Nonlinearity

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IOP Publishing | London Mathematical Society Nonlinearity

Nonlinearity **33** (2020) 5839–5860 https://doi.org/10.1088/1361-6544/ab9bab

Dynamics of a chemostat with periodic nutrient supply and delay in the growth

Pablo Amster[1,*], Gonzalo Robledo[2] and Daniel Sepúlveda[3]

[1] Departamento de Matemática, Universidad de Buenos Aires, Ciudad Universitaria Pabellón I—(C1428EGA)—Buenos Aires, Argentina
[2] Departamento de Matemáticas, Universidad de Chile, Casilla 653, Santiago, Chile
[3] Departamento de Matemáticas, Universidad Tecnológica Metropolitana, Las Palmeras 3360, Ñuñoa, Santiago, Chile

E-mail: pamster@dm.uba.ar

Received 28 January 2019, revised 27 April 2020
Accepted for publication 11 June 2020
Published 1 October 2020

Abstract

This paper introduces a new consideration in the well known chemostat model of a one-species with a periodic input of single nutrient with period ω, which is described by a system of differential delay equations. The delay represents the interval time between the consumption of nutrient and its metabolization by the microbial species. We obtain a necessary and sufficient condition ensuring the existence of a positive periodic solution with period ω. Our proof is based firstly on the construction of a Poincaré type map associated to an ω-periodic integro-differential equation and secondly on the existence of zeroes of an appropriate function involving the fixed points of the above mentioned map, which is proved by using Whyburn's Lemma combined with the Leray–Schauder degree. In addition, we obtain a uniqueness result for sufficiently small delays.

Keywords: chemostat, periodic solutions, delay differential equations
Mathematics Subject Classification numbers: 34K13, 34K60, 92D25.

(Some figures may appear in colour only in the online journal)

1. Introduction

The chemostat [21, 29, 31, 40] or continuous stirred-tank reactor (CSTR) is a continuous bioreactor with a constant volume V where one or several microbial species are cultivated in a liquid medium containing in abundance a broad set of resources with the exception of a specific nutrient that will be called the *limiting substrate* or *substrate*.

*Author to whom any correspondence should be addressed.

The chemostat and its mathematical modelling have an ubiquitous place in the study of bioprocesses and microbial ecology issues such as fermentation, anaerobic digestion, production of cellular biomass, competition and predation between microbial species, microbial evolution, etc.

In this article we consider and study a chemostat model described by the following ω-periodic system of delay differential equations (DDE):

$$\begin{cases} \dot{s}(t) = \dfrac{F}{V}s^0(t) - \dfrac{F}{V}s(t) - \gamma^{-1}\mu(s(t))x(t) & \text{if } t \geqslant 0, \\ \dot{x}(t) = x(t)\left\{\mu(s(t-\tau)) - \dfrac{F}{V}\right\} & \text{if } t \geqslant 0, \\ s(\theta) = \varphi(\theta) \quad \text{and} \quad x(0) = x_0 & \text{if } \theta \in [-\tau, 0], \end{cases} \tag{1}$$

where the maps $t \mapsto s(t)$ and $t \mapsto x(t)$ are, respectively, the densities of the substrate and the microbial species at time t.

As usual, the DDE system (1) considers two simultaneous and continuous mechanical processes:

(i) Continuous inputs: the device receives continuously (at rate $F > 0$) an input of liquid volume containing a variable concentration of substrate described by a positive function $t \mapsto s^0(t)$. In spite that the most common case in the literature is to consider a constant concentration, in this paper we will assume that $s^0(\cdot)$ is a continuous periodic function of period ω.

(ii) Continuous outputs: the device expulses continuously (at rate $F > 0$) towards the exterior an output of liquid volume containing a mixing of microbial biomass and substrate.

From now on, we will adopt the classical notation $D = F/V$ for the dilution rate. In addition, let us recall that the DDE system (1) describes two biological processes:

(iii) Substrate consumption: the absorption of the substrate by the microbial species, which will be described by a continuous and non negative function of type $f(s(t))x(t)$. That is, the consumption of substrate has a linear growth with respect to the microbial biomass concentration.

(iv) Biomass growth: the effects of the above mentioned consumption in the *per-capita* growth of the microbial species, which is described by a continuous and non negative function of type $g(s(t-\tau))x(t)$, where g is called the *uptake function*. The model described by the system (1) assumes that the consumption on nutrient has no immediate effects on the microbial growth. In fact, we follow an approach of Caperon [10], which considers the existence of a time interval $[t-\tau, t]$ that the microbial species take to metabolize the substrate.
As in the vast majority of the chemostat literature, the model assumes that the consumption of nutrient and the growth of microbial biomass have a coupling described by $g(r) = \gamma f(r) = \mu(r)$, where $\mu : [0, +\infty) \to [0, +\infty)$, being $\gamma > 0$ a yield constant which relates both processes.

With respect to the above function $\mu(\cdot)$, in this paper, we will assume that $\mu(\cdot)$ has the following properties:

(P) $\mu(\cdot)$ is C^1, $\mu'(s) > 0$ for any $s \geqslant 0$ and $\mu(0) = 0$,

and a classic example of uptake function $\mu(\cdot)$ satisfying **(P)** is given by the Monod's or Michaelis–Menten function:

$$\mu(s) = \frac{\mu_{\max} s}{k_s + s} \quad \text{with } D < \mu_{\max} \text{ and } k_s > 0, \tag{2}$$

which describes the growth of a wide range of microbial species.

The refinement of the basic assumptions of the chemostat model has stimulated an impressive amount of research in the qualitative theory of ordinary, impulsive and delay differential equations, propelling as the development of new techniques of nonlinear functional analysis as well as the innovative use of classical ones. In this theoretical and modelling context, we point out that the terms $s^0(\cdot)$ and D can be operated externally and are considered as inputs of the system. To consider ω-periodic inputs has shown some advantages: it can provide a better production of microbial biomass compared with constant inputs and allows to reproduce the essential features of simple microbial ecosystems, namely, a spatially homogeneous and time-varying environment, which are useful to study microbial physiology. Finally, the study of the ω-periodic and more general non autonomous chemostat models prompted some original research in topics as bifurcation theory, uniform persistence and existence of periodic solutions.

In spite of the fact that there exist several chemostat models described either by ω-periodic ODE systems or by autonomous DDE systems, to the best of our knowledge, it is quite surprising that there exist no simple models coupling delay and ω-periodicity. This fact stress the main contributions of this article: in the first place, we introduce a simple ω-periodic and delayed chemostat model and, in the second place, we prove the existence of ω-periodic solutions. Our results partially generalize those obtained for the undelayed case and use in a creative way two techniques: (i) the construction of Poincaré's translation operators tailored for a one-parameter family of integro-differential equations for the nutrient equation, and (ii) to construct a map defined over the fixed points of the above mentioned Poincaré operators and related to the biomass equation. We prove the existence of at least one zero of this map by means of the Whyburn's lemma and the Leray–Schauder's degree. Although, in a general sense, the use of Poincaré operators and the search of zeroes for maps has been used to cope with undelayed problems, we emphasize the novelty of our approach. We remark that, according to well known results of dissipativeness for periodic processes, the problem of finding periodic positive solutions can be reduced to that of proving the permanence of the positive solutions of (1). However, this latter problem may involve a lot of technicalities and subtleties such that it is not clear whether or not the methods for the non-delayed case (see [14] and [42, ch 13]) can be extended to the present context.

Structure of the article. Section 2 describes two systems which are particular cases of (1), an autonomous DDE version and an ω-periodic ODE; in section 3 the main results are established. The first result (theorem 1) states a sufficient condition for the chemostat washout; the second result (theorem 2) is a necessary and sufficient condition ensuring the existence of positive ω-periodic solutions of the model; the third result (theorem 3) concerns the uniqueness of positive ω-periodic solutions for small delays. Section 4 is devoted to the proofs of the main results. Section 5 introduces a numerical example inspired in the growth of the algae *Dunaliella tertiolecta* under a limitation of nitrate. A short discussion is presented in section 6 and we finish with an appendix devoted to some topological tools and results used in the paper.

Notation. As usual, the Banach space of the real valued continuous functions defined in $[-\tau, 0]$ with the supreme norm is denoted by $C([-\tau, 0], \mathbb{R})$ and its positive cone as $C^+([-\tau, 0], \mathbb{R}) := C([-\tau, 0], \mathbb{R}_0^+)$, where $\mathbb{R}_0^+ := [0, +\infty)$.

In addition, given $\varphi^* \in C^+([-\tau, 0], \mathbb{R})$ we will introduce the notation

$$\{0 \leqslant \varphi \leqslant \varphi^*\} = \left\{\varphi \in C^+([-\tau, 0], \mathbb{R}) : 0 \leqslant \varphi(\theta) \leqslant \varphi^*(\theta) \quad \text{for any } \theta \in [-\tau, 0]\right\}.$$

Moreover, the Banach space of the real valued continuous ω-periodic functions with supreme norm will be denoted by C_ω and its positive cone as C_ω^+. The average of a function $f \in C_\omega$ is denoted by

$$\mathcal{M}\{f\} := \frac{1}{\omega}\int_0^{\omega} f(t)\,\mathrm{d}t.$$

In order to prove the existence of ω-periodic solutions we may assume, without loss of generality, that the delay satisfies the property $\tau \in [0, \omega)$. Indeed, it is straightforward to verify that the existence of ω-periodic solutions of (1) with delay $\tau = n\omega + \tau^*$ ($n \in \mathbb{N}$ and $0 \leqslant \tau^* < \omega$) is equivalent to the existence of ω-periodic solutions of (1) with delay $\tau^* \in [0, \omega)$. Nevertheless, we emphasize that this assumption is only used to prove the sufficience part in theorem 2.

