)$ is defined, we have $a(t) = T$, and so

$$J(t) = \int_0^{a(t)} j(a,t)\, da.$$

Solving the equation in j from system (44), along the characteristic lines starting from $a = 0$, we obtain

$$j(a,t) = \exp\Big(-\int_0^a \mu_j(s)\, ds\Big) B(t-a).$$

Assuming for simplicity that $B(t) = kJ(t)$, we arrive at

$$J(t) = k\int_0^{a(t)} \exp\Big(-\int_0^a \mu_j(s)\, ds\Big) J(t-a)\, da.$$

Assume, again for simplicity, that $\mu_j = 0$. Then the above equation reduces to

$$J(t) = k\int_{t-a(t)}^{t} J(s)\, ds$$

which, by differentiation, gives

$$J'(t) = k[J(t) - J(t-a(t))(1-a'(t))].$$

On the other hand, differentiating the identity

$$w^* = \int_{t-a(t)}^{t} \frac{K}{J(s)+C} ds$$

we obtain

$$a'(t) = \frac{J(t-a(t)) - J(t)}{J(t)+C}. \tag{45}$$

Substituting $\dfrac{J(t-a(t))+C}{J(t)+C}$ for $(1-a'(t))$ in the expression of J', it yields

$$J'(t) = k\left[J(t) - J(t-a(t))\frac{J(t-a(t))+C}{J(t)+C}\right], \tag{46}$$

that is, a delay differential equation with the delay $a(t)$ being a solution of an ordinary differential equation whose coefficients are functions of J.

As a conclusion to this example, we have obtained a state-dependent delay differential equation, rather a system (45)-(46), starting from an equation without delay: obviously, the delay arises from the threshold condition.

4.2. *Modeling of state-dependent delays: example of a wrong model.* In this section we consider a stage-structured population model of single-species growth, where the individuals of the population have a life history that takes them through two stages, immature and mature.

The first version of this model, incorporating a constant delay, was presented by W. Aiello and H. Freedman in [1]. In an attempt to obtain a more realistic biological model, W. Aiello, H. Freedman and J. Wu ([2]), introduced a state-dependent delay in the model. We are going to present both models and we will discuss the validity of the latter one: we will show that this model misses several important issues, both at the level of its application and at the level of its mathematical properties. Then we will introduce a new model which, we believe, is more realistic. The revised model was described for the first time in a paper by A. Fathallah and O. Arino ([22]).

4.2.1. *The early model: a system of ordinary delay differential equations.* Let $x_i(t)$, $x_m(t)$ be the number of immature and mature individuals in the population, respectively, at time t. Supposing that the population being studied is in a closed homogeneous environment and that the time that passes from birth to maturity for an individual is a known constant value $\tau > 0$, the model proposed in [1] is, for $t \geq 0$:

$$\left\{ \begin{array}{l} x_i'(t) = \alpha x_m(t) - \gamma x_i(t) - \alpha e^{-\gamma\tau} x_m(t-\tau), \\ x_m'(t) = \alpha e^{-\gamma\tau} x_m(t-\tau) - \beta x_m^2(t), \end{array} \right. \tag{47}$$

with $x_i(t) = \varphi(t)$ for $t \in [-\tau, 0]$, $x_m(0) = x_m^0$ and α, β, γ positive constants.

From a mathematical analysis, W. Aiello and H. Freedman reach in [1] the following conclusions:

1. *There exists a unique equilibrium $E^* = (x_i^*, x_m^*)$ with $x_i^* > 0$, $x_m^* > 0$, which is globally asymptotically stable.*
2. *Let us consider this equilibrium as a function of τ, $E^*(\tau)$, and define the total carrying capacity as $K(\tau) := x_i^*(\tau) + x_m^*(\tau)$.*
   If the birth rate α is greater than the death rate γ of immature, which is a meaningful biological hypothesis, then there exists an optimal delay $\tau^* > 0$ which maximizes $K(\tau)$. This can be understood as an evolutionary strategy, consistent in changing maturation time to maximize the total population in a given environment.

But a constant delay term τ means that at any time t the time from birth to maturity for any new member will not be influenced by any changes in the population size, and then the over-crowding effects will not lead to any sort of destabilization of the equilibria.

