# NONAUTONOMOUS CHEMOSTATS WITH VARIABLE DELAYS*

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**Abstract.** The appearance of delay terms in a chemostat model can be fully justified since the future behavior of a dynamical system does not in general depend only 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 paper a chemostat model with time variable delays and wall growth, hence a nonautonomous problem, is investigated. The analysis provides sufficient conditions for the asymptotic stability of nontrivial equilibria of the chemostat with variable delays, as well as for the existence of nonautonomous pullback attractors.

**1. Introduction.** The chemostat model consists of microorganisms feeding on a single growth-limiting nutrient. It can be regarded as a laboratory idealization of nature to study competition for the same resource, e.g., a common food supply of a growth-limiting nutrient, between two or more populations [51] and thus has been widely used in theoretical ecology [3, 17, 18, 24, 41, 45, 47, 49], waste water treatment [1, 27], recombinant problems in genetically altered organisms [20, 21], etc. For derivation and analysis of chemostat models see [14, 36, 37, 38, 40, 48] and the references therein.

The chemostat models are usually described by a system of ODEs. 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 let $I$ be the input nutrient concentration which describes the quantity of nutrient available with the system at any time. Denote by $x(t)$ the concentration of the growth-limiting nutrient and by $y(t)$ the concentration of the microorganism at any time $t$. Under the assumption that the flow rate is fast enough such that there is no time for the microorganisms to either die or attach on to the container wall, the simplest form for a chemostat is

$$(1.1) \qquad x'(t) = D\left(I - x\right) - aU(x(t))y(t),$$

$$(1.2) \qquad y'(t) = -Dy(t) + cU(x(t))y(t),$$

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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, and $U$ is the functional response of the microorganism describing how the nutrient is consumed by the species which is known in the literature as the consumption function or uptake function. Basic assumptions on $U : \mathbb{R}^+ \to \mathbb{R}^+$ are given by

- $U(0) = 0, \quad U(x) > 0$ for all $x > 0$;
- $\lim_{x \to \infty} U(x) = L$, where $L < \infty$;
- $U$ is continuously differentiable;
- $U$ is monotonically increasing.

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

$$(1.3) \qquad\qquad U(x) = \frac{x}{\lambda + x},$$

where $\lambda > 0$ is the half-saturation constant [40].

When the flow rate is not fast enough, the microorganisms stay for a long time in the growth medium before they wash out; therefore the organisms may die naturally in the meantime. To accommodate the death of microorganisms due to the death in addition to the washout, we introduce the parameter $\gamma > 0$ to be the collective death rate coefficient of $y$ representing all the aforementioned factors such as aging, diseases, etc. On the other hand, when the flow rate is small, the dead biomass is not sent out of the system immediately and is subject to bacterial decomposition which in turn leads to regeneration of the nutrient. Expecting not 100% recycling of the dead material but only a fraction, we let constant $b \in (0, 1)$ describe the fraction of dead biomass that is recycled. Taking these phenomena into account modifies system (1.1)–(1.2) to

$$(1.4) \qquad\qquad x'(t) = D\,(I - x) - aU(x(t))y(t) + b\gamma y(t),$$

$$(1.5) \qquad\qquad y'(t) = -Dy(t) - \gamma y(t) + cU(x(t))y(t).$$

Note that ODEs (1.4) and (1.5) are valid only under the assumptions that processes of converting consumed nutrient by microorganisms and recycled dead microorganisms to their viable biomass are instantaneous. However, these assumptions are oversimplified and time delays exist in the conversion processes. In fact, time delays are natural in biological systems, since they allow the coexistence of competing populations as an unforced periodic solution. Statistical analysis of ecological data has also demonstrated that delay appears in the population dynamics of multiple species [43, 44]. Delay models are becoming more common and have appeared in various branches of biological modeling, such as the chemostat model [56], circadian rhythms [39], epidemiology [13], tumor growth [46], and neural networks [12].

A chemostat model with time delays, first studied by Caperon in [5], may result in a negative concentration of the nutrient. Later Bush and Cook proposed a chemostat model with a delay in the intrinsic growth rate of the microorganism but with no delay in the nutrient equation [4]. The chemostat model (1.4)–(1.5) with a time delay in the growth response of the consumer species may be represented as

$$x'(t) = D\,(I - x) - aU(x(t))y(t) + b\gamma y(t),$$

$$y'(t) = -Dy(t) - \gamma y(t) + cU(x(t - \tau))y(t).$$

In addition to a time delay in the growth response, the time delays involved in the decomposition process cannot be neglected for the chemostat system with material recycling [33, 34, 50]. Therefore introducing a time delay into material recycling gives

$$x'(t) = D\left(I - x\right) - aU(x(t))y(t) + b\gamma y(t - \tau),$$

$$y'(t) = -Dy(t) - \gamma y(t) + cU(x(t - \tau))y(t).$$

The formulations of delay terms in chemostat models depend on the underlying mechanism of conversion processes from nutrients and recycled dead microorganisms to viable biomass. If for each species the conversion processes require a fixed length of time, then the delays involved in the corresponding model should be discrete delays [4, 5, 19, 42]. If on the other hand the conversion processes depend on the amount of nutrient consumed and dead microorganisms recycled over a memory period in the past, then the delays involved in the corresponding model should be distributed delays. The distributed delays are infinite if the memory period is infinitely large and are finite if the memory period is finite [31, 54, 55]. Recent results of chemostat models with discrete or distributive delays can be found in [15, 23, 28, 29, 30, 52, 53, 54, 55] and references therein.