2. Delayed chemostat model

The ω-periodic DDE system (1) generalizes two well known chemostat models: the autonomous DDE system

$$\begin{cases} \dot{s}(t) = Ds^0 - Ds(t) - \gamma^{-1}\mu(s(t))x(t) & \text{if } t \geqslant 0 \\ \dot{x}(t) = x(t)\left\{\mu(s(t-\tau)) - D\right\} & \text{if } t \geqslant 0, \end{cases} \tag{3}$$

and the ω-periodic ODE system

$$\begin{cases} \dot{s}(t) = Ds^0(t) - Ds(t) - \gamma^{-1}\mu(s(t))x(t) & \text{if } t \geqslant 0 \\ \dot{x}(t) = x(t)\left\{\mu(s(t)) - D\right\} & \text{if } t \geqslant 0. \end{cases} \tag{4}$$

To the best of our knowledge, the system (3) has been considered in a work of Caperon [10], which proposes some approaches to explain the gap between consumption of nutrient and its effect on the species growth.

The mathematical study of (3) was started by Thingstad and Langeland in [45] and Bush and Cook in [9]. By using **(P)**, it is noticed that if the constant $\lambda = \mu^{-1}(D)$ verifies $\lambda \in (0, s^0)$, then $E^* = (\gamma[s^0 - \lambda], \lambda)$ is the unique positive equilibrium of (3). This constant λ is called the *break-even concentration*; this is, the minimal amount of substrate necessary to ensure a non-negative growth of the microbial species. The linearization of (3) around E^* and the study of the corresponding characteristic equation allowed to obtain sufficient conditions ensuring the local asymptotic stability of E^* as done in [5, 24, 32] and also to prove the existence of periodic solutions for a threshold delay [16, theorem 3.2]. Moreover, sufficient conditions for the global stability of E^* have been obtained by constructing a Lyapunov–Krasovskii functional in [17, 28].

It is important to point out the existence of complementary approaches describing the delay between consumption of nutrient and the corresponding growth of the microbial species. In particular, we highlight the model described by the DDE system:

$$\begin{cases} \dot{s}(t) = Ds^0 - Ds(t) - \gamma^{-1}\mu(s(t))x(t) & \text{if } t \geqslant 0 \\ \dot{x}(t) = x(t-\tau)\mu(s(t-\tau))\mathrm{e}^{-D\tau} - Dx(t) & \text{if } t \geqslant 0, \\ s(\theta) = \varphi(\theta) \quad \text{and} \quad x(\theta) = \psi(\theta) & \text{if } \theta \in [-\tau, 0], \end{cases} \tag{5}$$

which has been introduced by Freedman *et al* [15] and Ellermeyer [12].

In spite that the dilution rate D has been preferably chosen as ω-periodic input instead of s^0 (we refer the reader to [34, p 73] and [40, ch 7] for details), the ω-periodic ODE system (4) has been considered in several publications and its study has industrial and scientific motivations: on one hand, the nice compilation of results elaborated by Bailey [4] pointed out that periodically operated bioreactors can (at least from a theoretical point of view) improve

Table 1. Summary of the study of (4) and its operational parameters.

Inputs	Type	References
s^0	Continuous ω − periodic	[1, 2, 19, 22, 23, 39, 44]
s^0	Piecewise continuous ω − periodic	[18, 44]
s^0	Piecewise continuous	[14, 36, 37]
s^0	Almost periodic	[37]
s^0 and D	Continuous ω − periodic	[35, 44, 48, 50]
s^0 and D	Continuous	[11]
D	Continuous ω − periodic	[7, 26, 30, 33, 44]

the time-average performance of a bioprocess compared with a fixed parameters one. This work stimulated a big amount of optimal control oriented research where (4) is widely studied [1, 2, 22, 38]. On the other hand, the periodically operated chemostat allows to mimic some environmental fluctuations in aquatic ecosystems (e.g., light/dark cycles or substrate oscillations) and to study the effect of these variations in microalgae physiology, we refer the reader to [27] for details.

The study of (4) has stimulated mathematical research in several topics as bifurcation theory [1, 3, 44] and uniform persistence [14, 37]. The existence, uniqueness and attractivity on ω-periodic solutions has been studied initially by Hsu in [23], were numerical studies are carried out. In addition, in [39, theorem 2.1] Smith proved that the existence of an ω-periodic solution is equivalent to the existence of zeroes of a related map, which is verified by a refinement of the implicit function theorem. The uniqueness and the attractiveness results of ω-periodic solutions are proved by Hale and Somolinos in [19, corollary 5.6].

It is important to point out that (4) is a particular case of the model considered in [35, 48, 50], where s^0 and the dilution rate D are both ω-periodic. We also show a table summarizing the study of (4) and other related models with time-varying parameters (table 1).

Moreover, we have to emphasize that in [19, 23, 35, 39, 48, 50], the system (4) and its related ω-periodic models are considered as a previous step to the study of the system

$$\begin{cases} \dot{s}(t) = Ds^0(t) - Ds(t) - \displaystyle\sum_{i=1}^{n} \gamma_i^{-1}\mu_i(s(t))x_i(t) & \text{if } t \geqslant 0, \\ \dot{x}_i(t) = x_i(t)\left\{\mu_i(s(t)) - D\right\} & \text{if } t \geqslant 0, \end{cases} \tag{6}$$

which describes an scenario of pure and simple competition between n microbial species for the substrate. It is well known that if $t \mapsto s^0(t)$ is a positive constant function, the asymptotic behaviour of (6) is the *competitive exclusion*, namely, at most one microbial species will survive and the rest will become extinct (see [40, ch 2] for details). In this context, an ω-periodic input s^0 is introduced in order to promote the coexistence between all microbial species.

A careful revision of the chemostat literature shows a surprising fact: the lack of models which couple the autonomous DDE system (3) with the ω-periodic ODE system (4). This is due to the complexity of the problem, namely, the difficulty in to adapt the Poincaré operator approach to the delayed case and highlights in some way the contribution of our work.

3. Main results

Let us observe, in the first place, that system (1) with any non-negative initial condition (φ, x_0) such that $x_0 = 0$, becomes the scalar ODE

$$\dot{v} = Ds^0(t) - Dv. \tag{7}$$

Lemma 1. *The equation (7) has a unique ω-periodic solution $v^*(\cdot)$, which is positive and can be described by:*

$$v^*(t) = \int_{-\infty}^{t} \mathrm{e}^{-D(t-r)} Ds^0(r)\,\mathrm{d}r. \tag{8}$$

In addition, any solution $t \mapsto v(t)$ of (7) verifies

$$\lim_{t\to+\infty} (v(t) - v^*(t)) = 0. \tag{9}$$

Proof. As it was shown in [49, p 67], if $D > 0$ and $t \mapsto s^0(t)$ is bounded continuous on $\mathbb{R}$, then $t \mapsto v^*(t)$ defined by (8) is the unique solution of (7) which is bounded on $(-\infty, +\infty)$. On the other hand, as $t \mapsto s^0(t)$ is ω-periodic, it is straightforward to verify that $v^*(t)$ is ω-periodic too.

The proof of (9) can be followed directly by the transformation $w(t) = v^*(t) - v(t)$, which leads to

$$v(t) = v^*(t) + \{v(t_0) - v^*(t_0)\}\mathrm{e}^{-D(t-t_0)} \tag{10}$$

for an arbitrary $t_0 \geqslant 0$. □

Remark 1. It is important to note that:

(a) The ω-periodic function $t \mapsto (v^*(t), 0)$ is known as the 'washout' solution in the chemostat literature since one of its main goals is to produce microbial biomass. In this paper, we will call $t \mapsto (v^*(t), 0)$ the trivial solution and we define a non-trivial solution as any solution $t \mapsto (s(t), x(t))$ distinct from the trivial one with nonnegative components.

(b) It is straightforward to verify that $\mathcal{M}\{s^0\} = \mathcal{M}\{v^*\}$.

Remark 2. If $x(0) = x_0 > 0$, it is straightforward to see that $x(t) > 0$ for any $t \geqslant 0$. Moreover, as $t \mapsto s^0(t)$ is positive and continuous and $s(0) = \varphi(0) \geqslant 0$, it follows that $s(t) > 0$ at some interval $(0, \delta)$. Now, it is easy to prove that $s(t) > 0$ for any $t > 0$. Indeed, otherwise, there exists $t_1 = \min\{t > 0 : s(t) = 0\}$ verifying $\dot{s}(t_1) = Ds^0(t_1) > 0$, which cannot occur.

Remark 3. Note that any solution $t \mapsto (s(t), x(t))$ is defined on $[-\tau, +\infty)$. This follows from the fact that $s'(t) \leqslant D(s^0(t) - s(t))$, then s is bounded and, in consequence, the function $x(t)$ in the second equation has a bounded logarithmic derivative.

The main results state that the existence and non-existence of ω-periodic functions depend on the sign of $\mathcal{M}\{\mu(v^*)\} - D$:

Theorem 1. *If the following inequality is satisfied*

$$\mathcal{M}\{\mu(v^*)\} = \frac{1}{\omega}\int_0^{\omega} \mu(v^*(t))\,\mathrm{d}t \leqslant D, \tag{11}$$

then the trivial solution $t \mapsto (v^*(t), 0)$ of (1) is globally asymptotically stable for any initial condition $(\varphi, x_0) \in C^+([-\tau, 0], \mathbb{R}) \times \mathbb{R}_0^+$. That is

$$\lim_{t\to+\infty} \big(s(t) - v^*(t)\big) = 0 \quad \textit{and} \quad \lim_{t\to+\infty} x(t) = 0,$$

for any solution $t \mapsto (s(t), x(t))$ with initial condition (φ, x_0).