4.2.2. *A first model: a simple state-dependent delay equation.* As a supposedly more accurate biological representation, W. Aiello, H. Freedman and J. Wu ([2]) modified (47) by considering, instead of a fixed delay τ, a time to maturity which is a state-dependent delay as a function of the total population

$$z(t) = x_i(t) + x_m(t),$$

that is, in (47), τ is taken in the form $\tau(z(t))$.

Two objections may be raised to the choice of such a delay: the first one is to the delay term itself, which implies that the maturation time for any newborn at time t depends on the existing population size at that time t. This may be a good model for populations with a short maturation time. But, in many animal populations, the time to maturity is more susceptible to be influenced by the past history of individuals and the environment they have lived in from the beginning of their life. It is even possible that it is affected by the way the egg and the embryo (in the case of mammalian populations) have grown. The second objection is that this model does not preserve positiveness unless additional restrictions and assumptions are superimposed on the initial values. On the other hand, concerning the steady-state solutions, the conclusion obtained from this model is that if a unique equilibrium exists, then it is always stable and all multiple equilibria are unstable. This result does not reflect any of the biological facts about the existence of non-unique stable equilibria which have been observed in nature, for example in the case of Antartic whales (see [32]), also the case study of [2] and in prey-predator models (see [18], [43]), or the case considered in [13].

In the sequel we present an alternative version of the above model, which was proposed in [22].

4.3. *A variant: a delay state-dependent delay equation.* We modify the previous model by assuming that these are the environmental conditions prevailing at birth, rather than the ones existing at the time when maturity takes place, which influence the age to maturity. Using the same function τ as above, $\tau(z(s))$ is now the age at maturity of the individuals born at time s, in contrast to the actual age of those turning adult at time s, as previously assumed. So, individuals entering adulthood at time t have an age determined by the state of the environment at the time of their birth, $r(t)$, according to the following equation:

$$r(t) = t - \tau(z(r(t))). \tag{48}$$

The equations for the population densities have to be modified accordingly. Balancing influx and outflux in each of the two compartments, the immature and the mature ones, we arrive at the following system (expressed in terms of z and x_m instead of x_i and x_m):

$$\begin{cases} z'(t) = -\gamma z(t) + (\alpha+\gamma)x_m(t) - f(x_m(t))x_m(t), \\ {x_m}'(t) = \alpha x_m(r(t))r'(t)\exp[-\gamma\tau(z(r(t)))] - f(x_m(t))x_m(t). \end{cases} \tag{49}$$

More specific assumptions on the function τ are that it is a smooth increasing function of z, with

$$0 < \tau_0 \le \tau(z) \le \tau_M, \qquad \lim_{z\to 0}\tau(z) = \tau_0, \qquad \lim_{z\to+\infty}\tau(z) = \tau_M < +\infty.$$

In order to solve equation (49) it is necessary to specify initial values for the functions $z(t)$ and $x_m(t)$. We express them as follows:

$$\forall t \in [-\tau_M, 0], \qquad z(t) = \varphi(t) \ge 0, \qquad x_m(t) = \psi(t) \ge 0.$$

We use the pair (z, x_m) instead of (x_i, x_m). Both representations are obviously equivalent to each other. The only thing to keep in mind is a consistency property: not only z and x_m, but also the difference $z - x_m$, should be non-negative.

Regarding the function f, we may assume that it is a smooth increasing function such that

$$f(0) = 0 \le f(x) \le f_m := \lim_{x\to+\infty} f(x) < +\infty.$$

An important property of the model is the existence of an integral relationship, describing

x_i in terms of x_m, namely, we can check that

$$\frac{d}{dt}\left[\exp(\gamma t)x_i(t) - \alpha\int_{r(t)}^{t}\exp(\gamma s)x_m(s)\,ds\right] = 0.$$