However, in reality, time delays may be neither discrete nor distributive but simply varying with respect to time, due to the fluctuation of environments. For example, it has been observed that microorganisms in lakes can survive even at low levels of nutrients, with an oscillatory and low growth. Such a phenomenon cannot be fully justified by employing discrete or distributive delays terms in the chemostat models, and it motivates the idea of describing the inputs or delays as general time-dependent functions [6, 7, 8]. In this work we take into account the aforementioned important considerations and study the following chemostat model with varying delays:

$$(1.6) \qquad x'(t) = D\left(I - x(t)\right) - aU(x(t))y(t) + b\gamma y(t - \tau_1(t)),$$

$$(1.7) \qquad y'(t) = -Dy(t) - \gamma y(t) + cU(x(t - \tau_2(t)))y(t),$$

where $\tau_1(\cdot), \tau_2(\cdot) : \mathbb{R}_+ \to [0, h]$ $(h > 0)$ are continuous functions.

Equations (1.6)–(1.7) represent chemostats with variable delays, while the attachment of microorganism on the walls are neglected. However, very often the microorganisms grow not only in the growth medium but also along the walls of the container. This is either due to the ability of the microorganisms to stick on to the walls of the container or because the flow rate is not fast enough to wash these organisms out of the system. Naturally, 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 $y_2(t)$. These individuals may switch their categories at any time, i.e., the microorganisms on the walls may join those in the growth medium or the biomass in the medium may prefer walls.

Let $r_1$ and $r_2$ represent the rates at which the species stick on to and shear off from the walls, respectively; then $r_1y_1(t)$ and $r_2y_2(t)$ represent the corresponding terms of species changing the categories. Assume that the nutrient is equally available to both of the categories; therefore it is assumed that both categories consume the same amount of nutrient and at the same rate. Note that only $y_1(t)$ contributes to the material recycling of the dead biomass in the medium. Moreover, since the microorganisms on the wall are not washed out of the system, the term $-Dy_2(t)$ is

not included in the equation representing the growth of $y_2(t)$. The consideration of wall attachment results in the following chemostat model:

$$(1.8) \qquad x'(t) = D\left(I - x(t)\right) - aU(x(t))\left(y_1(t) + y_2(t)\right) + b\gamma y_1(t - \tau_1(t)),$$

$$(1.9) \qquad y_1'(t) = -\left(\gamma + D\right)y_1(t) + cU(x(t - \tau_2(t)))y_1(t) - r_1 y_1(t) + r_2 y_2(t),$$

$$(1.10) \qquad y_2'(t) = -\gamma y_2(t) + cU(x(t - \tau_2(t)))y_2(t) + r_1 y_1(t) - r_2 y_2(t).$$

In this paper we will study the asymptotic behaviors of systems (1.6)–(1.7) and (1.8)–(1.10) in the framework of nonautonomous dynamical systems. More specifically, we will discuss the positiveness and boundedness of solutions, stability of equilibrium solutions, and existence of pullback attractors for both systems (1.6)–(1.7) and (1.8)–(1.10). Note that the appearance of the variable delay functions $\tau_1(t)$ and $\tau_2(t)$ makes our models nonautonomous and, consequently, the classical theory of global attractors for dynamical systems is not applicable. Therefore new concepts of nonautonomous attractors from the recently developed theory of nonautonomous dynamical systems are required to study these systems.

The rest of the paper is organized as follows. In section 2 we provide necessary preliminaries of nonautonomous theory, in section 3 we study the chemostat system (1.6)–(1.7) with time delays but without wall growth, in section 4 we study the chemostat system (1.8)–(1.10) with time delays and wall growth, and in section 5 we provide some closing remarks.

**2. Nonautonomous dynamical systems.** In this section we provide some preliminary information from the theory of nonautonomous dynamical systems that we require in what follows. To facilitate the reader's access to the literature we give definitions in the context of systems with time delays. For nonautonomous dynamical system theory in a general context see [25, 26] and references therein.

To start, denote by $C_h = C([-h, 0]; \mathbb{R}^n)$ the Banach space of continuous functions $\phi : [-h, 0] \to \mathbb{R}^n$ equipped with the usual supremum norm $\|\phi\|_h := \sup_{\theta \in [-h,0]} \|\phi(\theta)\|$, where $\|\cdot\|$ is a norm on $\mathbb{R}^n$, which will often be the $\ell^1$ summation norm in what follows.

Consider a nonautonomous differential equation of form

$$(2.1) \qquad \dot{z}(t) = f(t, z_t),$$

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

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

for any given a continuous function $z(\cdot) : \mathbb{R} \to \mathbb{R}^n$ and $t \in \mathbb{R}$. When $z(\cdot)$ is a solution of (2.1), $z_t(\cdot)$ is said to be the solution segment at time $t$.

If an initial function $\phi \in C_h$ is prescribed at the initial time $t_0 \in \mathbb{R}$, the basic theory of delay differential equations (see [22]) implies under standard assumptions the existence of the unique solution $z(\cdot; t_0, \phi)$ of (2.1) on $[t_0 - h, \infty)$, which satisfies, in addition, the initial condition $z_{t_0}(\cdot) = \phi$, i.e., $z_{t_0}(\theta) = z(t_0 + \theta) = \phi(\theta)$ for all $\theta \in [-h, 0]$.