Theorem 2. *The system* (1) *has a non-trivial and positive ω-periodic solution if and only if*

$$\mathcal{M}\{\mu(v^*)\} = \frac{1}{\omega}\int_0^\omega \mu(v^*(t))\,\mathrm{d}t > D. \tag{12}$$

Furthermore, if $t \mapsto (s(t), x(t))$ is a non-trivial nonnegative ω-periodic solution then $0 < s(t) < v^*(t)$ and $x(t) > 0$ for any t.

Theorem 3. *The non-trivial ω-periodic solution $t \mapsto (s^*(t), x^*(t))$ of* (1) *is unique when the delay $\tau > 0$ is sufficiently small.*

Theorem 1 generalizes a result also obtained by Wolkowicz and Zhao with $\tau = 0$. Indeed, the statement (b) of corollary 2.3 from [48] (see also theorem 2.2 from [19]) says that (11) implies the global asymptotic stability of the trivial solution.

Theorem 2 partially extends a result obtained by Wolkowicz and Zhao with $\tau = 0$. Indeed, the statement (a) of corollary 2.3 from [48] says that (12) implies the existence and uniqueness of a positive ω-periodic solution $t \mapsto (s_0^*(t), x_0^*(t))$ such that

$$\lim_{t\to+\infty} \left(s(t) - s_0^*(t)\right) = 0 \quad \text{and} \quad \lim_{t\to+\infty} \left(x(t) - x_0^*(t)\right) = 0,$$

for any positive solution $t \mapsto (s(t), x(t))$ of (1) with $\tau = 0$.

Theorem 3 is a consequence of the above result of Wolkowicz and Zhao about the existence and uniqueness of an ω-periodic solution $t \mapsto (s_0^*(t), x_0^*(t))$ when $\tau = 0$, which combined with the continuity of the solutions of (1) with respect to the delay τ (see e.g., theorem 2.2 from [20, ch 2]), prompted us to obtain a uniqueness result for small delays.

The inequalities (11) and (12) can be seen also from a bioprocesses point of view as a generalization to the ω-periodic framework of the inequality $\mu^{-1}(D) = \lambda < s^0$ described in the section 2, which is equivalent to the existence of a unique positive equilibrium E^* of the autonomous DDE system (3). In fact, note that E^* is positive if and only if $\mu(s^0) > D$. Now if the constant $s^0 > 0$ is replaced by a positive and ω-periodic input $t \mapsto s^0(t)$, then the condition (12) generalizes this last inequality for ω-periodic inputs.

4. Proof of the main results

4.1. Proof of theorem 1

Let $t \mapsto (s(t), x(t))$ be a solution of the system (1) with initial condition $(\varphi, x_0) \in C([-\tau, 0], \mathbb{R}_0^+) \times \mathbb{R}_0^+$. If $x_0 = 0$, then we have that $x(t) \equiv 0$ and lemma 1 implies that $\lim\limits_{t\to+\infty} (v^*(t) - s(t)) = 0$. From now on, we will assume that $x_0 > 0$.

In addition, it will be useful to note that, given an arbitrary $t_0 \geqslant 0$, it follows that

$$v^*(t) - s(t) = [v^*(t_0) - s(t_0)]\mathrm{e}^{-D(t-t_0)} + \gamma^{-1}\int_{t_0}^{t} \mu(s(\xi))\mathrm{e}^{D(\xi-t)}x(\xi)\,\mathrm{d}\xi. \tag{13}$$

As a consequence, if $v^*(t_0) \geqslant s(t_0)$ then $v^*(t) > s(t)$ for any $t > t_0$.

The proof will consider two cases:

Case $\mathcal{M}\{\mu(v^*)\} < D$: we shall proceed in several steps.

Step (1): for any $\varepsilon > 0$, there exists $T := T_\varepsilon > 0$ such that

$$s(t) \leqslant v^*(t) + \varepsilon \quad \text{for any } t > T_\varepsilon. \tag{14}$$

In fact, the component $t \mapsto s(t)$ of the solutions of (1) has the following behaviour: either (i) $t \mapsto s(t) > v^*(t)$ for any $t \geqslant 0$ or (ii) there exists some $T_1 \geqslant 0$ such that $s(T_1) \leqslant v^*(T_1)$. From identity (13), we deduce:

In case (i), the non-negativeness of the solutions allows to prove that

$$0 \leqslant s(t) - v^*(t) \leqslant [s(0) - v^*(0)]\mathrm{e}^{-Dt},$$

and we can easily deduce that, given $\varepsilon > 0$, there exists $T := T_\varepsilon > 0$ such that (14) holds.

In case (ii), it follows that $s(t) < v^*(t)$ for any $t > T_1$ and (14) follows trivially.

Step (2): by the strict inequality in (11) there exists some $\varepsilon_0 > 0$ small enough such that

$$\frac{1}{\omega}\int_0^\omega \mu(v^*(t) + \varepsilon_0)\,\mathrm{d}t < D,$$

and the step 1 implies the existence of $T_{\varepsilon_0} > 0$ such that (14) is verified for ε_0, then **(P)** implies that, for any $t \geqslant T_{\varepsilon_0} + \tau$:

$$\int_t^{t+\omega} [\mu(s(\xi - \tau)) - D]\mathrm{d}\xi \leqslant \int_t^{t+\omega} [\mu(v^*(\xi - \tau) + \varepsilon_0) - D]\mathrm{d}\xi := c_0 < 0.$$

Since $t \mapsto v^*(t)$ is a positive continuous and ω-periodic function, it follows that $0 < v^*(t) \leqslant v^*_{\max} := \max\limits_{r\in[0,\omega]}\{v(r)\}$. The above inequality combined with **(P)** and the fact that any $t \geqslant T_{\varepsilon_0} + \tau$ can be written as $t = t_0 + n\omega + s$ with $t_0 = T_{\varepsilon_0} + \tau$, $n = \lfloor t/\omega \rfloor \in \mathbb{N}_0$ and $s \in [0, \omega]$ implies that

$$\ln\ x(t) \leqslant \ln\ x(t_0) + \lfloor t/\omega \rfloor c_0 + \big(\mu(v^*_{\max} + \varepsilon_0) - D\big)\,\omega,$$

then we can deduce that $x(t) \to 0$ when $t \to +\infty$.

Finally, we use (13) to prove the existence of a positive constant C_0 such that

$$\limsup_{t\to+\infty} |v^*(t) - s(t)| \leqslant C_0 \sup_{\xi \geqslant t_1} x(\xi)$$

for arbitrary $t_1 \geqslant 0$ and the result follows.

Case $\mathcal{M}\{\mu(v^*)\} = D$: the proof will be made in several steps.

Step (1): There exists $T > 0$ such that

$$s(t) < v^*(t) \quad \text{for any } t \geqslant T. \tag{15}$$

Indeed, we already know from (13) that the claim is true if $v^*(t_0) \geqslant s(t_0)$ for some t_0. Suppose otherwise that $s(t) > v^*(t)$ for all $t \geqslant 0$, then

$$\frac{1}{\omega}\int_t^{t+\omega} \mu(s(r))\,\mathrm{d}r > \frac{1}{\omega}\int_t^{t+\omega} \mu(v^*(r))\,\mathrm{d}r = D \quad \text{for any } t > 0.$$

Integrate the second equation of (1) and obtain that $x(t + \omega) > x(t)$ for any $t > \tau$, this fact implies that $\inf\limits_{t\geqslant 0} x(t) > 0$ and, consequently,

$$[s(t) - v^*(t)]' \leqslant -D[s(t) - v^*(t)] - \gamma^{-1}\mu(v^*(t))\inf_{\xi\geqslant 0} x(\xi) \leqslant -C_1$$

for some constant $C_1 > 0$. This, in turn, implies $s(t) - v^*(t) \to -\infty$, a contradiction.

Step (2): the solutions have the following property:

$$\limsup_{t\to+\infty} x(t) < +\infty, \quad \text{and} \quad \inf_{t\geqslant 0} s(t) > 0.$$

In addition, there exist positive constants c_1 and $c_2 > 0$ such that

$$c_1(v^*(t) - s(t)) \leqslant \mu(v^*(t)) - \mu(s(t)) \leqslant c_2(v^*(t) - s(t)) \quad \text{for all } t \geqslant T.$$

Indeed, integrating the second equation of (1) we deduce as in the previous step that $x(t+\omega) < x(t)$ for $t \geqslant T + \tau$ and, in particular, x is bounded from above. The proof that $\inf_{t\geqslant 0} s(t) > 0$ can be made by contradiction: if $\inf_{t\geqslant 0} s(t) = 0$, then the fluctuation lemma (see e.g. [41, p 154]) ensures the existence of a sequence $\{\sigma_n\}_n$ such that

$$\lim_{n\to+\infty} s(\sigma_n) = \lim_{n\to+\infty} \dot{s}(\sigma_n) = 0,$$

which combined with the boundedness of x implies that $s^0(\sigma_n) \to 0$, obtaining a contradiction with the positiveness and ω-periodicity of s^0.

The existence of c_1 and c_2 follows trivially from condition **(P)**.

