Dynamics of non-autonomous chemostat models

Tomás Caraballo, Xiaoying Han, Peter E. Kloeden and Alain Rapaport

Abstract Chemostat models have a long history in the biological sciences as well as in biomathematics. Hitherto most investigations have focused on autonomous systems, that is, with constant parameters, inputs and outputs. In many realistic situations these quantities can vary in time, either deterministically (e.g., periodically) or randomly. They are then non-autonomous dynamical systems for which the usual concepts of autonomous systems do not apply or are too restrictive. The newly developing theory of non-autonomous dynamical systems provides the necessary concepts, in particular that of a non-autonomous pullback attractor. These will be used here to analyze the dynamical behavior of non-autonomous chemostat models with or without wall growth, time dependent delays, variable inputs and outputs. The possibility of over-yielding in non-autonomous chemostats will also be discussed.

Tomás Caraballo
Dpto. Ecuaciones Diferenciales y Análisis Numérico, Universidad de Sevilla, Apdo. de Correos 1160, 41080-Sevilla, Spain. e-mail: caraball@us.es

Xiaoying Han
221 Parker Hall, Department of Mathematics and Statistics, Auburn University, Auburn, AL 36849 USA. e-mail: xzh0003@auburn.edu

Peter E. Kloeden
School of Mathematics and Statistics, Huazhong University of Science & Technology, Wuhan 430074, China, and Felix-Klein-Zentrum für Mathematik, TU Kaiserslautern, D-67663 Kaiserslautern, Germany. e-mail: kloeden@mathematik.uni-kl.de

Alain Rapaport
UMR INRA/SupAgro MISTEA, 2 place Viala, 34060 Montpellier, France, and MODEMIC team, INRIA, rte des Lucioles, 06 902 Sophia-Antipolis, France. e-mail: rapaport@supagro.inra.fr

1 Introduction

Traditional models of the chemostat assume fixed availability of the nutrient and its supply rate, as well as fast flow rates to avoid the tendency of microorganisms to attach to container walls. However, these assumptions become unrealistic when the availability of a nutrient depends on the nutrient consumption rate and input nutrient concentration and when the flow rate is not fast enough. On the other hand, the appearance of delay terms in chemostat models [4, 5] can be fully justified since the future behavior of a dynamical system does not in general only depend on the present but also on its history. Sometimes only a short piece of history provides the relevant influence (bounded or finite delay), while in other cases it is the whole history that has to be taken into account (unbounded or infinite delay). In this article we will discuss chemostat models with a variable nutrient supplying rate and a variable input nutrient concentration, along with time–variable delays and wall growth.

Denote by $x(t)$ the concentration of the growth-limiting nutrient and by $y(t)$ the concentration of the microorganism at any time t. When wall attachment is taken into account (see e.g. [3, 13, 16]), we can regard the consumer population $y(t)$ as an aggregate of two categories of populations, one in the growth medium, denoted by $y_1(t)$, and the other on the walls of the container, denoted by $y_2(t)$. Suppose that the nutrient is equally available to both of the categories, so it can be assumed that both categories consume the same amount of nutrient and at the same rate. Let D be the rate at which the nutrient is supplied and also the rate at which the contents of the growth medium are removed, and I be the input nutrient concentration which describes the quantity of nutrient available with the system at any time. Assume that D and I vary continuously in time (e.g., periodically [6] or randomly) in bounded positive intervals $D(t) \in [d_m, d_M]$ and $I(t) \in [i_m, i_M]$, respectively, for all $t \in \mathbb{R}$. In addition, let $\tau_1(t)$ and $\tau_2(t)$ be the time delay into material recycling and in the growth response of the consumer species, respectively. The consideration of variable inputs, variable delays and wall growth result in the following system of non-autonomous delay differential equations:

$$\frac{dx(t)}{dt} = D(t)[I(t) - x(t)] - aU(x(t))[y_1(t) + y_2(t)] + b\gamma y_1(t - \tau_1(t)), \qquad (1)$$

$$\frac{dy_1(t)}{dt} = -[\gamma + D(t)]y_1(t) + cU(x(t - \tau_2(t)))y_1(t) - r_1 y_1(t) + r_2 y_2(t), \qquad (2)$$

$$\frac{dy_2(t)}{dt} = -\gamma y_2(t) + cU(x(t - \tau_2(t)))y_2(t) + r_1 y_1(t) - r_2 y_2(t), \qquad (3)$$

where $a > 0$ is the maximal consumption rate of the nutrient and also the maximum specific growth rate of microorganisms, c with $0 < c \leq a$ is the growth rate coefficient of the consumer species, γ is the collective death rate of microorganisms, $b \in (0,1)$ is the fraction of dead biomass that is recycled, r_1 and r_2 are the rates at which the species stick on to and shear off from the walls respectively, and U is the uptake function describing how the nutrient is consumed by the species and satisfying:

(1) $U(0)=0$ and $U(x)>0$ for all $x>0$;
(2) $\lim_{x\to\infty} U(x)=L<\infty$;
(3) U is continuously differentiable;
(4) U is monotonically increasing.

In this article, when concrete computations are sought, we choose the uptake function to have the Michaelis-Menten or Holling type-II form, given by

$$U(x)=\frac{x}{\lambda+x}, \tag{4}$$

where $\lambda>0$ is the half-saturation constant. The results in all but the last section are collected from the papers [7, 8, 9].

2 Preliminaries on non-autonomous dynamical systems

Given a real number $h\geq 0$, denote by $C_h:=C([-h,0],\mathbb{R}^n)$ the Banach space of continuous functions mapping the interval $[-h,0]$ into $\mathbb{R}^n$ equipped with the usual supremum norm

$$\|\phi\|_{C_h}=\sup_{\theta\in[-h,0]}|\phi(\theta)|.$$

Note that $C_h\cong\mathbb{R}^n$ when $h=0$.

Consider the functional differential equation

$$\dot{z}(t)=f(t,z_t) \tag{5}$$

where $f:\mathbb{R}\times C_h\to\mathbb{R}^n$ is continuous and maps bounded sets into bounded sets and $z_t(\cdot)\in C_h$ is given by

$$z_t(\theta)=z(t+\theta),\quad \theta\in[-h,0],$$

for any given continuous function $z(\cdot):\mathbb{R}\to\mathbb{R}^n$ and $t\in\mathbb{R}$. Note that Equation (5) is a general formulation and includes ordinary differential equations $(h=0)$

$$\dot{z}(t)=f(t,z(t)),$$

in which case the state space C_h reduces to $\mathbb{R}^n$.