The unique solution of the initial value problems associated to (2.1) defines the solution map $\mathcal{S}(t, t_0) : C_h \ni \phi \mapsto z_t(\cdot; t_0, \phi) \in C_h$ for $t \geq t_0$, which is, in fact, a process (also called a two-parameters semigroup), i.e.,

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

As in the autonomous case, we look for invariant attracting sets. First, we introduce the Hausdorff semidistance between subsets $A$ and $B$ in a metric space $(X, d)$ as

$$\text{dist}(A, B) = \sup_{a \in A} \inf_{b \in B} d(a, b).$$

DEFINITION 2.1. *Let $\mathcal{S}$ be a process on a complete metric space $X$. A family $\{\mathcal{A}(t)\}_{t \in \mathbb{R}}$ of compact sets of $X$ is said to be a (global) pullback attractor for $\mathcal{S}$ if it satisfies*
- *invariance—$\mathcal{S}(t, t_0)\mathcal{A}(t_0) = \mathcal{A}(t)$ for all $t \geq t_0$; and*
- *pullback attraction—$\lim_{t_0 \to \infty} \text{dist}(\mathcal{S}(t, t - t_0)D, \mathcal{A}(t)) = 0$ for each $t \in \mathbb{R}$ and for all bounded subsets $D$ of $X$.*

Pullback attraction takes into account information about the system from the past and usually does not coincide with forward attraction, where the current time $t$ goes to $+\infty$ with the initial time held fixed. In autonomous systems both coincide since the dynamics depends only on the elapsed time $t - t_0$.

DEFINITION 2.2. *A family of nonempty subsets of $X$ $\{B(t)\}_{t \in \mathbb{R}}$ is said to be (pullback) absorbing with respect to the process $\mathcal{S}$ if, for $t \in \mathbb{R}$ and $D \subset X$ bounded, there exists $T_D(t) > 0$ such that for all $\tau \geq T_D(t)$*

$$\mathcal{S}(t, t - \tau)D \subset B(t).$$

The following results (see [26, 16, 35]) show that the existence of a family of compact absorbing sets implies the existence of a pullback attractor.

THEOREM 2.3. *Let $\mathcal{S}(t, t_0)$ 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 $\{\mathcal{A}(t)\}_{t \in \mathbb{R}}$ such that $\mathcal{A}(t) \subset B(t)$ for all $t \in \mathbb{R}$. Furthermore,*

$$\mathcal{A}(t) = \overline{\bigcup_{\substack{D \subset X \\ bounded}} \Lambda_D(t)},$$

*where*

$$\Lambda_D(t) = \bigcap_{T \geq 0} \overline{\bigcup_{t_0 \geq T} \mathcal{S}(t, t - t_0)D}.$$

Nevertheless, for our particular delay situation, we will use the next sufficient condition which ensures the existence of a pullback attractor.

THEOREM 2.4 (see [10, Theorem 4.1]). *Suppose that a process $Z(t, t_0)$ 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 for* (2.1).

We emphasize that it is possible to consider a more general definition of pullback attractor which attracts families of sets in a universe instead of only bounded sets (see [11, 32] for a detailed analysis of this theory). However, the present concept is enough for our interests here.

**3. Chemostats with delay and no wall growth.** In order to solve system (1.6)–(1.7), we need to fix the values of the solution not only at the initial time $t_0 \in \mathbb{R}$ but also in the interval $[t_0 - h, t_0]$, i.e., we need to find solutions to (1.6)–(1.7) for $t \geq t_0$ such that

(3.1) $\qquad x(t) = \phi_1(t - t_0), \ y(t) = \phi_2(t - t_0) \ \text{ for } t \in [t_0 - h, t_0],$

where $(\phi_1, \phi_2) \in C_h := C([-h, 0]; \mathbb{R}^2)$.

Notice that (1.6)–(1.7) can be written as the nonautonomous functional differential equation

$$\frac{dz(t)}{dt} = f(t, z_t) \tag{3.2}$$

where $f(\cdot, \cdot) : \mathbb{R} \times C_h \to \mathbb{R}^2$ is given by

$$f(t, \phi) = \begin{pmatrix} D(I - \phi_1(0)) - aU(\phi_1(0))\phi_2(0) + b\gamma\phi_2(-\tau_1(t)) \\ -(D + \gamma)\phi_2(0) + cU(\phi_1(-\tau_2(t)))\phi_2(0) \end{pmatrix} \text{ for } \phi := \begin{pmatrix} \phi_1 \\ \phi_2 \end{pmatrix} \in C_h,$$

and $z_t \in C_h$ denotes the function

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

for any continuous function $z : [-h, +\infty) \to \mathbb{R}^2$.

In order to solve the initial value problem for (3.2), one possibility is to address an initial value $\phi \in C_h$ at the initial time $t_0 \in \mathbb{R}$. Thanks to the properties of the function $f(\cdot, \cdot)$, namely, that it maps bounded sets from $\mathbb{R} \times C_h$ into bounded sets of $\mathbb{R}^2$ and is locally Lipschitz with respect to its second variable, one can ensure (see Hale and Verduyn Lunel [22]) the existence of a unique solution $z(\cdot; t_0, \phi)$ of (3.2) such that $z_{t_0}(\cdot; t_0, \phi) = \phi$, which means that $z_{t_0}(\theta; t_0, \phi) := z(t_0 + \theta; t_0, \phi) = \phi(\theta)$ for $\theta \in [-h, 0]$. Moreover, as under suitable assumptions (see Lemma 3.2 below) this solution is defined globally in time, we could construct a nonautonomous dynamical system (e.g., process) in the phase space $C_h$ in the following way: for any $t \geq t_0$, let $Z(t, t_0) : C_h \to C_h$ be the operator defined as

$$Z(t, t_0)\phi := z_t(\cdot; t_0, \phi) \quad \text{for } \phi \in C_h. \tag{3.3}$$

**3.1. Positiveness and boundedness of solutions.** The region of biological interests for our model is only positive and finite solutions. In this subsection we first show that solutions to (1.6)–(1.7) are nonnegative and bounded.