Step (3): any solution verifies $\liminf_{t\to+\infty} x(t) = 0$. Indeed, otherwise, suppose that $\liminf_{t\to+\infty} x(t) > 0$ and hence $\inf_{\xi\geqslant 0} x(\xi) > 0$. We deduce that

$$[v^*(t) - s(t)]' \geqslant -D[v^*(t) - s(t)] + \gamma^{-1}\mu(\inf_{\xi\geqslant 0} s(\xi)) \inf_{\xi\geqslant 0} x(\xi) \quad \text{for any } t \geqslant 0.$$

The above inequality implies that $v^*(t) - s(t) \geqslant C > 0$ for all $t \geqslant T$. Then for $N \in \mathbb{N}$ and $t \geqslant T + \tau$ we have that

$$\begin{aligned} x(t+N\omega) &= x(t)\mathrm{e}^{\int_{t-\tau}^{t-\tau+N\omega} \mu(s(r))\,\mathrm{d}r - ND\omega} \\ &= x(t)\mathrm{e}^{\int_{t-\tau}^{t-\tau+N\omega} [\mu(s(r))-\mu(v^*(r))]\,\mathrm{d}r} \\ &\leqslant \max_{\xi\geqslant 0} x(\xi)\mathrm{e}^{-NC\omega c_1}, \end{aligned}$$

and we conclude that $x(t) \to 0$ as $t \to +\infty$, a contradiction.

Step (4): we have that

$$\int_0^{+\infty} [v^*(r) - s(r)]\,\mathrm{d}r = +\infty.$$

Indeed, suppose that $\int_0^{+\infty} [v^*(r) - s(r)]\,\mathrm{d}r < +\infty$ and integrate the second equation of (1) between $t_0 + \tau$ and $t + \tau$ with $t \geqslant t_0 \geqslant T$, then we obtain that

$$\begin{aligned} \ln\ x(t+\tau) &= \ln\ x(t_0+\tau) + \int_{t_0}^{t} [\mu(s(r)) - \mu(v^*(r))]\,\mathrm{d}r + \int_{t_0}^{t} [\mu(v^*(r)) - D]\,\mathrm{d}r \\ &\geqslant \ln\ x(t_0+\tau) - c_2\int_{t_0}^{t} [v^*(r) - s(r)]\,\mathrm{d}r + \min_{t\in[0,\omega]}\int_0^t [\mu(v^*(r)) - D]\,\mathrm{d}r \end{aligned}$$

and hence $t \mapsto \ln x(t) \geqslant \delta_0 > -\infty$, obtaining a contradiction with the fact that $\liminf_{t\to+\infty} x(t) = 0$.

Step (5): end of proof: for $t \in [T+\tau, T+\tau+\omega]$ we may write as before

$$\begin{aligned} x(t+N\omega) &= x(t)\mathrm{e}^{\int_{t-\tau}^{t-\tau+N\omega} \mu(s(r))\,\mathrm{d}r - ND\omega} \\ &= x(t)\mathrm{e}^{\int_{t-\tau}^{t-\tau+N\omega} [\mu(s(r))-\mu(v^*(r))]\,\mathrm{d}r} \\ &\leqslant x(t)\mathrm{e}^{-c_1\int_{t-\tau}^{t-\tau+N\omega} [v^*(r)-s(r)]\,\mathrm{d}r} \\ &\leqslant \max_{\xi\geqslant 0} x(\xi)\mathrm{e}^{-c_1\int_{T+\omega}^{T+N\omega} [v^*(r)-s(r)]\,\mathrm{d}r}. \end{aligned}$$

Because the latter term tends to 0 as $N \to \infty$ independently of t, we deduce that $x(u) \to 0$ as $u \to +\infty$. Finally, for any t_0 and $t \geqslant t_0$ we have:

$$v^*(t) - s(t) \leqslant [v^*(t_0) - s(t_0)]\mathrm{e}^{-D(t-t_0)} + \gamma^{-1} \max_{\xi\geqslant t_0} x(\xi) \int_{t_0}^{t} \mu(s(\xi))\mathrm{e}^{-D(t-\xi)}\,\mathrm{d}\xi.$$

For $\eta > 0$, fix t_0 such that the last term in the previous inequality is smaller than η to obtain: $\limsup_{t\to+\infty}[v^*(t) - s(t)] \leqslant \eta$. Since η is arbitrary, we conclude that $v^*(t) - s(t) \to 0$ as $t \to +\infty$.

4.2. Proof of theorem 2

The necessity of condition (12) follows from theorem 1. Moreover, if $t \mapsto (s(t), x(t)) \neq (v^*(t), 0)$ is a non-negative ω-periodic solution of (1) we will prove that $0 < s(t) < v^*(t)$ for any t.

By ω-periodicity we have that

$$\int_0^{\omega} \{s^0(r) - s(r)\}\,\mathrm{d}r = \frac{\gamma^{-1}}{D}\int_0^{\omega} \mu(s(r))x(r)\,\mathrm{d}r > 0.$$

Because $\mathcal{M}\{v^*\} = \mathcal{M}\{s^0\}$, we have that

$$0 = \int_0^{\omega} \{s^0(r) - v^*(r)\}\,\mathrm{d}r < \int_0^{\omega} \{s^0(r) - s(r)\}\,\mathrm{d}r$$

and, consequently, there exists $t_0 \in [0, \omega]$ such that $s(t_0) < v*(t_0)$. By using (13) and the periodicity again, we deduce that $s(t) < v^*(t)$ for all t.

The sufficience of the condition (12) will be proved in several steps for the convenience of the reader.

Step 1: it is readily seen that if $L = \gamma^{-1}x(0) > 0$ is fixed, then upon integration of the second equation, system (1) is equivalent to

$$\dot{s}(t) = Ds^0(t) - Ds(t) - L\mu(s(t))\mathrm{e}^{\int_0^t [\mu(s(\xi-\tau))-D]\mathrm{d}\xi}. \tag{16}$$

Furthermore, we point out that as the right-hand side part of (1) is locally Lipschitz, the solutions are continuous with respect to the initial conditions (see e.g., [20, ch 2, theorem 2.2]) and this property is inherited by the solutions of (16). This fact will be useful later.

For any fixed $L > 0$, $\varphi \in C^+([-\tau, 0], \mathbb{R})$ and $\theta \in [-\tau, 0]$, we construct the Poincaré translation operator $P_L : C^+([-\tau, 0], \mathbb{R}) \to C^+([-\tau, 0], \mathbb{R})$ as follows:

$$P_L\varphi(\theta) = s_\varphi(\omega+\theta), \quad \text{where } s_\varphi(\cdot) \text{ is the solution of (16) with initial condition } \varphi.$$

Let us define the set $C^* := \{\varphi \in C([-\tau, 0], \mathbb{R}) : 0 \leqslant \varphi \leqslant v^* \text{ in } [-\tau, 0]\}$ and, in the same way as before, we can observe that if $\varphi \in C^*$ then $0 < s_\varphi(t) < v^*(t)$ for any $t > 0$, which proves that P_L is well defined over C^* and $P_L(C^*) \subset (C^*)^\circ$, the interior of C^*.

On the other hand, we can verify that operator P_L is compact. Indeed, the continuity of P_L follows from the continuous dependence on the initial conditions and, furthermore, because $0 \leqslant s_\varphi \leqslant v^*$ we deduce that $|\dot{s}_\varphi(t)|$ is bounded by a fixed constant for $t \geqslant 0$. As it was stated in the Introduction, we can assume that $\omega > \tau$, whence $|(P_L\varphi)'(t)|$ is bounded for $t \in [-\tau, 0]$ and $\varphi \in C^*$. Thus, the family $\{P_L\varphi : \varphi \in C^*\}$ is equicontinuous and the conclusion follows from the Arzelà–Ascoli theorem. Moreover, as C^* is forward invariant under P_L, Schauder's theorem implies the existence of at least one fixed point of P_L, which lies in $(C^*)^\circ$. On the other hand, the Poincaré operator is also defined when $L = 0$, for which there is a unique fixed point, namely the function $\varphi^* := v^*|_{[-\tau,0]}$.

Step 2: let us define the set $\mathcal{C} \subset C([-\tau, 0], \mathbb{R}) \times [0, +\infty)$ as follows:

$$\mathcal{C} := \{(\varphi, L) \in \{\varphi \in C([-\tau, 0], \mathbb{R}) : 0 < \varphi < \varphi^*\} \times (0, +\infty) : P_L\varphi = \varphi\} \cup \{(\varphi^*, 0)\},$$

which is equipped it the standard metric. Moreover, let us consider its fibers

$$\mathcal{C}_L := \{\varphi : (\varphi, L) \in \mathcal{C}\},$$

which are non-empty for any L. Now, let us consider the map $F : \mathcal{C} \to \mathbb{R}$, which is defined by

$$F(\varphi, L) := \int_0^\omega [\mu(s_\varphi(\xi - \tau)) - D]\, \mathrm{d}\xi,$$

where $s_\varphi(\cdot)$ is solution of (16) with initial condition φ.

Thus, the problem of finding positive ω-periodic solutions of (1) is equivalent to that of finding $(\varphi, L) \in \mathcal{C}$ such that $F(\varphi, L) = 0$. Indeed, if $t \mapsto (s(t), x(t))$ is a positive ω-periodic solution of (1), then the periodicity of $\ln x(t)$ implies that $\frac{1}{\omega}\int_0^\omega \mu(s(t - \tau))\, \mathrm{d}t = D$, whence $F(\varphi, L) = 0$ for $\varphi := s|_{[-\tau,0]}$ and $L = \gamma^{-1}x(0)$. Conversely, if $F(\varphi, L) = 0$ is verified for some $(\varphi, L) \in \mathcal{C}$ then it is straightforward to see that $\int_0^\omega [\mu(s_\varphi(\xi - \tau)) - D]\, \mathrm{d}\xi = 0$. Let us define $u(t) := s_\varphi(t + \omega)$ for any $t \geqslant -\tau$, which clearly satisfies $u(\theta) = \varphi(\theta)$ for $\theta \in [-\tau, 0]$.