Assume that an initial function $\psi\in C_h$ prescribed at the initial time $t_0\in\mathbb{R}$ is associated with (5) to form an initial value problem. The solution of this initial value problem for which an existence and uniqueness theorem holds then defines a solution map, $Z(t,t_0)$: $\psi\mapsto z_t(\cdot;t_0,\psi)\in C_h$ for $t\geq t_0$, which is, in fact, a process (also called a two-parameter semigroup) satisfying

- $Z(t,t_0):C_h\to C_h$ is a continuous map for all $t\geq t_0$;
- $Z(t_0,t_0)=Id_{C_h}$, the identity on C_h, for all $t_0\in\mathbb{R}$;
- $Z(t,t_0)=Z(t,s)Z(s,t_0)$ for $t\geq s\geq t_0$.

Definition 1. Let Z be a process on a complete metric space X. A family $\mathscr{A} = \{A(t)\}_{t\in\mathbb{R}}$ of compact subsets of X is called a pullback attractor for Z if it is

- invariant: $Z(t,t_0)A(t_0) = A(t)$ for all $t \geq t_0$;
- pullback attracting: for any nonempty bounded subset D of X

$$\mathrm{dist}_X\{Z(t,t-t_0)D, A(t)\} \to 0 \quad \text{as} \quad t_0 \to \infty \quad (\text{for each } \ t \in \mathbb{R})$$

where dist_X denotes the Hausdorff semi-distance.

Pullback attraction uses information about the dynamical system from the past in contrast with the usual forward convergence with $t \to \infty$ for fixed t_0 which uses information about the future.

Definition 2. A family $\{B(t)\}_{t\in\mathbb{R}}$ of nonempty subsets of X is said to be pullback absorbing with respect to a process Z if for each $t \in \mathbb{R}$, and every nonempty bounded subset D of X, there exists $T_D(t) > 0$ such that

$$Z(t,t-\sigma)D \subseteq B(t), \quad \text{for all } \ \sigma \geq T_D(t).$$

The following result (see [15]) shows that the existence of a family of compact absorbing sets implies the existence of a pullback attractor.

Theorem 1. *Let $Z(t,t_0)$ be a process on a complete metric space X. If there exists a family $\{B(t)\}_{t\in\mathbb{R}}$ of compact absorbing sets, then there exists a pullback attractor $\mathscr{A} = \{A(t)\}_{t\in\mathbb{R}}$ such that $A(t) \subset B(t)$ for all $t \in \mathbb{R}$. Furthermore,*

$$A(t) = \overline{\bigcup_{\substack{D\subset X \\ bounded}} \Lambda_D(t)} \quad where \quad \Lambda_D(t) = \bigcap_{T\geq 0} \overline{\bigcup_{t_0\geq T} Z(t,t-t_0)D}.$$

For the general case of (5) being a delay differential equation ($h \neq 0$), the next sufficient condition ensures the existence of a pullback attractor.

Theorem 2. *([11, Theorem 4.1]) Suppose that $Z(t,t_0)$ maps bounded sets of C_h into bounded sets of C_h, and there exists a family $\{B(t)\}_{t\in\mathbb{R}}$ of bounded absorbing sets for Z in C_h. Then there exists a pullback attractor $\mathscr{A}$ for equation* (5).

For the particular case of (5) being an ordinary differential equation ($h = 0$), the following theorem ensures the existence of an attractor in both the forward and pullback senses that consists of singleton sets, i.e., a single entire solution.

Theorem 3. *([14, 15]) Suppose that a process Z on $\mathbb{R}^n$ is uniform strictly contracting on a positively invariant pullback absorbing family $\{B(t)\}_{t\in\mathbb{R}}$ of nonempty compact subsets of $\mathbb{R}^n$, i.e., for each $R > 0$, there exist positive constants K and α such that*

$$|Z(t,t_0)x_0 - Z(t,t_0)y_0|^2 \ \leq \ Ke^{-\alpha(t-t_0)} \cdot |x_0 - y_0|^2, \quad \forall t \geq t_0, \ x_0, y_0 \in \mathbb{B}(0,R),$$

where $\mathbb{B}(0,R)$ is the closed ball in $\mathbb{R}^n$ centered at the origin with radius $R >$ 0. Then the process Z has a unique global forward and pullback attractor $\mathscr{A} =$

$\{A(t) : t \in \mathbb{R}\}$ with component sets consisting of singleton sets, i.e., $A(t) = \{\xi^*(t)\}$ for each $t \in \mathbb{R}$, where ξ^* is an entire solution of the process.

3 Properties of solutions

The existence and uniqueness of solutions to (1)-(3) with initial conditions

$$x(t) = \psi_1(t-t_0),\, y_1(t) = \psi_{21}(t-t_0),\, y_2(t) = \psi_{22}(t-t_0), \quad \forall t \in [t_0-h, t_0] \tag{6}$$

follow immediately from the continuity of the input functions $D(t)$ and $I(t)$ and the assumptions on the uptake function U. Therefore we have the unique solution $z(\cdot;t_0,\psi)$ of (1)-(3) such that $z_{t_0}(\cdot;t_0,\psi) = \psi$, i.e.,

$$z_{t_0}(\theta;t_0,\psi) := z(t_0+\theta;t_0,\psi) = \psi(\theta) \quad \text{for} \quad \theta \in [-h,0].$$

Consequently we can construct a non-autonomous dynamical system or process $Z(t,t_0) : C_h \to C_h$ in the phase space C_h defined for any $t \geq t_0$ as

$$Z(t,t_0)\phi = z_t(\cdot;t_0,\phi), \quad \phi \in C_h.$$

The positiveness and boundedness of solutions are stated in the following theorems.