On the other hand, reinterpreting the integral term in the above expression in terms of the immature population, one can see that this term provides (after division by $\exp(\gamma t)$) the population of immatures, that is to say,

$$x_i(t) = \alpha\int_{r(t)}^{t}\exp(\gamma(s-t))x_m(s)\,ds).$$

As a side remark, we can see that positivity of x_i is an immediate consequence of the same property for x_m. Such a relationship can be found also in the model with constant delay, but it does not hold in the *intermediate* model. If we now look at the function $r(t)$, differentiating equation (48) with respect to time yields

$$r'(t)[1+\tau'(z(r(t)))z'(r(t))] = 1.$$

The above formula indicates that $r'(t)$ can only change signs near values of time where it is unbounded. If, on the other hand, we assume that the initial value of the function $z(t)$ is suitably small, then we will have $r'(t) > 0$ on an interval past $t = 0$. If we make such an assumption, we will have

$${x_m}'(t) \geq -f(x_m(t))x_m(t)$$

in this interval, which ensures that $x_m(t)$ remains non-negative on the interval. In [22], the following result is proved:

PROPOSITION 6. *Consider system* (49) *under the above mentioned conditions on the functions defining the system, and assume moreover that* $|\tau'|_\infty \leq C$, *where* $C > 0$ *is some constant which depends on the coefficients of the system.*

Let (φ, ψ) *be a pair of non-negative continuous functions defined on* $[-\tau_M, 0]$, *and assume that the norms* $|\varphi|_\infty$, $|\varphi'|_\infty$ *and* $|\psi|_\infty$ *satisfy suitable smallness conditions determined solely in terms of the coefficients of the system. Then the Cauchy problem defined by* (49) *with* (φ, ψ) *as initial values has one and only one solution, defined and continuous on the whole positive axis. Moreover, the solution is non-negative, uniformly bounded and of class* $\mathcal{C}^1$.

Our main interest in the sequel is in the stability properties of equilibria and possible bifurcations. We will also stress the way this depends on the delay.

4.3.1. *Steady-state solutions.* Setting $x_m'(t) = z'(t) = 0$ in (49) we get

$$\begin{cases} -\gamma z^* + x_m^*[(\alpha+\gamma) - f(x_m^*)] = 0, \\ \qquad x_m^*[\alpha e^{-\gamma\tau(z^*)} - f(x_m^*)] = 0, \end{cases}$$

from which it is clear that there exists a trivial equilibrium. In [22] it is shown that $(0, 0)$ is a saddle point and all non-zero solutions are bounded away from zero, that is, there exists $\delta > 0$ such that $\liminf_{t\to+\infty} x_m(t) \geq \delta$.

Non-trivial equilibria $E^* = (z^*, x_m^*)$ are solutions of the following system:

$$\begin{cases} f(x_m^*) = \alpha e^{-\gamma\tau(z^*)}, \\ \quad x_m^* = \dfrac{\gamma z^*}{\gamma + \alpha(1 - e^{-\gamma\tau(z^*)})}. \end{cases}$$

Such equilibria exist and satisfy $z^* > x_m^* > 0$. Existence and conditions for uniqueness are given in [22]. In the sequel we assume that these conditions hold.

4.3.2. *Linearized stability.* We assume that the conditions for uniqueness of a positive equilibrium are satisfied. We shall examine the local stability of the non-trivial equilibrium E^*. For this purpose, the standard approach is to analyze the stability of the linearized equations about equilibrium (see [19], [23], [24], [26], [33]).

To get the variational system of (49) about E^* we consider solutions which are small perturbations of the equilibrium,

$$z(t) := z^* + y_1(t), \qquad x_m(t) := x_m^* + y_2(t).$$

Straightforward calculations lead us to the following system:

$$\begin{pmatrix} {y_1}'(t) \\ {y_2}'(t) \end{pmatrix} + \begin{pmatrix} 0 & 0 \\ G_1 & 0 \end{pmatrix} \begin{pmatrix} y_1'(t-\tau^*) \\ y_2'(t-\tau^*) \end{pmatrix} = \begin{pmatrix} F_1 & F_2 \\ 0 & G_2 \end{pmatrix} \begin{pmatrix} y_1(t) \\ y_2(t) \end{pmatrix} + \begin{pmatrix} 0 & 0 \\ G_3 & G_4 \end{pmatrix} \begin{pmatrix} y_1(t-\tau^*) \\ y_2(t-\tau^*) \end{pmatrix} \tag{50}$$