In order to verify that $t \mapsto s_\varphi(t)$ is ω-periodic, it is seen that

$$\begin{aligned}
\dot{u}(t) &= Ds^0(t + \omega) - Ds_\varphi(t + \omega) - L\mu(s_\varphi(t + \omega))\mathrm{e}^{\int_0^{t+\omega} [\mu(s_\varphi(\xi-\tau))-D]\mathrm{d}\xi} \\
&= Ds^0(t) - Du(t) - L\mu(u(t))\mathrm{e}^{\int_0^{\omega} [\mu(s_\varphi(\xi-\tau))-D]\mathrm{d}\xi}\mathrm{e}^{\int_\omega^{t+\omega} [\mu(s_\varphi(\xi-\tau))-D]\mathrm{d}\xi} \\
&= Ds^0(t) - Du(t) - L\mu(u(t))\mathrm{e}^{\int_0^{t} [\mu(u(\xi-\tau))-D]\mathrm{d}\xi},
\end{aligned}$$

which implies that $t \mapsto u(t)$ is solution of (16) with initial condition φ. Then, by the theorem of existence and uniqueness of solutions we conclude that $s_\varphi(t) = s_\varphi(t + \omega)$.

Summarizing, the fact that $F(\varphi, L) = 0$ implies the existence of a positive ω-periodic solution $t \mapsto (s(t), x(t))$ of (1), with

$$s(t) := s_\varphi(t) \quad \text{and} \quad x(t) := L\gamma\mathrm{e}^{\int_0^t [\mu(s_\varphi(\xi-\tau))-D]\mathrm{d}\xi}.$$

Step 3: there exists a constant k such that $\|\varphi - \varphi^*\|_\infty \leqslant kL$ for any $(\varphi, L) \in \mathcal{C}$.

Indeed, let $(\varphi, L) \in \mathcal{C}$ and fix $t_0 \in (0, \omega]$ at which the maximum value of the function $v^* - s_\varphi$ over $(0, \omega]$ is achieved, then $(v^* - s_\varphi)'(t_0) \geqslant 0$. On the other hand, as

$$(v^*(t) - s_\varphi(t))' = D(s_\varphi(t) - v^*(t)) + L\mu(s_\varphi(t))\mathrm{e}^{\int_0^t [\mu(s_\varphi(\xi-\tau)-D]\mathrm{d}\xi},$$

since $(\varphi^*, 0)$ and (φ, L) belong to $\mathcal{C}$ combined with the fact that $\tau < \omega$, it follows that

$$\max_{\theta\in[-\tau,0]}\{\varphi^*(\theta) - \varphi(\theta)\} \leqslant \max_{t\in[0,\omega]}\{v^*(t) - s_\varphi(t)\} = v^*(t_0) - s_\varphi(t_0),$$

which implies that

$$\|\varphi^* - \varphi\|_\infty \leqslant \max_{t\in[-\tau,\omega]}\{v^*(t) - s_\varphi(t)\} \leqslant \frac{L}{D}\mu(s_\varphi(t_0))\mathrm{e}^{\int_0^{t_0}[\mu(s_\varphi(\xi-\tau)-D]\mathrm{d}\xi}.$$

Because $s_\varphi \leqslant v^*$ and μ is nondecreasing, we deduce that

$$\|\varphi^* - \varphi\|_\infty \leqslant kL$$

for some constant k which is independent of L.
Step 4: in order to prove the existence of $(\varphi, L) \in \mathcal{C}$ such that $F(\varphi, L) = 0$, it suffices to prove that $F : \mathcal{C} \to \mathbb{R}$ is a continuous function which changes sign over a connected subset of $\mathcal{C}$.

The continuity of F follows by using again the continuous dependence on the initial conditions for the system (1).

Notice that the assumption (12) can be written as $F(\varphi^*, 0) > 0$. This fact, combined with the continuity of F and the previous step implies that $F(\varphi, L) > 0$ for any $(\varphi, L) \in \mathcal{C}$ with $L > 0$ small enough.

Now, we claim that $F(\varphi, L) < 0$ for any $(\varphi, L) \in \mathcal{C}$ with sufficiently large values of L. Indeed, by using the fact that $s_\varphi(\omega + \theta) = P_L\varphi(\theta) = \varphi(\theta)$ for $\theta \in [-\tau, 0]$, we can see that

$$\max_{t\in[-\tau,\omega]} s_\varphi(t) = \max_{t\in(0,\omega]} s_\varphi(t).$$

Fix $t_0 \in (0, \omega]$ such that $s_\varphi(\cdot)$ reaches its maximum value on $[-\tau, \omega]$ at t_0, then $s_\varphi(t_0) > 0$ and $\dot{s}_\varphi(t_0) \geqslant 0$ or, equivalently

$$0 < Ds_\varphi(t_0) \leqslant Ds^0(t_0) - L\mu(s_\varphi(t_0))\mathrm{e}^{\int_0^{t_0}[\mu(s_\varphi(\xi-\tau)-D]\mathrm{d}\xi} \leqslant Ds^0(t_0) - L\mu(s_\varphi(t_0))\mathrm{e}^{-D\omega}.$$

The previous inequality implies that $\mu(s_\varphi(t_0)) \leqslant \frac{C}{L}$ for some constant C which, combined with the properties of μ proves that $s_\varphi(t_0) = \max_{-\tau\leqslant t\leqslant\omega} s_\varphi(t) \to 0$ when $L \to +\infty$ and consequently $F(\varphi, L) < 0$ for large values of L.

Next, fix $0 < L_0 < L_1$ such that $(-1)^j F(\varphi_j, L_j) > 0$ for any $\varphi_j \in \mathcal{C}_{L_j}$. It is easy to verify that the set

$$\mathcal{K} := \bigcup_{L\in[L_0,L_1]} \mathcal{C}_L$$

is compact. Indeed, it is easy to see that $\mathcal{K} \subset C^*$ is equicontinuous because the bound for $|\dot{\varphi}(\theta)| = |\dot{s}_\varphi(\theta + \omega)|$ with $\theta \in [-\tau, 0]$ can be chosen independently of $L \in [L_0, L_1]$ due to

$$D(s^0(t) - v^*(t)) - L_1\mu(v^*(t))\mathrm{e}^{\int_0^t[\mu(v^*(\xi-\tau))-D]} < \dot{s_\varphi}(t) \leqslant Ds^0_{\max}.$$

Moreover, continuous dependence also implies that if $(\varphi_n, L_n) \in \mathcal{K}$ is such that verifies $(\varphi_n, L_n) \to (\varphi, L)$, then $s^{L_n}_{\varphi_n}$, namely, the solutions of (16) with parameter L_n and initial condition φ_n, converge to s^L_φ uniformly on $[\omega - \tau, \omega]$ which, in turn, implies that $(\varphi, L) \in \mathcal{K}$.

The proof will follow if there exists a connected component of $\mathcal{K}$ that connects the fibers $\mathcal{C}_{L_0}$ and $\mathcal{C}_{L_1}$. Indeed, otherwise, by Whyburn's lemma (see appendix for details) there exist two disjoint closed sets $\mathcal{F}_j$ such that $\mathcal{C}_{L_j} \subset \mathcal{F}_j$ and $\mathcal{K} = \mathcal{F}_0 \cup \mathcal{F}_1$ and an open set $\Omega \subset \{0 < \varphi < \varphi^*\} \subset C^*$ such that

$$\mathcal{F}_0 \subset \Omega, \tag{17}$$

$$\mathcal{F}_1 \cap \Omega = \emptyset \tag{18}$$

and

$$\partial\Omega \cap \mathcal{K} = \emptyset. \tag{19}$$

Let us define the map $P : \overline{\Omega} \times [L_0, L_1] \to C([-\tau, 0], \mathbb{R})$ as follows

$$P(\varphi, L) = P_L(\varphi),$$

where P_L is the same map defined previously. By using again the Theorem of continuous dependence with respect to the initial conditions from [20, pp 43 and 44] it can be proved that P is continuous and its compactness can be verified straightforwardly.

Now let us define the map $G : \overline{\Omega} \times [L_0, L_1] \to C([-\tau, 0], \mathbb{R})$ as $G(\varphi, L) = \varphi - P(\varphi, L)$ and denote $G_L(\varphi) = G(\varphi, L)$.

By using (19), we can see that G_L is different from zero on $\partial\Omega$ for any $L \in [L_0, L_1]$ since by definition the zeroes of G are in $\mathcal{K}$. By homotopy invariance property of the Leray–Schauder degree (see appendix for details), this implies that the degree verifies

$$\deg(G_{L_0}, \Omega, 0) = \deg(G_{L_1}, \Omega, 0) = 0. \tag{20}$$

Indeed, notice that the last degree is 0 since identity (18) implies that $\Omega \cap \mathcal{C}_{L_1} = \emptyset$, that is, G_{L_1} does not vanish in Ω. Thus, the conclusion follows from the solution property of the Leray–Schauder's degree. On the other hand, property (17) implies that $\mathcal{C}_{L_0} \subset \Omega$ and hence G_{L_0} cannot be zero outside of Ω. By using the excision property of the degree, we have that

$$\deg(G_{L_0}, \Omega, 0) = \deg(G_{L_0}, \{\varphi \in C([-\tau, 0], \mathbb{R}) : 0 < \varphi < \varphi^*\}, 0).$$

In order to compute the last above degree, for any $\varphi \in C([-\tau, 0], \mathbb{R})$ we construct a truncated function $\hat{\varphi} \in C^*$ defined by

$$\hat{\varphi}(t) = \begin{cases} \varphi(t) & \text{if } 0 < \varphi(t) < \varphi^*(t), \\ \varphi^*(t) & \text{if } \varphi(t) \geqslant \varphi^*(t), \\ 0 & \text{if } \varphi(t) \leqslant 0, \end{cases}$$

and the operator $\hat{P}_L : C([-\tau, 0], \mathbb{R}) \to C([-\tau, 0], \mathbb{R})$ defined by $\hat{P}_L(\varphi) := P_L(\hat{\varphi})$. The continuity and compactness is a direct consequence from the continuity of $\varphi \mapsto \hat{\varphi}$ and the compactness of P_L.