Theorem 4. *For any non-negative continuous initial condition* (6) *on* $[t_0-h,t_0]$*, the solutions to* (1)-(3) *are non-negative.*

Proof. We will show that if a solution starts in the octant $\mathbb{R}^3_+ = \{(x,y_1,y_2) : x \geq 0, y_1 \geq 0, y_2 \geq 0\}$, then it remains there forever. In fact, by continuity, each solution has to take value 0 before it reaches a negative value. With $x = 0$ and $y_1 \geq 0$, $y_2 \geq 0$, equation (1) reduces to

$$x'(t) = D(t)I(t) + b\gamma y_1(t-\tau_1(t)),$$

and thus $x(t)$ is strictly increasing at $x = 0$. With $y_1 = 0$ and $x \geq 0$, $y_2 \geq 0$, the reduced ODE for $y_1(t)$ is

$$y_1'(t) = r_2 y_2 \geq 0,$$

hence $y_1(t)$ is non-decreasing at $y_1 = 0$. Similarly, y_2 is non-decreasing at $y_2 = 0$. Therefore, $(x(t), y_1(t), y_2(t)) \in \mathbb{R}^3_+$ for any t. □

Theorem 5. *Assume that $D : \mathbb{R} \to [d_m, d_M]$ where $0 < d_m < d_M < \infty$, and $I : \mathbb{R} \to [i_m, i_M]$ where $0 < i_m < i_M < \infty$ are continuous. In addition assume that $\tau_1'(t) \leq M_1 < 1$ for all $t \in \mathbb{R}$. Then solutions to* (1)-(3) *are bounded for any bounded initial conditions provided that*

$$\mu := \min\{\delta, \gamma - c\} > 0 \quad \text{where} \quad \delta := d_m - \frac{M_1}{1-M_1}\gamma - c. \tag{7}$$

Proof. Define over $\mathbb{R}\times C_h$ the functional $v(\cdot,\cdot,\cdot,\cdot)$ as

$$v(t,\phi_1,\phi_{21},\phi_{22}) := \phi_1(0)+b\phi_{21}(0)+b\phi_{22}(0)+\frac{b\gamma}{1-M_1}\int_{-\tau_1(t)}^{0}\phi_{21}(s)ds. \qquad (8)$$

Given a solution $z(\cdot)=(x(\cdot),y_1(\cdot),y_2(\cdot))$ of (1)-(3) corresponding to an initial datum $(\psi_1,\psi_{21},\psi_{22})\in C_h$, define the function $\nu(t):=\nu(t,z_t)$ for $t\in\mathbb{R}$. After a change of variable in the integral in (8) we obtain

$$\nu(t)=x(t)+by_1(t)+by_2(t)+\frac{b\gamma}{1-M_1}\int_{t-\tau_1(t)}^{t}y_1(s)ds.$$

Then the time derivative of $\nu(t)$ along solutions to (1)-(3) is

$$\begin{aligned}\frac{d\nu(t)}{dt} &= D(t)I(t)-D(t)x(t)-aU(x(t))(y_1(t)+y_2(t))+b\gamma y_1(t-\tau_1(t))\\ &\quad -b[\gamma+D(t)]y_1(t)-b\gamma y_2(t)+bcU(x(t-\tau_2(t))(y_1(t)+y_2(t))\\ &\quad +\frac{b\gamma}{1-M_1}(y_1(t)-(1-\tau_1'(t))y(t-\tau_1(t))).\end{aligned}$$

Since $\tau_1'(t)\le M_1<1$, we have $-\frac{1}{1-M_1}(1-\tau_1'(t))\le -1$. Also using the facts that $U(x)\le 1$ for $x\ge 0$, $d_m\le D(t)\le d_M$ and $i_m\le I(t)\le i_M$ for any t, we have

$$\begin{aligned}\frac{d\nu(t)}{dt} &\le d_Mi_M-d_mx(t)-b(\gamma+d_m)y_1(t)-b\gamma y_2(t)+bc(y_1(t)+y_2(t))+\frac{b\gamma}{1-M_1}y_1(t)\\ &\le d_Mi_M-d_mx(t)-b\left(\gamma+d_m-c-\frac{b\gamma}{1-M_1}\right)y_1(t)-b(\gamma-c)y_2(t)\\ &\le d_Mi_M-d_mx(t)-b\delta y_1(t)-b(\gamma-c)y_2(t).\end{aligned}$$

where δ is as defined in (7). Now define the region

$$\Omega := \{(x,y_1,y_2)\in\mathbb{R}_+^3 : d_mx+b\delta y_1+b(\gamma-c)y_2\le d_Mi_M\}.$$

If a trajectory starts at time t_0 from a point in $\mathbb{R}_+^3\setminus\Omega$, then the functional $\nu(\cdot,\cdot,\cdot,\cdot)$ along a trajectory starting from this point would be decreasing for all times $t\ge t_0$ such that $(x(t),y_1(t),y_2(t))\in\mathbb{R}_+^3\setminus\Omega$. Therefore

$$\begin{aligned}\nu(t,x_t,(y_1)_t,(y_2)_t) &\le \nu(t,x_{t_0},(y_1)_{t_0},(y_2)_{t_0})\\ &\le x(t_0)+by_1(t_0)+by_2(t_0)+\frac{b\gamma}{1-M_1}\int_{t_0-\tau_1(t)}^{t_0}y_1(s)ds\\ &\le |\psi_1|+b\left(1+\frac{\gamma h}{1-M_1}\right)|\psi_{21}|+b|\psi_{22}|,\end{aligned}$$

which implies that

$$\begin{aligned}\|(x(t),y_1(t),y_2(t))\| &:= x(t)+y_1(t)+y_2(t)\\ &\leq \frac{1}{b}\nu(t,x_t,(y_1)_t,(y_2)_t) \leq \frac{1}{b}|\psi_1| + \left(1+\frac{\gamma h}{1-M_1}\right)|\psi_{21}|+|\psi_{22}|. \quad (9)\end{aligned}$$

If a trajectory starts from or enters the region Ω at $t_1 \geq t_0$ and stays in Ω forever, then by the definition of Ω we have that for any time $t \geq t_0$, $d_m x(t) + b\delta y_1(t) + b(\gamma - c)y_2(t) \leq d_M i_M$, which implies that

$$\|(x(t),y_1(t),y_2(t))\| \leq \frac{d_m}{b\mu}x(t) + \frac{\delta}{\mu}y_1(t) + \frac{\gamma - c}{\mu}y_2(t) \leq \frac{d_M i_M}{b\mu}. \quad (10)$$

If a trajectory starts from, enters or re-enters the region Ω at times $t_{2i-1} \geq t_0$ and exits at time t_{2i}, $(i = 1,2,\cdots)$, then (9) holds for all times (t_{2i}, t_{2i+1}) and (10) holds for all times (t_{2i-1}, t_{2i}).