LEMMA 3.1.    *Given any nonnegative initial conditions $\phi \geq 0$ on $[t_0 - h, t_0]$, solutions to (1.6)–(1.7) are nonnegative.*

*Proof.* We first show that if a solution starts in the quadrant $\mathbb{R}_+^2 = \{(x, y) : x \geq 0, y \geq 0\}$, it remains there forever. By continuity of solutions, each solution has to take value 0 before it reaches a negative value. In fact, since the time derivative of $y(t)$ evaluated at $y = 0$, $y'(t)|_{y=0} = 0$, $y$ is nondecreasing at $y = 0$ and thus will never take negative values. Consequently the time derivative of $x(t)$ evaluated at $y = 0$, $x'(t)|_{x=0} = DI + b\gamma y(-\tau_1(0)) > 0$, implies that $x$ will bounce back to the positive region once it reaches 0. Therefore solutions to (1.6)–(1.7) are nonnegative for all $t \geq t_0$.    □

LEMMA 3.2.    *Assume that $\tau_1'(t) \leq M_1 < 1$. Then, solutions to (1.6)–(1.7) corresponding to initial conditions in a bounded set of $C_h$, at the initial time $t_0 \in \mathbb{R}$, are bounded for all $t > t_0$, provided that*

$$\delta := D - \frac{M_1}{1 - M_1}\gamma - c > 0. \tag{3.4}$$

*Proof.* Let $(x(t), y(t))$ be a solution to (1.6)–(1.7), and define the function

$$u(t) := u(x(t), y(t)) = x(t) + by(t) + \frac{b\gamma}{1 - M_1} \int_{t - \tau_1(t)}^{t} y(s)ds.$$

Then, the time derivative of $u$ is

$$
\begin{aligned}
\frac{du}{dt} = {} & DI - Dx(t) - aU(x(t))y(t) + b\gamma y(t - \tau_1(t)) \\
& - b(\gamma + D)y(t) + bcy(t)U(x(t - \tau_2(t))) \\
& + \frac{b\gamma}{1 - M_1}\left[y(t) - (1 - \tau_1'(t)) \cdot y(t - \tau_1(t))\right].
\end{aligned}
$$

It follows from $\tau_1'(t) \le M_1 < 1$ that $\frac{1}{1-M_1}(1 - \tau_1'(t)) \ge 1$. Hence, by using the fact that $U < 1$, we have

$$
\begin{aligned}
\frac{du}{dt} & \le DI - Dx(t) - b\left(D - \frac{M_1}{1 - M_1}\gamma - c\right) \cdot y(t) \\
& = DI - Dx(t) - b\delta y(t),
\end{aligned}
$$

where $0 < \delta < D$ is defined in (3.4).

Now define

$$
\Omega := \{(x, y) \in \mathbb{R}_+^2 : Dx + b\delta y \le DI\}.
$$

We next study the upper bounds of solutions case by case.

(a) If a trajectory $(x(\cdot), y(\cdot))$ starts from $t_0$ in $\mathbb{R}_+^2 \setminus \Omega$, then the corresponding function $u(t) = u(x(t), y(t))$ would be decreasing for all times $t \ge t_0$ such that $(x(t), y(t)) \in \mathbb{R}_+^2 \setminus \Omega$, i.e.,

(3.5)

$$
\begin{aligned}
u(x(t), y(t)) & \le u(x(t_0), y(t_0)) = x(t_0) + by(t_0) + \frac{b\gamma}{1 - M_1}\int_{t_0 - \tau_1(t_0)}^{t_0} y(s)\,ds \\
& \le |\phi_1| + b\left(1 + \frac{\gamma h}{1 - M_1}\right)|\phi_2|.
\end{aligned}
$$

Since $b \in (0, 1)$, $u(t) \ge bx(t) + by(t)$ and hence $x(t) + y(t) \le u(t)/b$. Therefore (3.5) implies that $x(t) + by(t)$ is bounded above, i.e.,

(3.6)        $\|(x(t), y(t))\| := x(t) + y(t) \le \dfrac{|\phi_1|}{b} + \left(1 + \dfrac{\gamma h}{1 - M_1}\right)|\phi_2|.$

(b) If a trajectory starts from or enters region $\Omega$ at time $t_1 \ge t_0$ and stays there forever, then by the definition of $\Omega$ we have $Dx(t) + b\delta y(t) \le DI$ for $t \ge t_1$, which implies that

(3.7)        $\|(x(t), y(t))\| = x(t) + y(t) < \dfrac{D}{b\delta}x(t) + y(t) \le \dfrac{DI}{b\delta}.$

(c) If a trajectory starts from/enters/reenters region $\Omega$ at time $t_{2i-1} \ge t_0$ and exits at time $t_{2i}$ $(i = 1, 2, \ldots)$, then (3.6) holds for all times $(t_{2i}, t_{2i+1})$ and (3.7) holds for all times $(t_{2i-1}, t_{2i})$.