with

$$\begin{cases} F_1 = -\gamma, \\ F_2 = \alpha + \gamma - (f^* + f'^* x_m^*), \\ G_1 = \alpha x_m^* e^{-\gamma\tau^*} \tau'(z^*) = x_m^* f^* \tau'(z^*), \\ G_2 = -(f^* + f'^* x_m^*), \\ G_3 = -\gamma G_1, \\ G_4 = \alpha e^{-\gamma\tau^*} = f^* \end{cases} \tag{51}$$

where we have introduced the notations

$$\tau^* := \tau(z^*), \qquad f^* := f(x_m^*), \qquad f'^* := f'(x_m^*).$$

We seek a solution of (50) of the form $y_1(t) = ue^{\lambda t}$, $y_2(t) = ve^{\lambda t}$, which leads to the following *characteristic equation* in λ:

$$P(\lambda) + Q(\lambda) e^{-\lambda\tau^*} = 0 \tag{52}$$

where

$$\begin{cases} P(\lambda) = \lambda^2 - \lambda(F_1 + G_2) + F_1 G_2, \\ Q(\lambda) = \lambda(F_2 G_1 - G_4) + F_1 G_4 - F_2 G_3. \end{cases}$$

4.3.3. *Non-state dependent delay implies stability.* In system (49), if the maturation time is constant, then E^* is locally asymptotically stable.

In order to prove this assertion, let us consider $\tau(z) = \tilde{\tau}$ constant in system (49), so that $\tau'(z^*) = 0$. Then we get the following characteristic equation:

$$(\lambda + \gamma)(\lambda + f^* + f'^* x_m^* - f^* e^{-\lambda\tilde{\tau}}) = 0.$$

Therefore $\lambda = -\gamma < 0$ is an eigenvalue always negative. The proof is finished if we can show that every root of the equation

$$\lambda + f^* + f'^* x_m^* - f^* e^{-\lambda\tilde{\tau}} = 0$$

has a negative real part.

Setting $\lambda = \mu + i\nu$, we get the following equation for the real part μ:

$$\mu + f'^* x_m^* = -f^*(1 - e^{-\mu\tilde{\tau}} \cos \nu\tilde{\tau}).$$

The assumption $\mu \geq 0$ yields that $\mu + f'^* x_m^* \leq 0$, so $\mu < -f'^* x_m^* < 0$, which is a contradiction.

Following the same procedure as in [1], [33], it can be shown that E^* is also globally asymptotically stable if the delay τ is constant.

It should be noticed that the local result about stability remains valid if the delay is state-dependent with $\tau'(z^*) = 0$.

4.3.4. *Stability and loss of stability.* Here, we consider the issues of stability changes for the equilibrium E^* as the delay is increased, bearing in mind that the roots of the characteristic equation (52) are functions of delays.

To this end, suppose that $\tau = \tau(z)$ is not constant and $\tau'(z^*) \neq 0$. In the sequel, we take $\tau'(z^*) = 1$, which can always be achieved through normalization.

We fix x_m^* , therefore also the values of f^* and f'^* and we let $\tau^* = (1/\gamma)\ln(\alpha/f^*)$ vary as a result of α being increased. Since the characteristic equation (52) is a quasipolynomial, if there exists a transition from stability to instability it must correspond to a purely imaginary root $\lambda = i\nu \neq 0$.

In particular, ν should be a real root of the algebraic equation

$$|P(i\nu)| = |Q(i\nu)| \Leftrightarrow \nu^4 + A\nu^2 + B = 0 \tag{53}$$

with

$$\begin{cases} A = F_1^2 + G_2^2 - (F_2G_1 - G_4)^2, \\ B = F_1^2G_2^2 - (F_2G_3 - F_1G_4)^2. \end{cases}$$

Existence of non-zero real solutions $\nu_\pm > 0$ for equation (53) is implied by the following conditions:

a) If $B < 0$, then there is one and only one positive solution $\nu_+ > 0$.

b) If $B > 0$ and $A < 0$ such that $A^2 > 4B$, then there are exactly two positive solutions $\nu_+ > \nu_- > 0$, where

$$\nu_+{}^2 = \frac{-A + \sqrt{A^2 - 4B}}{2}, \qquad \nu_-{}^2 = \frac{-A - \sqrt{A^2 - 4B}}{2}. \tag{54}$$

c) Otherwise, that is, if $B > 0$ and $A > 0$ or $A < 0$ such that $A^2 < 4B$, then equation (53) has no real solution.