To summarize, for any $t > t_0$, we have

$$\begin{aligned}\|z_t\| = \|(x_t, y_{1t}, y_{2t})\| &= x(t+\theta) + y_1(t+\theta) + y_2(t+\theta)\\ &\leq \max\left\{\frac{|\psi_1|}{b} + \left(1+\frac{\gamma h}{1-M_1}\right)|\psi_{21}|+|\psi_{22}|, \frac{d_M i_M}{b\mu}\right\}.\end{aligned}$$

Therefore, given any $(\psi_1, \psi_{21}, \psi_{22}) \in C_h$ with $|\psi_1| + |\psi_{21}| + |\psi_{22}| \leq r$, we have $z_t = (x_t, y_{1t}, y_{2t}) \in \mathbb{B}_{C_h}(0, \tilde{r})$ for $t \geq t_0$, where

$$\tilde{r} := \max\left\{\frac{r}{b}, r\left(1+\frac{\gamma h}{1-M_1}\right), \frac{d_M i_M}{b\mu}\right\}. \qquad \square$$

In the next section we will discuss the existence of non-autonomous attractors for different variations of system (1)-(3). Geometric details of the attractors are provided for some special cases.

4 Pullback attractors for non-autonomous chemostat models

In this section we discuss the existence and properties of the pullback attractors for the chemostat system (1)-(3). In particular, we will study the system with wall growth and variable delays, wall growth and variable inputs, and the special case with no wall growth.

4.1 Chemostats with wall growth, variable delays and fixed inputs

When $D(t) = D$, $I(t) = I$, $\tau_1(t) \neq 0$ and $\tau_2(t) \neq 0$, the existence of a pullback absorbing set can be proved by using the Razumikhin technique, which uses a Lyapunov function rather than a functional. The reader can find an interesting motivation for the Razumikhin technique in the book by Hale and Lunel [12, pp. 151]. More precisely, our result is a consequence of the uniformly ultimately boundedness of the solutions according to Theorem 4.3 on pp.159 in [12]. To make the result more accessible to the reader, we first recall the following notation.

Given a continuous function $V : \mathbb{R} \times \mathbb{R}^n \to \mathbb{R}$ and an initial function $\phi \in C_h$, the (upper Dini) derivative of V along the solutions of (5) is defined to be

$$\dot{V}(t,\phi(0)) = \limsup_{\varepsilon\to 0^+} \frac{1}{\varepsilon}[V(t+\varepsilon, z(t+\varepsilon;t,\phi) - V(t,\phi(0))]. \tag{11}$$

Theorem 6. *Assume that $D(t) = D$, $I(t) = I$ and $\tau_1'(t) \leq M_1 < 1$. Then the non-autonomous dynamical system generated by* (1)-(3) *possesses a pullback attractor in C_h provided that*

$$\min\left\{D - \frac{M_1}{1-M_1}\gamma - c, \gamma - c\right\} > 0 \quad \textit{and} \quad \min\{D, \gamma - c\} > b\gamma.$$

Proof. Since we are interested in only non-negative solutions, consider the function

$$V(t,x,y_1,y_2) := x + y_1 + y_2 = \|(x,y_1,y_2)\|.$$

Given any initial value $\phi \in C_h$ we consider the solution $z(\cdot;t,\phi){:=}(x(\cdot),y_1(\cdot),y_2(\cdot))$ of (1)-(3) passing through (t,ϕ) and we will check the assumptions in Theorem 4.3 from [12]. Observe that when V is differentiable, the upper Dini derivative coincides with the derivative of the function V along solutions of the problem (5). However, the Lyapunov function will not always be differentiable, but only continuous. Hence we can write $x(t) = \phi_1(0)$, $y_1(t) = \phi_{21}(0)$ and $y_2(t) = \phi_{22}(0)$ at time t.

By letting $u(s) = s/2$ and $v(s) = 2s$, we have

$$u(\|(x,y_1,y_2)\|) \leq V(t,x,y_1,y_2) \leq v(\|(x,y_1,y_2)\|).$$

The time derivative of V along the solution of (1)-(3) through (t,ϕ) satisfies

$$\begin{aligned}\dot{V}(t,\phi(0)) &= DI - D\phi_1(t) - (\gamma+D)\phi_{21}(0) - \gamma\phi_{22}(0) + b\gamma\phi_{21}(-\tau_1(t)) \\ &\qquad - [aU(\phi_1(0)) - cU(\phi_1(-\tau_2(t)))](\phi_{21}(0)+\phi_{22}(0)) \\ &\leq DI - D\phi_1(0) - (\gamma+D-c)\phi_{21}(0) - (\gamma-c)\phi_{22}(0) + b\gamma\phi_{21}(-\tau_1(t)).\end{aligned}$$

For any $q > 1$, define $p(s) = qs$. Provided that $V(t+\theta,\phi(\theta)) < p(V(t,\phi(0)))$ for $\theta \in [-h,0]$, we have

$$\phi_{21}(-\tau_1(t)) < q(\phi_1(0) + \phi_{21}(0) + \phi_{22}(0)).$$

Consequently,

$$\dot{V}(t,\phi(0)) \leq DI-(D-b\gamma q)\phi_1(0)-(\gamma+D-c-b\gamma q)\phi_{21}(0)-(\gamma-c-b\gamma q)\phi_{22}(0)$$
$$\leq DI-G_q[\phi_1(0)+\phi_{21}(0)+\phi_{22}(0)]=DI-G_q\|\phi(0)\|,$$

where $G_q=\min\{D,\gamma-c\}-b\gamma q$.

Fix $q=1+\varepsilon$, then $G_q>0$ when ε is small enough and $\min\{D,\gamma-c\}>b\gamma$. Letting

$$w(s)=\begin{cases}0, & s\leq DI/G_q,\\ \frac{1}{2}(G_q s-DI), & s>DI/G_q,\end{cases}$$

we have $\dot{V}(t,\phi(0))\leq -w(\|\phi(0)\|)$ for any $\|\phi(0)\|\geq 0$. It follows immediately from Theorem 4.3 on pp. 159 in [12] that the solutions to (1)-(3) are uniformly ultimately bounded, i.e., there exists $\beta>0$ such that for any $\alpha>0$, there is a constant $T_\alpha>0$, which is independent of t, such that

$$\|z(t;t_0,\phi)\|\leq\beta,\quad \forall t\geq t_0+T_\alpha,\quad \forall t_0\in\mathbb{R},\, \phi\in C_h,\, \|\phi\|_{C_h}\leq\alpha.$$

This implies that the absorbing sets exist, in both the pullback and forward senses. The existence of a non-autonomous attractor then follows immediately from Theorems 2 and 5. □