In summary, for any $t > t_0$ the $\ell^1$ norm of solutions $(x(t), y(t))$ in $\mathbb{R}^2$ satisfies

$$
\|(x(t), y(t))\| = x(t) + y(t) \le \max\left\{\frac{|\phi_1|}{b} + \left(1 + \frac{\gamma h}{1 - M_1}\right)|\phi_2|, \frac{DI}{b\delta}\right\},
$$

and consequently

$$\|(x_t, y_t)\|_h = x(t+\theta) + y(t+\theta) \leq \max\left\{\frac{|\phi_1|}{b} + \left(1 + \frac{\gamma h}{1 - M_1}\right)|\phi_2|, \frac{DI}{b\delta}\right\}.$$

It follows immediately that for any $(\phi_1, \phi_2) \in C_h$ with $|\phi_1| + |\phi_2| \leq d$, we have $(x_t, y_t) \in \mathcal{B}_{C_h}(0, R_1)$, where

$$R_1 = \max\left\{\frac{d}{b}, d\left(1 + \frac{\gamma h}{1 - M_1}\right), \frac{DI}{b\delta}\right\}$$

and

$$\mathcal{B}_{C_h}(0, R_1) := \{(\phi_1, \phi_2) \in C_h : |\phi_1| + |\phi_2| \leq R_1\}. \qquad \square$$

Condition (3.4) implies that the boundedness of the solution depends on the nutrient supplying rate, the growth rate and the collective death rate of the microorganism, and the stiffness of delay in material recycling ($\tau_1'(t)$). In principle, in order for the concentration of both the nutrient and the microorganism to be bounded, the nutrient supplying rate has to be larger than the microorganism growth rate. Moreover, the difference between the nutrient supplying rate and the microorganism growth rate has to be larger than a multiplication of the collective death rate, which depends on the stiffness of delay in material recycling—roughly, the larger the stiffness, the larger the difference ought to be, and vice versa.

**3.2. Stability analysis.** In this subsection we will establish results on stability of the chemostat model (1.6)–(1.7) with variable delay functions $\tau_1(\cdot), \tau_2(\cdot) \in C^1(\mathbb{R}; [0, h])$, and where the uptake function $U$ is given by (1.3). It is straightforward to check that $(I, 0)$ is one feasible equilibrium and it is asymptotically stable when $D + \gamma \geq c$. In fact, when $D + \gamma \geq c$, it follows directly from (1.7) that $y'(t) \leq -(D + \gamma - c)y(t)$ for all $t$. Therefore $y = 0$ is an asymptotically stable equilibrium of (1.7), and substituting $y = 0$ into (1.6) gives immediately $x = I$.

Note that any nontrivial equilibrium $(x^*, y^*)$ of system (1.6)–(1.7) should satisfy

$$D(I - x^*) - \frac{ax^*}{\lambda + x^*}y + b\gamma y^* = 0,$$

$$-Dy^* - \gamma y^* + \frac{cx^*}{\lambda + x^*}y^* = 0.$$

From this we have

(3.8) $$x^* = \frac{(D + \gamma)\lambda}{c - D - \gamma}, \quad y^* = \frac{cD(I - x^*)}{a(D + \gamma) - bc\gamma},$$

whenever $c - D - \gamma \neq 0$, $a(D + \gamma) - bc\gamma \neq 0$.

We will be interested only in those positive solutions due to the biological meaning of the variables of our problem. This requires that the constants in our problem must satisfy

(3.9) $$c - D - \gamma > 0, \ a(D + \gamma) - bc\gamma > 0,$$

or, written in an equivalent way,

(3.10) $$\frac{cb\gamma}{a} < D + \gamma < c.$$

To this end, we will analyze the stability properties of the positive equilibrium $(x^*, y^*)$ by constructing an appropriate Lyapunov function. We will obtain sufficient conditions involving the parameters associated to the delay function, along with other parameters in the model, in order to ensure the stability of the positive stationary point in (3.8).

THEOREM 3.3. *In addition to condition* (3.10), *assume that* $\tau_1(\cdot), \tau_2(\cdot) : \mathbb{R}_+ \to [0, h]$ *and* $\tau_1'(t) \leq M_1 < 1$. *Then the equilibrium solution* $(x^*, y^*)$ *in* (3.8) *for system* (1.6)–(1.7) *is globally asymptotically stable provided*

$$(3.11) \qquad \frac{1}{D+\gamma}\left(e^{(D+\gamma)h} - 1\right) + \frac{1}{1-M_1}h < \frac{2a}{bc\gamma}.$$

*Remark* 3.4. Notice that what this result says is that in order to have stability of the positive equilibrium, either the delay parameter $h$ needs to be small enough or the parameters $b\gamma$ and $c$ must be small with respect to $a$. Biologically this means that the microorganism has a rather short memory of its past, or has the capability for consuming the nutrient at a larger rate than its growth rate and reproduction rate from recycling.