Moreover, note that $\mathrm{Im}(\hat{P}_L) \subset \{\varphi \in C([-\tau, 0], \mathbb{R}) : 0 < \varphi < \varphi^*\}$. Then, any fixed point φ of $\lambda\hat{P}_L$ with $\lambda \in [0, 1]$ verifies $\varphi = \lambda\hat{P}_L\varphi < \varphi^* \leqslant v^*_{\max}$. Thus taking $R > v^*_{\max}$ we can see that $\lambda\hat{P}_L$ has no fixed point on $\partial B_R(0)$ for $\lambda \in [0, 1]$ and then the homotopy property implies that

$$\deg(I - \hat{P}_L, B_R(0), 0) = \deg(I, B_R(0), 0) = 1.$$

In addition, $\hat{P}_L$ has no fixed points outside $\{0 < \varphi < \varphi^*\}$ and coincides with P_L on this set, then the excision property of Leray–Schauder's degree implies that

$$\deg(I - P_L, \{\varphi \in C([-\tau, 0], \mathbb{R}) : 0 < \varphi < \varphi^*\}, 0) = \deg(I - \hat{P}_L, B_R(0), 0) = 1.$$

As the previous identity is valid for any $L > 0$, we can deduce that

$$\deg(G_{L_0}, \{\varphi \in C([-\tau, 0], \mathbb{R}) : 0 < \varphi < \varphi^*\}, 0) = 1,$$

which contradicts (20). This proves the existence of a connected set $X \subset \mathcal{C}$ containing points in $\mathcal{C}_{L_0}$ and $\mathcal{C}_{L_1}$. By the intermediate value theorem we deduce the existence of $(\varphi, L) \in X$ such that $F(\varphi, L) = 0$.

4.3. Proof of theorem 3

The proof will be made in two steps:

An auxiliary result: in spite of the next result has been previously proved by Wolkowicz and Zhao [48] (see also [50, corollary 5.2.1]) in a more general version, which considers ω-periodic uptake functions $\mu(t, \cdot)$ and dilution rates $D(t)$ together decay rates for the species. The restriction to our model allows an alternative proof, which has a remarkable simplicity.

Lemma 2. *Let $t \mapsto (s_0^*(t), x_0^*(t))$ be a positive ω-periodic solution of (1) provided by theorem 2 when $\tau = 0$. Then this solution is unique and globally asymptotically stable.*

Proof. When $\tau = 0$, the change of variables $v := s + \gamma^{-1}x$ and a straightforward computation shows that the undelayed system (1) is equivalent to

$$\begin{cases} \dot{s} = D(s^0(t) - s) - \mu(s)(v - s), \\ \dot{v} = D(s^0(t) - v). \end{cases}$$

As done in lemma 1, we can verify that $(v - v^*)' = -D(v - v^*)$ is such that $v(t) - v^*(t) \to 0$ when $t \to +\infty$ due to

$$v(t) - v^*(t) = [v(t_0) - v^*(t_0)]\mathrm{e}^{-D(t-t_0)} \quad \text{for any } t_0 \geqslant 0. \tag{21}$$

A direct consequence from (21) is the boundedness of any solution $t \mapsto (s(t), x(t))$. In turn, $t \mapsto \dot{x}(t)$ is bounded as well, which implies that $t \mapsto x(t)$ is uniformly continuous.

Moreover, there exist ε and $\delta > 0$, possibly dependent of the initial conditions such that $0 < \delta < s(t) < v(t) < v^*(t) + \varepsilon$ for t large enough which, in turn, combined with **(P)** implies that $\mu(s(t)) - \mu(s_0^*(t)) = a(t)[s(t) - s_0^*(t)]$ with $t \mapsto a(t)$ bounded and greater than a constant $\alpha > 0$ for all t.

With the change of variables $w = x - x_0^*$, we can see that

$$\dot{w} = [\mu(s_0^*(t)) - D]w + x[\mu(s_0^*(t)) - \mu(s(t))] = r(t)w(t) + x(t)a(t)(v(t) - v^*(t)),$$

with $r(\cdot)$ defined as follows:

$$r(t) := \mu(s_0^*(t)) - D - \gamma^{-1}x(t)a(t).$$

Note that $t \mapsto x(t)$ is not integrable in $[0, +\infty)$. Indeed; otherwise; as x is uniformly continuous, the Barbalat's lemma [25, lemma 8.2] implies that $x(t) \to 0$ and consequently $s(t) - v^*(t) \to 0$ when $t \to +\infty$. Then, the condition (12) implies the existence of $c > 0$ such that $\int_t^{t+\omega}[\mu(s(\xi))-D]\,\mathrm{d}\xi \geqslant c>0$ for some t large enough, which implies $x(t+\omega)\geqslant x(t)\mathrm{e}^{c\omega}$, contradicting the boundedness of x.

Note also that, because $\mathcal{M}(\mu(s_0^*))=D$, for arbitrary $t_1>t_0\geqslant 0$ we have

$$\int_{t_0}^{t_1}[\mu(s_0^*(\xi))-D]\,\mathrm{d}\xi \leqslant \max_{0\leqslant\eta\leqslant\omega}\int_0^{\eta}[\mu(s_0^*(\xi))-D]\,\mathrm{d}\xi := B.$$

Thus, for all $\sigma\geqslant 0$

$$R_\sigma(t):=\int_\sigma^t r(\xi)\,\mathrm{d}\xi \leqslant B-\alpha\gamma^{-1}\int_\sigma^t x(\xi)\,\mathrm{d}\xi \to -\infty$$

as $t\to+\infty$. For fixed $t_0>0$, we use (21) to see that

$$w(t)=w(t_0)\mathrm{e}^{R_{t_0}(t)}+[v(t_0)-v^*(t_0)]\int_{t_0}^t x(\xi)a(\xi)\mathrm{e}^{R_\xi(t)-D(\xi-t_0)}\,\mathrm{d}\xi$$

and from the boundedness of $x(\cdot)$ and $a(\cdot)$, combined with $R_\xi(t)\leqslant B$ we obtain:

$$|w(t)-w(t_0)\mathrm{e}^{R_{t_0}(t)}|\leqslant C|v(t_0)-v^*(t_0)|\int_{t_0}^t \mathrm{e}^{-D(\xi-t_0)}\,\mathrm{d}\xi \leqslant \frac{C}{D}|v(t_0)-v^*(t_0)|$$

for some constant $C>0$. Letting $t\to+\infty$ we see that $|w(t)|\leqslant\frac{C}{D}|v(t_0)-v^*(t_0)|$ and, since t_0 is arbitrary we deduce that $x(t)-x_0^*(t)\to 0$ as $t\to+\infty$. This, in turn, implies $s(t)-s_0^*(t)\to 0$ as $t\to+\infty$.

□

End of proof: let us consider the mapping

$$\Phi:\mathcal{A}\times\mathbb{R}\to C_\omega\times C_\omega$$

given by

$$\Phi(s,x,\tau)(t):=(\dot{s}(t),\dot{x}(t))-N(s,x)(t)$$

where $\mathcal{A}\subset C_\omega^1\times C_\omega^1$ is defined as

$$\mathcal{A}:=\{(s,x):0<s<v^*,x>0\}$$

and $N(s,x)(t)$ is the Nemitskii operator defined by right-hand side of (1). A straightforward computation shows that Φ is of class C^1 and

$$D_{(s,x)}\Phi(s,x,\tau)(\varphi,\psi)(t)=\left(\dot{\varphi}(t)+a(t)\varphi(t)+b(t)\psi(t),\dot{\psi}(t)+c(t)\varphi(t-\tau)+d(t)\psi(t)\right),$$

where

$$\begin{array}{ll} a(t)=D+\gamma^{-1}\dot{\mu}(s(t))x(t), & b(t)=\gamma^{-1}\mu(s(t)) \\ c(t)=-x(t)\dot{\mu}(s(t-\tau)), & d(t)=-[\mu(s(t-\tau))-D]. \end{array}$$

Firstly, by lemma 2 we can see that

$$\Phi(s_0^*,x_0^*,0)=0,\quad \text{where } x_0^*(t)=\gamma(v^*(t)-s_0^*(t)).$$

Secondly, it can be verified that the map $(\varphi, \psi) \mapsto D_{(s,x)}\Phi(s_0^*, x_0^*, 0)(\varphi, \psi)$ is an isomorphism from $C_\omega^1 \times C_\omega^1$ to $C_\omega \times C_\omega$. Indeed, $D_{(s,x)}\Phi(s_0^*, x_0^*, 0)(\varphi, \psi) = (0, 0)$ is equivalent to say that (φ, ψ) is an ω-periodic solution of the ω-periodic system

$$\dot{u} = A(t)u \quad \text{with } A(t) = \begin{bmatrix} -[D + \gamma^{-1}\dot{\mu}(s_0^*(t))x_0^*(t)] & -\gamma^{-1}\mu(s_0^*(t)) \\ x_0^*(t)\dot{\mu}(s_0^*(t)) & \mu(s_0^*(t)) - D \end{bmatrix}. \tag{22}$$

Set $\xi = \varphi + \gamma^{-1}\psi$, then $\dot{\xi}(t) = -D\xi(t)$ and, as $\xi \in C_\omega$ we can deduce that $\xi = 0$. Then we have that

$$\dot{\varphi}(t) = [\mu(s_0^*(t)) - D - \gamma^{-1}\dot{\mu}(s_0^*(t))x_0^*(t)]\varphi(t)$$

and note that $\varphi = 0$, indeed, otherwise φ does not vanish and, by ω-periodicity it follows that $\int_0^\omega [\mu(s_0^*(t)) - D - \gamma^{-1}\dot{\mu}(s_0^*(t))x_0^*(t)]\,\mathrm{d}t = 0$. By **(P)** this yields $0 = \int_0^\omega [\mu(s_0^*(t)) - D]\,\mathrm{d}t = \int_0^\omega \gamma^{-1}\dot{\mu}(s_0^*(t))x_0^*(t)\,\mathrm{d}t > 0$, a contradiction and consequently we have $\varphi = \psi = 0$. In other words; $D_{(s,x)}\Phi(s_0^*, x_0^*, 0)$ is injective; which is equivalent to say that the unique C_ω solution of (22) is $t \mapsto u(t) \equiv 0$.