4.2 *Chemostat with wall growth, variable inputs and no delays*

For the special case with no delays, $\tau_1(t)=\tau_2(t)=0$ the system (1) - (3) consists of ordinary differential equations. In addition to the existence of non-autonomous attractors we will be able to obtain more geometric details of the attractor. To this end, we make the following change of variables:

$$\alpha(t)=\frac{y_1(t)}{y_1(t)+y_2(t)},\qquad z(t)=y_1(t)+y_2(t). \tag{12}$$

Assuming that $U(x)=\dfrac{x}{\lambda+x}$, system (1) - (3) then attains the form

$$x'(t)=D(t)[I(t)-x(t)]-\frac{ax(t)}{\lambda+x(t)}z(t)+b\gamma\alpha(t)z(t), \tag{13}$$

$$z'(t)=-\gamma z(t)-D(t)\alpha(t)z(t)+\frac{cx(t)}{\lambda+x(t)}z(t), \tag{14}$$

$$\alpha'(t)=-D(t)\alpha(t)(1-\alpha(t))-r_1\alpha(t)+r_2(1-\alpha(t)). \tag{15}$$

Observe that $\alpha(t)$ satisfies the Riccati equation (15) and is not coupled with $x(t)$ and $z(t)$. For any positive y_1 and y_2 we have $0<\alpha(t)<1$ for all t. Note that $\alpha'|_{\alpha=0}$

$= r_2 > 0$ and $\alpha'|_{\alpha=1} = -r_1 < 0$, so the interval $(0,1)$ is positively invariant. This is the biologically relevant region.

When $D(t) = D$ is a constant, there is a unique asymptotically stable steady state $\alpha^* \in (0,1)$ given by

$$\alpha^* := \frac{D + r_1 + r_2 - \sqrt{(D + r_1 + r_2)^2 - 4Dr_2}}{2D}. \tag{16}$$

Hence when $t \to \infty$, replacing $\alpha(t)$ by α^* in equations (13) and (14) we have

$$\frac{dx(t)}{dt} = D(I(t) - x(t)) - \frac{ax(t)}{\lambda + x(t)} z(t) + b\gamma\alpha^* z(t) \tag{17}$$

$$\frac{dz(t)}{dt} = -\gamma z(t) - D\alpha^* z(t) + \frac{cx(t)}{\lambda + x(t)} z(t). \tag{18}$$

More details of the long term dynamics of the solutions to (17) - (18) are established in the following theorem.

Theorem 7. *Assume that $D(t) = D$ for all $t \in \mathbb{R}$, and $I : \mathbb{R} \to [i_m, i_M]$ with $0 < i_m < i_M < \infty$ is continuous, $a \geq c$, $b \in (0,1)$ and $\gamma > 0$. Then system (17) - (18) has a pullback attractor $\mathscr{A} = \{A(t) : t \in \mathbb{R}\}$ inside the non-negative quadrant. Moreover,*

(i) the entire solution $(w^*(t), 0)$ is asymptotically stable (in the usual forwards sense) in $\mathbb{R}^2_+$, where

$$w^*(t) = De^{-Dt} \int_{-\infty}^{t} I(s) e^{Ds} ds,$$

and the pullback attractor $\mathscr{A}$ has a singleton component subset $A(t) = \{(w^*(t), 0)\}$ for all $t \in \mathbb{R}$, provided $\gamma + D\alpha^* > c$;

(ii) the pullback attractor $\mathscr{A}$ also contains points strictly inside the positive quadrant in addition to the set $\{(w^*(t), 0)\}$, provided

$$\gamma + D\alpha^* < \frac{cDi_M}{\lambda(a - c + \gamma - b\gamma\alpha^* + D) + Di_M} := \varphi_D(i_M). \tag{19}$$

Proof. (i) When $\gamma + D\alpha^* > c$,

$$\frac{dz(t)}{dt} = -\left(\gamma + D\alpha^* - \frac{cx(t)}{\lambda + x(t)}\right) z(t) \leq 0,$$

which implies that $z(t)$ decreases to 0 as $t \to \infty$ for any $z(t_0) \geq 0$. Consequently, $x(t)$ satisfies $\frac{dx(t)}{dt} = D(I(t) - x(t))$ and has a nontrivial nonautonomous equilibrium

$$x(t) = x(t_0) e^{-D(t - t_0)} + De^{-Dt} \int_{t_0}^{t} I(s) e^{Ds} ds,$$

which converges to $w^*(t)$ as $t \to \infty$ or $t_0 \to -\infty$.

(ii) Let $u(t) := x(t) + z(t)$, then

$$u'(t) = D(I(t) - x(t)) + \frac{(c-a)x(t)}{\lambda + x(t)} z(t) + b\gamma\alpha^* z(t) - \gamma z(t) - D(t)\alpha^* z(t).$$

On the one hand,

$$\begin{aligned} u'(t) &\leq D(I(t) - x(t)) - (\gamma - b\gamma\alpha^* + D\alpha^*) z(t) \\ &< DI(t) - Dx(t) - D\alpha^* z(t) \leq Di_M - D\alpha^* u(t). \end{aligned}$$

On the other hand,

$$\begin{aligned} u'(t) &\geq D(I(t) - x(t)) - (a - c + \gamma + D\alpha^* - b\gamma\alpha^*) z(t) \\ &\geq DI(t) - Dx(t) - (a - c + \gamma - b\gamma\beta^* + D) z(t) \\ &> Di_m - (a - c + \gamma - b\gamma\beta^* + D) u(t). \end{aligned}$$

Therefore we have the upper and lower bounds for $u(t)$ as

$$l := \frac{Di_M}{a - c + \gamma - b\gamma\alpha^* + D} < u(t) < \frac{i_M}{\alpha^*}. \tag{20}$$

For $\varepsilon > 0$ small, define T_ε to be the trapezoid

$$T_\varepsilon := \{(x,z) \in \mathbb{R}^2_+ : x \geq \varepsilon,\ \ z \geq \varepsilon,\ \ \frac{Di_M}{a - c + \gamma - b\gamma\alpha^* + D} \leq x + z \leq \frac{i_M}{\alpha^*}\},$$

then T_ε is absorbing. In addition, we have the following inequalities satisfied on the boundaries of T_ε:

$$\begin{aligned} x'(t)\big|_{x=\varepsilon} &= D(I(t) - \varepsilon) + (b\gamma\alpha^* - \frac{a\varepsilon}{\lambda + \varepsilon}) z(t) > 0, \\ z'(t)\big|_{z=\varepsilon} &> \left(-\gamma + D\alpha^* + \frac{c(l-\varepsilon)}{\lambda + l - \varepsilon}\right)\varepsilon > 0, \\ (x(t) + z(t))'\big|_{x+z=i_M/\alpha^*} &< 0, \quad (x(t) + z(t))'\big|_{x+z=l} > 0. \end{aligned}$$