*Proof.* First we introduce the following transformation:

$$\tilde{x}(t) = x(t) - x^*, \qquad \tilde{y}(t) = \ln \frac{y(t)}{y^*},$$

$$\widetilde{U}(\cdot) = U(\cdot + x^*) - U(x^*).$$

Then system (1.6)–(1.7) can be rewritten as

$$\tilde{x}'(t) = -D\tilde{x}(t) - ay^* e^{\tilde{y}(t)}\widetilde{U}(\tilde{x}(t)) - ay^* U(x^*)\left(e^{\tilde{y}(t)} - 1\right)$$

$$(3.12) \qquad\qquad + b\gamma y^*\left(e^{\tilde{y}(t-\tau_1(t))} - 1\right),$$

$$(3.13) \qquad \tilde{y}'(t) = c\widetilde{U}(\tilde{x}(t - \tau_2(t))).$$

We next construct the required Lyapunov function step by step. First define

$$V_1(\tilde{x}(t)) := \int_0^{\tilde{x}(t)} \widetilde{U}(s)ds.$$

Since $U(x)$ is increasing with respect to $x$, we have $V_1(\tilde{x}(t)) > 0$ for unless $x(t) = x^*$. Differentiating $V_1(t) := V_1(\tilde{x}(t))$ with respect to $t$ gives

$$\frac{dV_1(t)}{dt} = -D\tilde{x}(t)\widetilde{U}(\tilde{x}(t)) - ay^* e^{\tilde{y}(t)}\widetilde{U}^2(\tilde{x}(t)) - (aU(x^*) - b\gamma)\, y^*(e^{\tilde{y}(t)} - 1)\widetilde{U}(\tilde{x}(t))$$

$$- b\gamma y^*(e^{\tilde{y}(t)} - e^{\tilde{y}(t-\tau_1(t))})\widetilde{U}(\tilde{x}(t)).$$

Observing that

$$e^{\tilde{y}(t)} - e^{\tilde{y}(t-\tau_1(t))} = \int_{t-\tau_1(t)}^t e^{\tilde{y}(s)}\tilde{y}'(s)ds = c\int_{t-\tau_1(t)}^t \widetilde{U}(\tilde{x}(s - \tau_2(s)))ds,$$

and using the inequality $pq \leq \frac{1}{2}(p^2 + q^2)$, we have

$$\frac{dV_1(t)}{dt} = -D\tilde{x}(t)\widetilde{U}(\tilde{x}(t)) - ay^* e^{\tilde{y}(t)}\widetilde{U}^2(\tilde{x}(t)) - (aU(x^*) - b\gamma)\, y^*(e^{\tilde{y}(t)} - 1)\widetilde{U}(\tilde{x}(t))$$

$$- bc\gamma y^* \cdot \widetilde{U}(\tilde{x}(t)) \cdot \int_{t-\tau_1(t)}^t \widetilde{U}(\tilde{x}(s - \tau_2(s)))ds$$

$$\leq -D\tilde{x}(t)\widetilde{U}(\tilde{x}(t)) - ay^*e^{\tilde{y}(t)}\widetilde{U}^2(\tilde{x}(t)) - (aU(x^*) - b\gamma)\,y^*(e^{\tilde{y}(t)} - 1)\widetilde{U}(\tilde{x}(t))$$

$$+\frac{1}{2}bc\gamma y^*\left\{\int_{t-\tau_1(t)}^{t} e^{\tilde{y}(s)}ds \cdot \widetilde{U}^2(\tilde{x}(t - \tau_2(t)))\right.$$

(3.14)
$$\left.+\int_{t-\tau_1(t)}^{t} e^{\tilde{y}(s)}\widetilde{U}^2(\tilde{x}(s - \tau_2(s)))ds\right\}.$$

Second, define

$$V_2(\tilde{y}(t)) := \int_0^{\tilde{y}(t)} (e^s - 1)\,ds.$$

Then $V_2(\tilde{y}(t)) > 0$ unless $y(t) = y^*$, and differentiating $V_2(t) := V_2(\tilde{y}(t))$ with respect to $t$ in solutions to (3.12)–(3.13) gives

(3.15)
$$V_2'(t) = \left(e^{\tilde{y}(t)} - 1\right)\tilde{y}'(t) = c\left(e^{\tilde{y}(t)} - 1\right)\widetilde{U}(\tilde{x}(t - \tau_2(t))).$$

Finally, define

$$V_3(\tilde{x}(t), \tilde{y}(t)) = \frac{1}{2(1 - M_1)}bc\gamma y^*\int_{t-\tau_1(t)}^{t}\int_v^{t} e^{\tilde{y}(s)}\widetilde{U}^2(\tilde{x}(s - \tau_2(s)))dsdv.$$

Then $V_3(\tilde{x}(t), \tilde{y}(t)) > 0$ unless $x(t) = x^*$ and $y(t) = y^*$, and the derivative of $V_3(t) := V_3(\tilde{x}(t), \tilde{y}(t))$ with respect to $t$ is

$$V_3'(t) = \frac{1}{2(1 - M_1)}bc\gamma y^*\left\{e^{\tilde{y}(t)}\widetilde{U}^2(\tilde{x}(t - \tau_2(t)))\tau_2(t)\right.$$

(3.16)
$$\left.-\int_{t-\tau_2(t)}^{t} e^{\tilde{y}(s)}\widetilde{U}^2(\tilde{x}(s - \tau_2(s)))ds \cdot (1 - \tau_1'(t))\right\}.$$

Now consider the function

$$V(t) := V(\tilde{x}(t), \tilde{y}(t)) = V_1(\tilde{x}(t - \tau_2(t))) + \alpha V_2(\tilde{y}(t)) + V_3(\tilde{y}(t))$$

with $\alpha = (aU(x^*) - b\gamma)\,y^*/c$. Then in the solutions of (3.12)–(3.13), by using (3.14)–(3.16) and that $\tau_1'(t) \leq M_1 < 1$ we obtain

$$\frac{dV(t)}{dt} \leq -D\tilde{x}(t - \tau_2(t))\widetilde{U}(\tilde{x}(t - \tau_2(t))) - ay^*e^{\tilde{y}}\widetilde{U}^2(\tilde{x}(t - \tau_2(t)))$$