Now we will prove that the map $(\varphi, \psi) \mapsto D_{(s,x)}\Phi(s_0^*, x_0^*, 0)(\varphi, \psi)$ is surjective: let us consider any vector function $t \mapsto f(t) = (\zeta(t), \theta(t)) \in C_\omega \times C_\omega$. The surjectiveness is equivalent to the existence of an ω-periodic solution of the non-homogeneous system

$$\dot{v} = A(t)v + f(t). \tag{23}$$

Any solution $t \mapsto v(t)$ of (23) has the form

$$v(t) = X(t)v(0) + \int_0^t X(t)X^{-1}(s)f(s)\,\mathrm{d}s,$$

where $X(t)$ is a fundamental matrix of (22) with $X(0) = I$. A direct consequence of the injectiveness is that $\det[X(\omega) - I] \neq 0$. Then, we can consider the initial condition $v(0) = [I - X(\omega)]^{-1}\int_0^\omega X(\omega)X^{-1}(s)f(s)\,\mathrm{d}s$ and it follows easily that $v(\omega) = v(0)$ which is equivalent to $v \in C_\omega$.

The open mapping Theorem allows to prove that the inverse of the map $(\varphi, \psi) \mapsto D_{(s,x)}\Phi(s_0^*, x_0^*, 0)(\varphi, \psi)$ is continuous.

By the implicit function theorem, we deduce the existence of a (locally unique) continuous branch of positive ω-periodic solutions $(s(\tau), x(\tau))$ for τ small. We claim that, making τ smaller if necessary, there are no other positive ω-periodic solutions. Indeed, otherwise there exists a sequence $\tau_n \to 0$ together with two distinct positive C_ω-solutions (s_n^1, x_n^1) and (s_n^2, x_n^2). Passing to a subsequence, we can use theorem 2.2 from [20, ch 2] to verify that they converge uniformly to some limits (s^j, x^j), which are C_ω-solutions of the non-delayed problem. Because $\mathcal{M}(\mu(s_n^j)) = D$ for all n, so does $\mathcal{M}(\mu(s^j))$; thus we deduce that $s^j \neq v^*$ and lemma 2 says that $(s^j, x^j) = (s_0^*, x_0^*)$ for $j = 1, 2$. Thus, for n large both sequences enter into the neighbourhood provided by the implicit function theorem, which yields a contradiction.

5. Numerical simulation

In order to illustrate our results we performed numerical simulations considering a Monod or Michaelis–Menten type function (2) and a nutrient supply of type

$$s^0(t) = \Lambda + \varepsilon\ \sin(2\pi t),$$

Table 2. Parameters and their interval bounds.

Parameter	Units	Meaning	Values
D	l/day	Dilution rate	Arbitrary
Λ	μmol l^{-1}	Input nutrient concentration when $\varepsilon = 0$	[80, 120]
$\mu_{\max}$	l/day	Maximum growth gate	[1.2, 1.6]
k_s	μmol l^{-1}	Half-saturation constant	[0.01, 0.2]
γ	μm^3 μmol^{-1}	Growth yield	[0.15, 0.6]

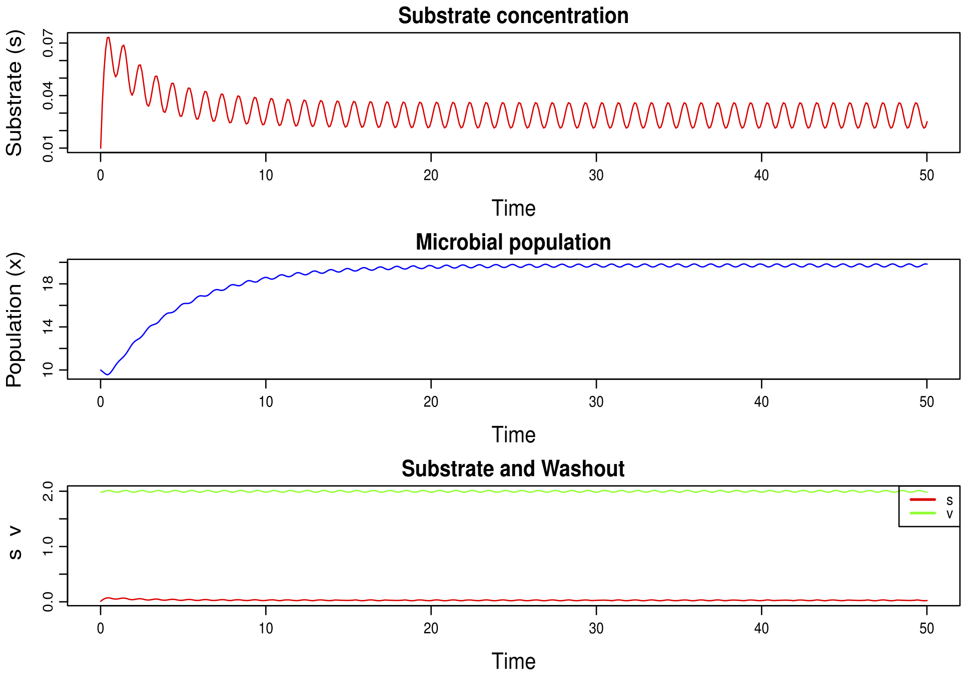

Figure 1. Numerical example with parameters $D = 0.2, \Lambda = 2, \varepsilon = 0.5, \tau = 0.33, \mu_{\max} = 1.6, k_s = 0.2, \quad \gamma = 10, \quad \varphi \equiv 0.01, \quad x(0) = 10$ and $\mathcal{M}\{\mu(v^*)\} \approx 1.469\,077 > D$.

with the parameters and units from [46, p 491], which are described in the following table (table 2):

The above parameters have been estimated when studying the growth of the microalgae *D. tertiolecta* under a limitation of nitrate. The reader is referred to [6] for a deeper study of this topic.

We carried our numerical simulations by using the library PBSddesolve in R [43] with parameters from the above table and three delays lower than the period 1.

The figures 1 and 2 were carried out with initial conditions $(0.01, 10)$ and $(0.08, 10) \in C([-\tau, 0], \mathbb{R}) \times \mathbb{R}$ respectively. The parameters are chosen such that (12) is verified and both figures confirm theorem 2. Nevertheless, the figures also suggest the uniqueness and attractiveness of the ω-periodic solution $t \mapsto (s^*(t), x^*(t))$.

The figure 3 is carried out with an initial condition $(0.08, 10) \in C([-\tau, 0], \mathbb{R}) \times \mathbb{R}$. The parameters are chosen such that (11) is verified and the theorem 1 is confirmed.

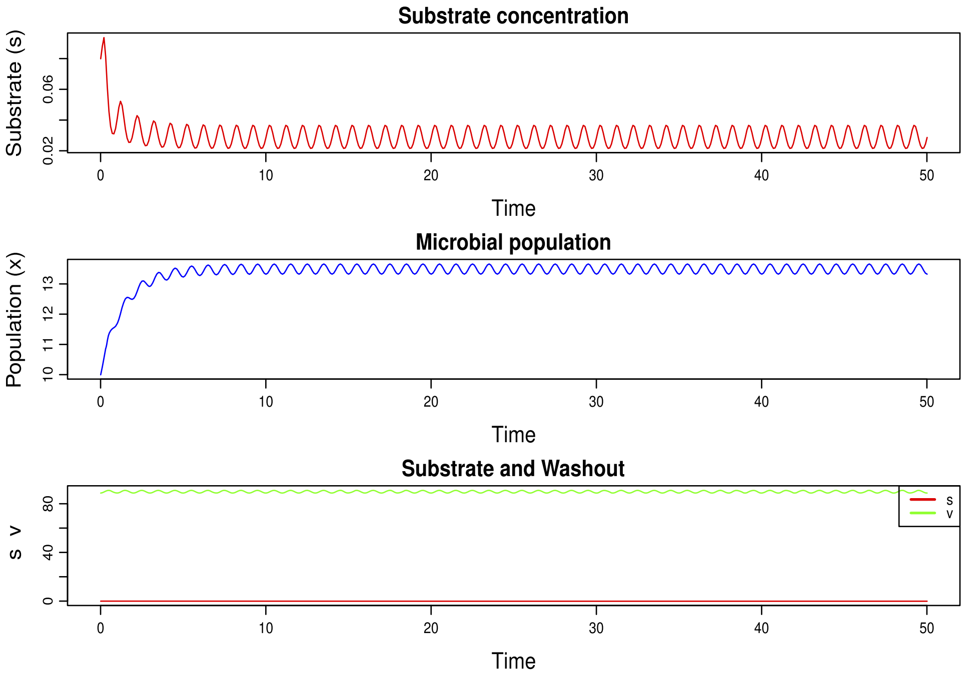

Figure 2. Numerical example with parameters $D = 0.7, \Lambda = 90, \varepsilon = 10$, $\tau = 0.014, \mu_{\max} = 1.2, k_s = 0.02,\ \gamma = 0.15,\ \varphi \equiv 0.08,\ x(0) = 10$ and $\mathcal{M}\{\mu(v^*)\} \approx 1.211\,731 > D$.