Let us notice that, taking the values given in (51) for F_i, $i = 1, 2$ and for G_i, $i = 1, 2, 3, 4$, we can write the coefficients A, B as

$$\begin{cases} A = \gamma^2 + (f^* + f'^* x_m^*)^2 - f^{*2}[(\alpha + \gamma - f^* - f'^* x_m^*)x_m^* - 1]^2, \\ B = \gamma^2(f^* + f'^* x_m^*)^2 - \gamma^2 f^{*2}[(\alpha + \gamma - f^* - f'^* x_m^*)x_m^* + 1]^2. \end{cases} \tag{55}$$

Therefore

$$\lim_{\alpha\to+\infty} B = -\infty$$

and then, for each $\alpha > 0$ big enough, we can assure the existence of a unique real positive solution of equation (53), $\nu_+(\alpha) > 0$.

Now we have to show that these roots provide purely imaginary solutions $\lambda(\alpha) = i\nu_+(\alpha)$ of the characteristic equation (52):

$$e^{-i\nu_+(\alpha)\tau^*(\alpha)} = \frac{P(i\nu_+(\alpha))}{Q(i\nu_+(\alpha))}.$$

A straightforward calculation gives the following asymptotic expression for $\nu_+(\alpha)$:

$$\nu_+(\alpha) \sim x_m^* f^* \alpha \quad (\alpha \to +\infty)$$

which provides

$$\lim_{\alpha\to+\infty} \frac{P(i\nu_+(\alpha))}{Q(i\nu_+(\alpha))} = i$$

and also

$$\lim_{\alpha\to+\infty} \tau^*(\alpha) = \lim_{\alpha\to+\infty} \frac{1}{\gamma} \log \frac{\alpha}{f^*} = +\infty.$$

Equation for $\nu_+(\alpha)$ can be written as

$$e^{i\theta_+(\alpha)} = R_+(\alpha)$$

where

$$\theta_+(\alpha) = \nu_+(\alpha)\tau^*(\alpha), \qquad R_+(\alpha) = \frac{P(i\nu_+(\alpha))}{Q(i\nu_+(\alpha))}$$

so that θ_+ is an increasing continuous function for $\alpha > 0$ large enough, such that, $\lim_{\alpha\to+\infty} \theta_+(\alpha) = +\infty$ and R_+ is a continuous function for $\alpha > 0$ big enough, such that $|R_+(\alpha)| = 1$ and $\lim_{\alpha\to+\infty} R_+(\alpha) = i$. Then we can choose a continuous argument function $\operatorname{Arg} R_+(\alpha)$ such that $R_+(\alpha) = \exp(i\operatorname{Arg} R_+(\alpha))$ with $\lim_{\alpha\to+\infty} \operatorname{Arg} R_+(\alpha) = \pi/2$.

Therefore $\theta_+(\alpha) - \operatorname{Arg} R_+(\alpha)$ is an increasing continuous function for $\alpha > 0$ large enough, from which we can assure the existence of an infinite family of real values $\{\alpha_k\}$, $k \geq k_0 > 0$, k integer, such that

$$\theta_+(\alpha_k) - \operatorname{Arg} R_+(\alpha_k) = \frac{\pi}{2} + 2k\pi.$$

This implies the existence of an infinite family of purely imaginary roots $\lambda_k = i\nu_+(\alpha_k)$ of the characteristic equation (52).