(3.17)
$$+\frac{1}{2}bc\gamma y^*\widetilde{U}^2(\tilde{x}(t - \tau_2(t)))\left\{\int_{t-\tau_1(t)}^{t} e^{\tilde{y}(s)}ds + \frac{1}{1 - M_1}e^{\tilde{y}(t)}\tau_2(t)\right\}.$$

From (1.7) we have $y'(t) \geq -(D + \gamma)y(t)$, from which it follows that

$$y(s) \leq y(t)e^{(D+\gamma)(t-s)}$$

and hence

$$y^*\int_{t-\tau_1(t)}^{t} e^{\tilde{y}(s)}ds = \int_{t-\tau_1(t)}^{t} y(s)ds \leq y(t)\int_{t-\tau_1(t)}^{t} e^{(D+\gamma)(t-s)}ds$$

$$= \frac{y(t)}{D + \gamma}\left(e^{(D+\gamma)\tau_1(t)} - 1\right).$$

Inserting this into (3.17) gives

$$
\begin{aligned}
\frac{dV(t)}{dt} \leq{} & -D\tilde{x}(t-\tau_2(t))\widetilde{U}(\tilde{x}(t-\tau_2(t))) \\
& - \left\{ a - \frac{1}{2}bc\gamma \left[ \frac{1}{D+\gamma}\left(e^{(D+\gamma)\tau_1(t)} - 1\right) + \frac{1}{1-M_1}\tau_2(t) \right] \right\} y(t)\widetilde{U}^2(\tilde{x}(t-\tau_2(t))) \\
\leq{} & - \left\{ a - \frac{1}{2}bc\gamma \left[ \frac{1}{D+\gamma}\left(e^{(D+\gamma)h} - 1\right) + \frac{1}{1-M_1}h \right] \right\} y(t)\widetilde{U}^2(\tilde{x}(t-\tau_2(t))) \\
\leq{} & 0.
\end{aligned}
$$

The stability of $(x^*, y^*)$ follows immediately from the negativeness of $V'(t)$.     □

We have obtained sufficient conditions for the asymptotic stability of positive equilibrium solutions to the system (1.6)–(1.7). Next we will study the system from a pullback point of view, which can provide useful insight in addition to the forward stability of equilibrium points.

**3.3. Existence of pullback attractors.** In this subsection we will establish the sufficient conditions for the existence of a nonautonomous pullback attractor. To this end, we first prove the existence of a pullback absorbing set by using the Razumikhin technique, which uses a Lyapunov function rather than a functional (see, e.g., [9] for a differential equation with random delays). The reader can find an interesting motivation for the Razumikhin technique in the book by Hale and Verduyn Lunel [22, p. 151]. In a few words, in addition of the first reason already mentioned that one has to construct Lyapunov functions rather than functionals, another important reason is that in order to have negativeness of the derivative of the Lyapunov function along the solutions of the differential functional equation, it is only necessary to work with those initial conditions which are dominated, in some way, by their values at the final time of the interval $[-h, 0]$, i.e., by the value at time $t = 0$. More precisely, our result will be a consequence of the uniformly ultimately boundedness of the solutions of our problem which is ensured by Theorem 4.3 on p. 159 in [22]. 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 (2.1) is defined to be

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

*Remark* 3.5. Observe that when $V$ is differentiable, the upper Dini derivative coincides with the derivative of the function $V$ along the solutions of the problem (2.1), but the Lyapunov function will not always be differentiable, but only continuous.

Notice that, according to our notation, $z(t; t, \phi) = \phi(0)$. This will allow us to write the proofs of Lemma 3.6 and later Lemma 4.5 in a more elegant way.

Let us now prove the existence of an absorbing set in the following lemma.

LEMMA 3.6. *There exist bounded pullback absorbing sets for the nonautonomous dynamical system generated by* (1.6)–(1.7) *provided that*

$$
D - \max\{c, \gamma\} > 0.
$$

*Proof.* Consider the function $V : \mathbb{R} \times \mathbb{R}^2 \to \mathbb{R}$ defined by

$$
V(t, x, y) = \|(x, y)\| := |x| + |y|, \ t, x, y \in \mathbb{R}.
$$

As we are interested only in nonnegative solutions, when we restrict this function to points $(x, y)$ in the nonnegative quadrant we have that $V(t, x, y) = x + y$. Then, given an initial value $\phi \in C_h$ we consider the solution $z(\cdot; t, \phi) := (x(\cdot), y(\cdot))$ of (1.6)–(1.7) passing through $(t, \phi)$ and we will check the assumptions in Theorem 4.3 from [22]. In light of Remark 3.5, we have that $x(t) = \phi_1(0), y(t) = \phi_2(0)$.