6. Discussion

We studied a model of a one species chemostat with ω-periodic input of a single substrate whose metabolization has a delay with respect to its consumption, which is described by the DDE system (1). Previous studies have been made for the undelayed case, where the change of variables $v = s + \gamma^{-1}x$ leads to a nonlinear triangular system, whose study allows to obtain necessary and sufficient conditions for the existence, uniqueness and attractivity, which coincides with the average inequality (12). Nevertheless, the delayed case induces technical difficulties which prompt to follow a completely different approach managing to obtain an existence result, we also proved the uniqueness for small delays. We point out that if we consider D and s^0 as ω-periodic inputs in the model (1), the proof of our three results could be made in similar way as in this work and the differences will be only technical. Obviously, the constant D must be replaced by $\mathcal{M}(D)$ in (11) and (12).

As we stated on the introduction and section 2, the undelayed system (1) has industrial and biologic motivations. We expect that our results could contribute to deepen those researches. In addition and contrarily to the undelayed case, an extensive bifurcation analysis and a uniform persistence study for (1) remains to be done (figure 4).

Our numerical simulations show the attractiveness of a non-trivial ω-periodic solution, we expect to carry out a more complete study of the uniqueness and attractiveness problem in a future work. We have in mind two approaches to cope with this problem: to construct a Lyapunov–Krasovskii functional as in [17, 28], the second approach is to employ some new

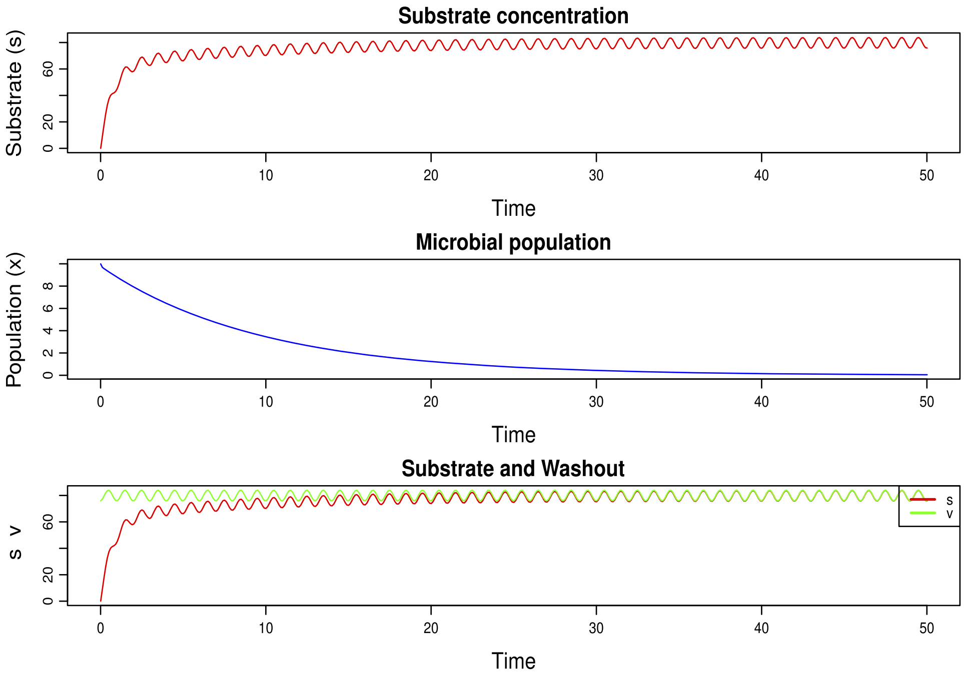

Figure 3. Numerical example with parameters $D = 1.3, \Lambda = 80, \varepsilon = 20$, $\tau = 0.014, \mu_{\max} = 1.2, k_s = 0.2$, $\gamma = 0.6$, $\varphi \equiv 0.08$, $x(0) = 10$ and $\mathcal{M}\{\mu(v^*)\} \approx 1.208\,972 < D$.

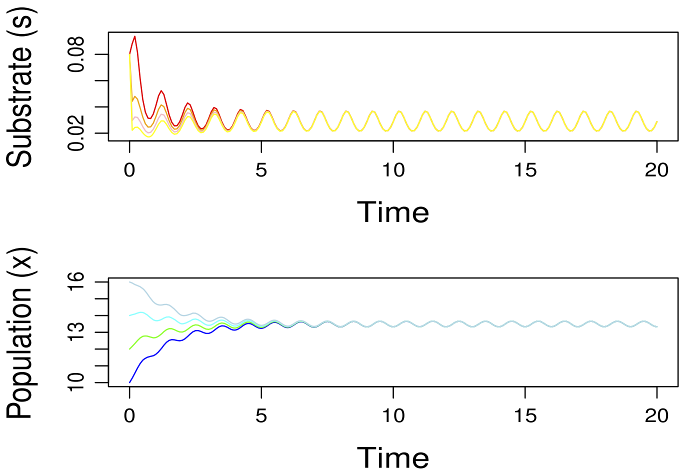

Figure 4. Numerical simulations with the parameters of figure 2 and initial conditions $x_1(0) = 10, x_2(0) = 12, x_3(0) = 14, x_4(0) = 16$ and $\varphi_1 = \varphi_2 = \varphi_3 = \varphi_4 \equiv 0.08$.

results from nonautonomous dynamical systems (pullback and forward attractors) as done in [11] and references therein.

Another interesting problem is to address a competitive periodic chemostat described by the equations

$$\begin{cases} \dot{s}(t) = Ds^0(t) - Ds(t) - \displaystyle\sum_{i=1}^{n} \gamma_i^{-1} \mu_i(s(t)) x_i(t) & \text{if } t \geqslant 0, \\ \dot{x}_i(t) = x_i(t) \left\{ \mu_i(s(t-\tau_i)) - D \right\} & \text{if } t \geqslant 0, \\ s(\theta) = \varphi(\theta) \quad \text{and} \quad x_i(0) = x_{i,0} \ (i = 1, \ \ldots, \ n) & \text{if } \theta \in [-\tau_i, 0], \end{cases} \tag{24}$$

which generalizes the ODE system (6) to a DDE framework. In [17, theorem1] it was proved that if $t \mapsto s^0(t)$ is a positive constant function, the asymptotic behaviour of (24) is the competitive exclusion. In addition, the competitive exclusion has also be proved for competitive versions of the system (5) as done in [13].

As we stated in section 2, the existence of ω-periodic solutions of (4) was useful to prove the existence of ω-periodic solutions for (6). Similarly, we hope that the main results of this paper will be useful to find sufficient condition ensuring the existence of ω-periodic solutions for (24).

Acknowledgments

We thank the anonymous referees for the careful reading of the manuscript and fruitful remarks. The authors are also grateful to Miguel Montenegro (Department of Mathematics, Universidad Tecnológica Metropolitana—Chile) for his valuable help carrying out our numerical simulations and using R solver. The first author is partially supported by project UBACyT 20020160100002BA. Daniel Sepúlveda acknowledges the support of the grant FONDECYT Iniciación Científica 11190457 (Chile).

Appendix A. Technical results

For the convenience of the reader, we briefly describe two subjects that played a key role in the proof of theorem 2.

Whyburn's lemma. The following result was introduced by Whyburn in [47, p 12]:

Lemma 3. *Let (X, d) be a metric space, and let $K \subset X$ be compact. If K_0 and K_1 are disjoint closed subsets of K such that no connected subset of K intersects both of them, then there exist disjoint closed sets $C_0, C_1 \subset K$ such that $K_0 \subset C_0$, $K_1 \subset C_1$ and $K = C_0 \cup C_1$.*

In addition, under the assumptions of lemma 3 it is easy to prove the existence of an open bounded set Ω containing C_0 such that $\Omega \cap C_1 = \emptyset$ and $\partial\Omega \cap K = \emptyset$. Take for instance $\Omega = \bigcup_{x \in C_0} B(x, \varepsilon/2)$, where $\varepsilon = \min\limits_{u \in C_0, v \in C_1} d(u, v)$.

Leray–Schauder degree. Let E be a Banach space and $\Omega \subset E$ be an open and bounded subset. The Leray–Schauder degree [8] is a function that assigns to each operator $F = I - K : \overline{\Omega} \to E$ with K compact and $0 \notin F(\partial\Omega)$ an integer with the following properties:

(a) Normalization:

$$\deg(I, \Omega, 0) = \begin{cases} 1 & \text{if } 0 \in \Omega, \\ 0 & \text{if } 0 \notin \Omega. \end{cases}$$

(b) Solution: if $\deg(F, \Omega, 0) \neq 0$, then F vanishes in Ω.
(c) Excision: if $\Omega_1 \subset \Omega$ is open and F does not vanish in $\overline{\Omega} \backslash \Omega_1$, then

$$\deg(F, \Omega, 0) = \deg(F, \Omega_1, 0).$$

(d) Homotopy invariance: if $K : \overline{\Omega} \times [0, 1] \to E$ is compact such that $K(x, \lambda) \neq x$ for $x \in \partial\Omega$ and $\lambda \in [0, 1]$, then $\deg(I - K(\cdot, \lambda), \Omega, 0)$ is constant.

ORCID iDs

Pablo Amster https://orcid.org/0000-0003-2829-7072
Gonzalo Robledo https://orcid.org/0000-0002-6674-7823
Daniel Sepúlveda https://orcid.org/0000-0002-3129-393X

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