Hence T_ε is invariant and this implies that there exists a pullback attractor $\mathscr{A} = \{A(t) : t \in \mathbb{R}\}$ in T_ε. □

When $I(t) = I$ is fixed and $D(t) \in [d_m, d_M]$ varies continuously in time, a pullback attractor of the form $\mathscr{A}_\alpha = \{A_\alpha(t) : t \in \mathbb{R}\}$ in the unit interval $(0,1)$ exists, since the unit interval is positively invariant (see e.g., [15]), and its component subsets are given by

$$A_\alpha(t) = \bigcap_{t_0 < t} \alpha\left(t, t_0, [0,1]\right), \qquad \forall t \in \mathbb{R}.$$

These component subsets have the form $A_\alpha(t) = \left[\alpha_l^*(t), \alpha_u^*(t)\right]$, where $\alpha_l^*(t)$ and $\alpha_u^*(t)$ are entire bounded solutions of the Riccati equation. Differential inequalities can be used to obtain bounds on these entire solutions as

$$A_\alpha(t) = [\alpha_l^*(t), \alpha_u^*(t)] \subset \left[\frac{r_2}{r_1+r_2+d_M}, \frac{r_2}{r_1+r_2}\right] := [\underline{\alpha}, \overline{\alpha}].$$

To investigate the case where the pullback attractor consists of a single entire solution, we need to find conditions under which $\alpha_l^*(t) \equiv \alpha_u^*(t)$ for any $t \in \mathbb{R}$. To this end, let $\Delta_\alpha(t) = \alpha_u^*(t) - \alpha_l^*(t)$. Then

$$\begin{aligned}\Delta_\alpha'(t) &= D(t)\left(\alpha_u^*(t)+\alpha_l^*(t)\right)\Delta_\alpha(t) - \left(D(t)+r_1+r_2\right)\Delta_\alpha(t)\\ &\le d_M \cdot 2\alpha_u^*(t)\Delta_\alpha(t) - (d_m+r_1+r_2)\Delta_\alpha(t)\\ &\le \left(\frac{2d_M r_2}{r_1+r_2} - d_m - r_1 - r_2\right)\Delta_\alpha(t).\end{aligned}$$

Thus, when $2d_M r_2 < d_m(r_1+r_2) + (r_1+r_2)^2$, we have

$$0 \le \Delta_\alpha(t) \le e^{\left(\frac{2d_M r_2}{r_1+r_2} - d_m - r_1 - r_2\right)(t-t_0)}\Delta_\alpha(t_0) \to 0 \quad \text{as } t\to\infty \quad \text{or} \quad t_0 \to -\infty.$$

Since $d_m < d_M$, this holds, e.g., if $d_M(r_2 - r_1) < (r_1+r_2)^2$. It essentially puts a restriction on the width of the interval in which $D(t)$ can takes its values, unless $r_1 > r_2$. Note that $\alpha^*(t)$ is also asymptotically stable in the forward sense in this case.

Therefore for t (or $-t_0$) sufficiently large, $x(t)$ and $z(t)$ components of the system (13)–(15) satisfy

$$x'(t) = D(t)(I - x(t)) - \frac{ax(t)}{\lambda + x(t)}z(t) + b\gamma\alpha^*(t)z(t), \tag{21}$$

$$z'(t) = -\gamma z(t) - D(t)\alpha^*(t)z(t) + \frac{cx(t)}{\lambda + x(t)}z(t). \tag{22}$$

The following theorem is proved in [7].

Theorem 8. *Assume that $I(t) = I$ and $D : \mathbb{R} \to [d_m, d_M]$ with $0 < d_m < d_M < \infty$ is continuous, $a \ge c$, $b \in (0,1)$ and $\gamma > 0$. Then system (21) - (22) has a pullback attractor $\mathscr{A} = \{A(t) : t \in \mathbb{R}\}$ inside the non-negative quadrant. Moreover,*

(i) the axial steady state solution $(I,0)$ is asymptotically stable in the non-negative quadrant and the pullback attractor $\mathscr{A}$ has a singleton component subset $A(t) = \{(I,0)\}$ for all $t \in \mathbb{R}$, provided $\gamma + d_m\underline{\alpha} > c$;
(ii) the pullback attractor $\mathscr{A}$ also contains points strictly inside the positive quadrant in addition to the point $\{(I,0)\}$, provided

$$\gamma + d_M\overline{\alpha} < \frac{cd_m I}{\lambda(a - c + \gamma + d_M - b\gamma\overline{\alpha}) + d_m I} : \varphi_I(d_m). \tag{23}$$

4.3 Chemostat with no wall growth or delays

In the special case where $\tau_1(t) = \tau_2(t) = 0$ and the wall growth is neglected (see e.g. [17]), system (1) - (3) reduces to the system of ODEs

$$\frac{dx(t)}{dt} = D(t)\,[I(t) - x(t)] - \frac{ax(t)}{\lambda + x(t)} y(t), \tag{24}$$

$$\frac{dy(t)}{dt} = -D(t)y(t) + \frac{ax(t)}{\lambda + x(t)} y(t). \tag{25}$$

We are able to obtain more details of the attractor for this special case, as stated in the following theorem, which is also proved in [7].