Henceforth, stability changes occur if some eigenvalues cross the imaginary axis as α increases. That is, the quantity of interest is the sign of

$$\frac{d}{d\alpha}(\operatorname{Re} \lambda(\alpha))_{\lambda = i\nu_+(\alpha)}.$$

An implicit differentiation in the characteristic equation (52) yields

$$\begin{aligned}\lambda'_\alpha(\alpha) &= \frac{P(\partial Q/\partial\alpha) - Q(\partial P/\partial\alpha) - \lambda(\tau^*)'_\alpha PQ}{Q(\partial P/\partial\lambda) - P(\partial Q/\partial\lambda) + \tau^* PQ} \\ &= \frac{(\lambda G_1 - G_3)P - (\lambda/\gamma\alpha)PQ}{(2\lambda - F_1 - G_2)Q - (F_2 G_1 - G_4)P + \tau^* PQ}\end{aligned}$$

where $(u)'_\alpha$ means differentiation with respect to α.

A somewhat simple but lengthy calculation yields asymptotically as $\alpha \to +\infty$:

$$\lambda'_\alpha(i\nu_+(\alpha)) \sim \frac{x_m^* f^*(f^* x_m^* \alpha + i\gamma)}{\gamma + i\alpha x_m^* f^* \log \alpha}$$

so that

$$\mathrm{Sign}\,(\mathrm{Re}\,\lambda'_\alpha(i\nu_+)) = \mathrm{Sign}\,(\alpha\gamma x_m^{*2} f^{*2}(1+\log\alpha)) > 0 \quad (\alpha \to +\infty).$$

4.3.5. *Conclusion of the section.* We have considered three models of the same population dynamics, the first one with a constant delay, the second one with a simple state-dependent delay and the third one with a delayed state-dependent delay. The results are as follows:

1. With a constant delay, we have that any non-trivial equilibrium, when it exists, is locally asymptotically stable and there is no change in the stability.
2. With a delay of the type $\tau = \tau(z(t))$, there is no change in stability either. This is the result found by W. Aiello, H. Freedman and J. Wu ([2]).
3. With a delay of the type $\tau = \tau(z(r(t)))$, conditions for a Hopf bifurcation to take place are met: we found an infinite family of values of the parameter α at which the characteristic equation has imaginary roots.

In terms of modeling, the above results show a striking contrast between the case of constant or ordinary state-dependent delay and what we called a delayed state-dependent delay. This tells us notably that not all models of delays are equal, and that choosing a wrong model of delay may be misleading.

Our analysis is only partial: we did not conclude that a bifurcation is indeed taking place. As far as we know, no Hopf bifurcation theorem for such equations is currently to be found in the literature. It should be also noticed that, in fact, linearization has been a problem in the case of state-dependent delay differential equations (see [16]). Some results have recently been obtained by O. Arino and E. Sánchez ([8]), for a class of state-dependent delay equations including the one presented here, namely, an extension of the saddle-point theorem and the center manifold theorem to such equations.

5. General conclusion. The examples discussed in this work illustrate the effect of delay on oscillations and stability. They show that this effect is rather more complex than it was initially thought: the old *dogma* according to which increasing the delay results in increased unstable oscillations does not seem to be generally true. A typical situation where it holds is the logistic delay differential equation. The characteristic equation associated with the logistic equation, which is of the form

$$\exp(-\lambda\tau) = F(\lambda),$$

with the function $\alpha \mapsto |F(i\alpha)|$, $\alpha \in \mathbf{R}$, increasing. For the logistic equation, it can be seen that the derivative is positive at every α. From the monotonicity, it can be concluded that each time a root crosses the imaginary axis, it does it from left to right as the delay increases. It is also immediate to see that, under the assumption of monotonicity, the modulus of the imaginary root is increasing to $+\infty$ as the delay approaches $+\infty$, which indicates faster and faster oscillations. Phrased in terms of stability, the dogma tells us that stability will be lost for delay large enough and will not be recovered. This is precisely stated in Theorem 5 for logistic-like equations.

Even a simple second order scalar delay differential equation may make the dogma fail, although it will hold in this case for large values of the delay. It is even more so for delay equations where the equilibrium depends on the delay, which is the case in the classes of equations considered in Section 3 as well as the model dealt with in Section 4. In such cases, the characteristic equation is of the form

$$\exp(-\lambda\tau) = F(\lambda, \tau).$$

Let us mention that a systematic study of characteristic equations of this type has been undertaken by E. Beretta and Y. Kuang in [11].