Theorem 9. *Assume that $I(t) = I$ fixed and $D : \mathbb{R} \to [d_m, d_M]$ with $0 < d_m < d_M < \infty$ is continuous. Then the non-autonomous dynamical system generated by the system of ODEs* (24)–(25) *has a pullback attractor $\mathscr{A} = \{A(t) : t \in \mathbb{R}\}$ in $\mathbb{R}^2_+$. Moreover,*

(i) when $a < d_m$, the axial steady state solution $(I,0)$ is asymptotically stable in the non-negative quadrant and the pullback attractor $\mathscr{A}$ has a singleton component subset $A(t) = \{(I,0)\}$ for all $t \in \mathbb{R}$;
(ii) when $a > (1 + \lambda/I)d_M$, the pullback attractor $\mathscr{A}$ also contains points strictly inside the positive quadrant in addition to the point $\{(I,0)\}$;
(iii) when $d_m < a < \frac{d_m(\lambda d_m + d_M I)^2}{(\lambda d_m + d_M I)^2 - \lambda I d_m^2}$, the pullback attractor $\mathscr{A}$ consists of the axial point $\{(I,0)\}$ and a single entire solution ξ^* that is uniformly bounded away from the axes as well as heteroclinic entire solutions between them, i.e., its component subsets are

$$A(t) = \left\{(x,y) \in \mathbb{R}^2_+ : x + y = I; \xi^*(t) \le x \le I\right\} \quad \textit{for} \quad t \in \mathbb{R}.$$

Assume that $D(t) = D$ fixed and $I : \mathbb{R} \to [i_m, i_M]$ with $0 < i_m < i_M < \infty$ is continuous. Then the non-autonomous dynamical system generated by the system of ODEs (24)–(25) *has a pullback attractor $\mathscr{A} = \{A(t) : t \in \mathbb{R}\}$ in $\mathbb{R}^2_+$. Moreover,*

(i) when $D > a$, the entire solution $(x^*(t), y^*(t)) = (w^*(t), 0)$ is asymptotically stable in $\mathbb{R}^2_+$ and the pullback attractor has singleton component sets $A(t) = \{(w^*(t), 0)\}$ for every $t \in \mathbb{R}$;
(ii) when $ai_m > D(\lambda + i_M)$, the pullback attractor has nontrivial component sets that include $(w^*(t), 0)$ and strictly positive points;
(iii) when $D < a$ and $a\left(\lambda^2 + \lambda(2i_M - i_m) + i_M^2\right) < D(\lambda + i_M)^2$, the pullback attractor contains a nontrivial entire solution that attracts all other strictly positive entire solutions.

5 Random chemostat models

It practice input and output parameters may vary slightly in a random manner, taking values in bounded intervals about an ideal or mean value. The system (1)–(3) without delays then becomes a system of pathwise random ordinary differential equations (RODEs):

$$x'(t) = D_t(\omega)\,(I_t(\omega) - x(t)) - a\frac{x(t)}{m + x(t)}\,(y_1(t) + y_2(t)) + b\gamma y_1(t), \tag{26}$$

$$y_1'(t) = -\,(\gamma + D_t(\omega))\,y_1(t) + c\frac{x(t)}{m + x(t)}y_1(t) - r_1 y_1(t) + r_2 y_2(t), \tag{27}$$

$$y_2'(t) = -\gamma y_2(t) + c\frac{x(t)}{m + x(t)}y_2(t) + r_1 y_1(t) - r_2 y_2(t), \tag{28}$$

where the inputs are perturbed by real noise, i.e., D_t and I_t are continuous and essentially bounded with values

$$D_t(\omega) \in d\cdot[1-\varepsilon_D, 1+\varepsilon_D], \quad I_t(\omega) \in i\cdot[1-\varepsilon_I, 1+\varepsilon_I], \quad d > 0,\ i > 0,\ \varepsilon_D, \varepsilon_I < 1.$$

Bounded noise can be modeled in various ways. For example, given a stochastic process Z_t such as an Ornstein-Uhlenbeck process, D or I could be the stochastic process defined by [2]

$$\zeta(Z_t(\omega)) := \zeta_0\Big(1 - 2\varepsilon\frac{Z_t(\omega)}{1 + Z_t(\omega)^2}\Big), \tag{29}$$

where ζ_0 and ε are positive constants with $\varepsilon \in (0,1]$. This takes values in the interval $\zeta_0[1-\varepsilon, 1+\varepsilon]$ and tends to peak around the points $\zeta_0(1 \pm \varepsilon)$, so is suitable for a noisy switching scenario. Another possibility is the stochastic process

$$\eta(Z_t(\omega)) := \eta_0\Big(1 - \frac{2\varepsilon}{\pi}\arctan Z_t(\omega)\Big), \tag{30}$$

where η_0 and ε are positive constants with $\varepsilon \in (0,1]$, which takes values in the interval $\eta_0[1-\varepsilon, 1+\varepsilon]$ and is centered on η_0.

In the theory of random dynamical systems the driving noise process is represented abstractly by a canonical driving system $\theta_t(\omega)$ on the sample space Ω, and the system is analyzed in a pathwise fashion. The solutions to the system of RODEs (26)–(28) generate a cocycle mapping, and the non-autonomous system has a skew–product like structure with the noise process acting as a measure theoretical rather than topological autonomous dynamical system (see [1, 8, 15] for more details). A random attractor is a pullback attractor for this system and consists of random subsets, reducing to a single stochastic process when the random sets are singleton sets. Counterparts of the deterministic results above (without delay) are given in [8]. Convergence to a random attractor is pathwise in the pullback sense. Forward convergence also holds, but in the weaker sense of in probability due to the possibility of large deviations. Random delays could also be considered as in e.g., [10], but this has not yet been done in the chemostat context.

6 Over-yield in non-autonomous chemostats

For a given amount of nutrient that is fed in a chemostat during a given period of time T, one can compare the biomass production over the time period, depending on the way the amount of nutrient is distributed over the time period. We say that there exists a biomass *over-yielding* when a time varying input produces more biomass than a constant input. To illustrate the effect of over-yielding in non-autonomous chemostats, we consider the chemostat model with wall growth, variable inputs and non delays as in Section 4.2.

When $D(t) = D$ is constant an $I(\cdot)$ a non-constant T-periodic function with

$$\frac{1}{T}\int_t^{t+T} I(s)ds = \bar{I} ,$$

a periodic solution of system (17)-(18) has to fulfill the equations

$$0 = D(\bar{I}-\bar{x}) - a\frac{1}{T}\int_t^{t+T} U(x(s))z(s)ds + b\gamma\alpha^*\bar{z} , \tag{31}$$

$$0 = -(\gamma + D\alpha^*)\bar{z} + c\frac{1}{T}\int_t^{t+T} U(x(s))z(s)ds , \tag{32}$$

where $\bar{x}$, $\bar{z}$ denote the average values of the variables $x(\cdot)$, $z(\cdot)$ over the period T. Combining equations (31) and (32), one obtains the relation

$$D(\bar{I}-\bar{x}) = \left[\frac{a(\gamma+D\alpha^*)}{c} - b\gamma\alpha^*\right]\bar{z} . \tag{33}$$

One can also write from equation (18)

$$0 = \frac{1}{T}\int_t^{t+T} \frac{z'(s)}{z(s)}ds = -(\gamma+D\alpha^*) + c\frac{1}{T}\int_t^{t+T} U(x(s))ds .$$

As the function $U(\cdot)$ is concave and increasing, one deduces the inequality $\bar{x} > x^*$, where x^* stands for the steady state of the variable $x(\cdot)$ with the constant input $I(t) = \bar{I}$. Similarly, x^* satisfies the equality $cU(x^*) = \gamma + D\alpha^*$. One can then compare the corresponding biomass variables, with the help of equation (33), and obtain:

$$\left[b\gamma\alpha^* - \frac{a(\gamma+D\alpha^*)}{c}\right](\bar{z} - z^\star) > 0 .$$

We conclude that an over-yielding occurs when the condition

$$bc\gamma\alpha^* > a(\gamma + D\alpha^*) \tag{34}$$

is fulfilled. One can see that the nutrient recycling of the dead biomass ($b\gamma \neq 0$) is essential to obtain an over-yielding.