In all the examples but one considered in this work, the property of instability induced by the delay holds at least for large delay. The exception is the example provided by J. Cushing, where stability is recovered for large delay. This sets an open issue: is it possible to find general conditions for instability or, on the contrary, stability, to hold for large delay? More importantly, is it possible to relate such properties as stability switches to inner mechanisms of the modeled population dynamics? The work done by W. Gurney, R. Nisbet and coworkers (see ([27], [31]) is a step in this direction.

References

[1] W. G. Aiello and H. I. Freedman, *A time-delay model of single-species growth with stage structure*, Math. Biosci. 101 (1990), 139–153.

[2] W. G. Aiello, H. I. Freedman and J. Wu, *Analysis of a model representing stage-structured population growth with state-dependent time delay*, SIAM J. Appl. Math. 52 (1992), 855–869.

[3] W. Alt, *Some periodicity criteria for functional differential equations*, Manuscripta Math. 23 (1978), 295–318.

[4] O. Arino, K. P. Hadeler and M. L. Hbid, *Existence of periodic solutions for delay differential equations with state dependent delay*, J. Diff. Equat. 144 (1998), 263–301.

[5] O. Arino, M. L. Hbid and R. Bravo de la Parra, *A mathematical model of growth of population of fish in the larval stage: density-dependent effects*, Math. Biosci. 150 (1998), 1–20.

[6] O. Arino and E. Sánchez, *Linear theory of abstract functional differential equations of retarded type*, J. Math. Anal. Appl. 191 (1995), 547–571.

[7] O. Arino and E. Sánchez, *A variation of constants formula for an abstract functional differential equation of retarded type*, Diff. Int. Equat. 9 (1996), 1305–1320.

[8] O. Arino and E. Sánchez, *A saddle point theorem for functional state-dependent delay equations* (submitted).

[9] O. Arino, E. Sánchez and A. Fathallah, *State-dependent delay differential equations in population dynamics: modeling and analysis*, Fields Institute Comm. 29 (2001), 19–36.

[10] J. Bélair and M. C. Mackey, *Consumer memory and price fluctuations on commodity markets: an integrodifferential model*, J. Dynamics Diff. Equat. 1 (1989), 299–325.

[11] E. Beretta and Y. Kuang, *Geometric stability switch criteria in delay differential systems with delay dependent parameters*, SIAM J. Math. Anal. 33 (2002), 1144–1165.

[12] G. Bocharov and K. P. Hadeler, *Structured population models, conservation laws and delay equations*, J. Diff. Equat. 168 (2000), 212–237.

[13] Y. Cao, J. Fan and T. C. Gard, *The effects of state-dependent time delay on a stage-structured population growth model*, Nonlinear Anal. 19 (1992), 95–105.

[14] S. N. Chow and J. Mallet-Paret, *Integral averaging and bifurcation*, J. Diff. Equat. 26 (1977), 112–159.

[15] K. L. Cooke, *Functional differential equations: some models and perturbation problems*, in: Diff. Equat. Dyn. Systems (Mayaguez, 1965), Academic Press, 1967, 167–183.

[16] K. Cooke and W. Huang, *On the problem of linearization for state-dependent delay differential equations*, Proc. Amer. Math. Soc. 124 (1996), 1417–1426.

[17] J. M. Cushing, *Volterra integrodifferential equations in population dynamics*, in: Mathematics of Biology, M. Iannelli (ed.), Liguori Editore, 1981, 81–148.

[18] D. L. De Angelis, R. A. Goldstein and R. V. O'Neill, *A model for trophic interaction*, Ecology 56 (1975), 881–892.

[19] O. Diekmann, S. A. van Gils, S. M. Verduyn Lunel and H.O. Walther, *Delay Equations. Functional, Complex and Nonlinear Analysis*, Applied Math. Sciences 110, Springer, 1995.

[20] O. Diekmann, M. Gyllenberg, H. Huang, M. Kirkilionis, J. A. J. Metz and H. R. Thieme, *On the formulation and analysis of general deterministic structured population models. II. Nonlinear theory*, J. Math. Biol. 43 (2001), 157–189.

[21] O. Diekmann, M. Gyllenberg, J. A. J. Metz and H. R. Thieme, *On the formulation and analysis of general deterministic structured population models. I. Linear theory*, J. Math. Biol. 36 (1998), 349–388.

[22] A. Fathallah and O. Arino, *On a model representing stage-structured population growth with state-dependent time delay*, J. Biol. Systems 5 (1997), 469–488.

[23] H. I. Freedman and V. S. Hari Rao, *Stability criteria for a system involving two time delays*, SIAM J. Appl. Math. 46 (1986), 552–560.

[24] K. Gopalsamy, *Stability and Oscillations in Delay Differential Equations of Population Dynamics*, Kluwer, 1992.

[25] A. Grabosch and H. J. A. M. Heijmans, *Cauchy problems with state-dependent time evolution*, Japan J. Appl. Math. 7 (1990), 433–457.

[26] S. Grossman and J. A. Yorke, *Asymptotic behaviour and stability criteria for delay-differential equations*, J. Diff. Equat. 12 (1972), 236–255.

[27] W. S. C. Gurney and R. M. Nisbet, *Fluctuations, periodicity, generation separation and the expression of larval competition*, Theor. Popul. Biol. 28 (1985), 150–180.

[28] J. K. Hale and S. M. Verduyn Lunel, *Introduction to Functional Differential Equations*, Applied Mathematical Sciences 99, Springer, 1993.

[29] N. D. Hayes, *Roots of the transcendental equation associated with a certain difference-differential equation*, J. London Math. Soc. 25 (1950), 226–232.

[30] G. E. Hutchinson, *Circular causal systems in ecology*, Ann. New York Acad. Sci. 50 (1948), 221–246.

[31] A. E. Jones, R. M. Nisbet, W. S. C. Gurney and S. P. Blythe, *Period to delay ratio near stability boundaries for systems with delayed feedback*, J. Math. Anal. Appl. 135 (1988), 354–368.

[32] D. D. Jones and C. J. Walters, *Catastrophe theory and fisheries regulation*, J. Fish. Res. Bull. Can. 33 (1976), 2829–2833.

[33] Y. Kuang, *Delay Differential Equations with Applications in Population Dynamics*, Math. in Sci. and Eng. 191, Academic Press, 1993.

[34] Y. Kuang and H. L. Smith, *Slowly oscillating periodic solutions of autonomous state-dependent delay equations*, Nonlinear Anal. 19 (1992), 872–885.

[35] M. C. Mackey and L. Glass, *Oscillations and chaos in physiological control systems*, Science 197 (1977), 287–289.

[36] P. Magal and O. Arino, *Existence of periodic solutions for a state-dependent delay differential equation*, J. Diff. Equat. 165 (2000), 61–95.

[37] J. M. Mahaffy, *A test for stability of linear differential delay equations*, Quart. Appl. Math. 43 (1982), 193–200.

[38] J. M. Mahaffy, J. Bélair and M. C. Mackey, *Hematopoietic model with moving boundary condition and state-dependent delay: applications in erythropoiesis*, J. Theor. Biol. 190 (1998), 135–146.

[39] J. Mallet-Paret and R. D. Nussbaum, *Boundary layer phenomena for differential-delay equations with state-dependent time lags, I*, Arch. Rat. Mech. Anal. 120 (1992), 99–146.

[40] J. Mallet-Paret, R. D. Nussbaum and P. Paraskevopoulos, *Periodic solutions for functional differential equations with multiple state-dependent time lags*, Topological Methods Nonlinear Anal. 3 (1994), 101–162.

[41] R. D. Nussbaum, *Periodic solutions of some nonlinear autonomous functional differential equations*, Annali Mat. Pura Appl. (4) 101 (1974), 263–306.

[42] V. Volterra, *Sur la théorie mathématique des phénomènes héréditaires*, J. Math. Pures Appl. 7 (1928), 249–298.

[43] G. F. Webb, *Theory of Nonlinear Age-Dependent Population Dynamics*, Dekker, 1985.

[44] J. A. Yorke, *Asymptotic stability for one dimensional differential equations*, J. Diff. Equat. 7 (1970), 189–202.