Consider now the chemostat model without wall, $I(\cdot) = I$ constant and $D(\cdot)$ a non-constant T-periodic function with

$$\frac{1}{T}\int_t^{t+T} D(s)ds = \bar{D}\ .$$

From equations (24)-(25) a periodic solution has to fulfill

$$I = x(t) + y(t) \tag{35}$$

$$0 = \frac{1}{T}\int_t^{t+T} \frac{y'(s)}{y(s)}ds = -\bar{D} + a\frac{1}{T}\int_t^{t+T} U(x(s))ds \tag{36}$$

From equation (36), one obtains, as before, the inequality $\bar{x} > x^*$ and thus $\bar{y} < y^*$. Consequently over-yielding never occurs.

For the chemostat model with a wall and periodic $D(\cdot)$, we have not been able to prove if an over-yielding is possible, although numerical simulations tend to show that it is not.

Remark 1. For more general time varying inputs (i.e. not necessarily periodic), one can also study the influence of the variations of the inputs on the characteristics of the pullback attractor. Indeed Theorems 7, 8 and 9 provide precise conditions for which the pullback attractor is larger than the single *wash-out* trajectory $\{(w^*(\cdot), 0)\}$ (i.e. absence of biomass). When enlarging the input set $[i_m, i_M]$ or $[d_m, D_M]$ allows the pullback attractor to be larger than the single wash-out, one can consider that a biomass survival (and thus an over-yielding) could occur.

- Statements (ii) in Theorem 9 (chemostat with no wall) show that enlarging the input sets does not help the dynamics to avoid the wash-out.
- In statements (ii) of Theorems 8 and 9 (chemostat with wall), one can check that the functions $\varphi_D(\cdot)$, $\varphi_I(\cdot)$ as defined in (19) and (23), respectively, could be increasing or decreasing depending on the values of the parameters. Therefore, enlarging the input set could be beneficial for the biomass survival, which is different from the no wall case.

Acknowledgements This work has been partially supported by the Spanish Ministerio de Economía y Competitividad project MTM2011-22411 and the Consejería de Innovación, Ciencia y Empresa (Junta de Andalucía) under grant 2010/FQM314 and Proyecto de Excelencia P12-FQM-1492.

References

1. L. Arnold, *Random Dynamical Systems*, Springer-Verlag, Berlin, 1998.
2. Y. Asai and P.E. Kloeden, Numerical schemes for random ODEs via stochastic differential equations, *Commun. Appl. Analysis* **17** (2013), no. 3 & 4, 521–528.
3. M. Ballyk, D. Jones and H. Smith, The biofilm model of Freter: a review, In *Structured population models in biology and epidemiology*, Editors: P. Magal and S. Ruan, Springer (2008) 265–302.
4. E. Beretta and Y. Takeuchi Qualitative properties of chemostat equations with time delays: boundedness, local and global asymptotic stability. *Differential Equations Dynamical Syst.*, **2** (1994) 19–40.
5. E. Beretta and Y. Takeuchi Qualitative properties of chemostat equations with time delays II *Differential Equations Dynamical Syst.*, **2** (1994) 263–288.
6. G.J. Butler, S.B. Hsu and P. Waltman. A mathematical model of the chemostat with periodic washout rate *SIAM J. Appl. Math.*, **45** (1985) 435–449.
7. T. Caraballo, X. Han and P. E. Kloeden, Chemostats with time-dependent inputs and wall growth, *Applied Mathematics and Information Sciences* (to appear).
8. T. Caraballo, X. Han and P. E. Kloeden, Chemostats with random inputs and wall growth, *Math. Methods Appl. Sci.* (to appear).
9. T. Caraballo, X. Han and P. E. Kloeden, Non-autonomous chemostats with variable delays, *J. Theor. Pop. Dyn.* (submitted).
10. T. Caraballo, P.E. Kloeden and J. Real, Discretization of asymptotically stable stationary solutions of delay differential equations with a random stationary delay *J. Dynam. Differential Equations* **18** (2006) no. 4, 863–880.
11. T. Caraballo, J.A. Langa and J.C. Robinson, Attractors for differential equations with variable delays, *J. Math. Anal. Appl.* **260** (2001) no. 2, 421–438.
12. J. K. Hale and S. M. Verduyn Lunel, Introduction to functional-differential equations, *Applied Mathematical Sciences. Springer-Verlag, New York*, **99** (1993).
13. D. Jones, H. Kojouharov, D. Le and H.L. Smith, The Freter model: A simple model of biofilm formation. *J. Math. Biol.* **47** (2003) 137–152.
14. P.E. Kloeden and T. Lorenz, Pullback incremental stability, *Nonautonomous & Random Dynamical Systems* (2013) 53–60 DOI: 10.2478/msds-2013-0004.
15. P.E. Kloeden and M. Rasmussen, *Nonautonomous Dynamical Systems,* American Mathematical Society Providence, RI, (2011).
16. S.S. Pilyugin and P. Waltman, The simple chemostat with wall growth, *SIAM J. Appl. Math.* **59** (1999) 1552–1572.
17. H.L. Smith and P. Waltman, *The Theory of the Chemostat: Dynamics of Microbial Competition*, Cambridge University Press , Cambridge, UK (1995).
18. V. Sree Hari Rao and P. Raja Sekhara Rao, *Dynamic Models and Control of Biological Systems,* Springer-Verlag, Heidelberg (2009).
19. H. Topiwala and G. Hamer, Effect of wall growth in steady state continuous culture, *Biotech. Bioeng.* **13** (1971) 919–922.