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

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

Second, the time derivative of $V$ along the solutions of (1.6)–(1.7) satisfies

$$\begin{aligned}
\dot{V}(t, \phi(0)) &= DI - D(\phi_1(0) + \phi_2(0)) - aU(\phi_1(0))\phi_2(0) \\
&\quad + b\gamma\phi_2(-\tau_1(t)) - \gamma\phi_2(0) + cU(\phi_1(-\tau_2(t)))\phi_2(0) \\
&\leq DI - D(\phi_1(0) + \phi_2(0)) + b\gamma\phi_2(-\tau_1(t)) + (c - \gamma)\phi_2(0).
\end{aligned}$$

Define $p(s) = s/b$; then $p(s) > s$ since $0 < b < 1$. Provided that $V(t + \theta, \phi(\theta)) < p(V(t, \phi(0)))$ for $\theta \in [-h, 0]$, we have

$$\phi_2(-\tau_1(t)) < \frac{1}{b}(\phi_1(0) + \phi_2(0)),$$

and consequently

$$\begin{aligned}
\dot{V}(t, \phi(0)) &\leq DI - D(\phi_1(0) + \phi_2(0)) + \gamma(\phi_1(0) + \phi_2(0)) + (c - \gamma)\phi_2(0) \\
&\leq DI - G[\phi_1(0) + \phi_2(0)] = DI - G\|\phi(0)\|,
\end{aligned}$$

where

$$G = D - \max\{c, \gamma\}.$$

As our hypothesis ensures that $G > 0$, let

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

then $\dot{V}(t, \phi(0)) \leq -w(\|\phi(0)\|)$ for any $\|\phi(0)\| \geq 0$. It follows immediately from Theorem 4.3 on p. 159 in [22] that the solutions to (1.6)–(1.7) are uniformly ultimately bounded, i.e., there exists $\beta > 0$ such that for any $\alpha > 0$, there is a constant $T_\alpha > 0$ 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 pullback and forward senses.    ☐

*Remark* 3.7. It is worth mentioning that the existence of pullback (and forward) absorbing sets requires weaker conditions than the ones required for $Z(t, t_0)$ to map bounded sets into bounded sets. First, only the continuity of the delay terms is required in Lemma 3.6, while differentiability of $\tau_1(t)$ and boundedness of $\tau_1'(t)$ are required in Lemma 3.2. Moreover, the condition $D - \max\{c, \gamma\} > 0$ provided in Lemma 3.6 is automatically fulfilled if the condition $D - \frac{M_1}{1 - M_1}\gamma - c > 0$ provided in Lemma 3.2 is satisfied.

The following theorem follows immediately from Lemma 3.2, Lemma 3.6, and Theorem 2.4.

THEOREM 3.8.    *Assume that $\tau_1'(t) \leq M_1 < 1$. The nonautonomous dynamical system generated by* (1.6)–(1.7) *possesses a pullback attractor in $C_h$ provided that*

$$D - \frac{M_1}{1 - M_1}\gamma - c > 0.$$

In this section we studied the chemostat model with variable delays but no wall growth. In the next section we will study the chemostat model with variable delays, taking into account the growth of microorganisms on the wall.

**4. Chemostat with time delays and wall growth.** The assumption that we have on model (1.6)–(1.7) is that the microorganisms grow only in the growth medium, but not along the walls of the container. However, when the washout rate is not fast enough, wall growth becomes an important factor to be considered. In this section we study the chemostat model with variable time delays and with wall growth taken into account. For convenience sake, we restate (1.8)–(1.10) here:

$$x'(t) = D\left(I - x(t)\right) - aU(x(t))\left(y_1(t) + y_2(t)\right) + b\gamma y_1(t - \tau_1(t)),$$

$$y_1'(t) = -\left(\gamma + D\right)y_1(t) + cU(x(t - \tau_2(t)))y_1(t) - r_1 y_1(t) + r_2 y_2(t),$$

$$y_2'(t) = -\gamma y_2(t) + cU(x(t - \tau_2(t)))y_2(t) + r_1 y_1(t) - r_2 y_2(t).$$

Assume that

(4.1)
$$x(t) = \phi_1(t - t_0), \quad y_1(t) = \phi_{21}(t - t_0), \quad y_2(t) = \phi_{22}(t - t_0) \qquad \text{for } t \in [t_0 - h, t_0],$$

where $(\phi_1, \phi_{21}, \phi_{22}) \in C([-h, 0]; \mathbb{R}^3) := \tilde{C}_h$, and write $\phi = (\phi_1, \phi_{21}, \phi_{22})$. Then (1.8)–(1.10) can be written as the nonautonomous functional differential equation

(4.2)                                             $$\frac{dz(t)}{dt} = g(t, z_t),$$

where $g(\cdot, \cdot) : \mathbb{R} \times \tilde{C}_h \to \mathbb{R}^3$ is given by

$$g(t, \phi) = \begin{pmatrix} D(I - \phi_1(0)) - aU(\phi_1(0))(\phi_{21}(0) + \phi_{22}(0)) + b\gamma\phi_{21}(-\tau_1(t)) \\ -(\gamma + D)\phi_{21}(0) + cU(\phi_1(-\tau_2(t)))\phi_{21}(0) - r_1\phi_{21}(0) + r_2\phi_{22}(0) \\ -\gamma\phi_{22}(0) + cU(\phi_1(-\tau_2(t)))\phi_{22}(0) + r_1\phi_{21}(0) - r_2\phi_{22}(0) \end{pmatrix},$$

and $z_t \in \tilde{C}_h$ is the function given by $z_t(\theta) := z(t + \theta)$, $\theta \in [-h, 0]$ for any continuous function $z : [-h, \infty) \to \mathbb{R}^3$.

The existence and uniqueness of solutions to (4.2) with initial conditions (4.1) can be easily established under the assumptions on the uptake function $U$. Therefore we have the unique solution $z(\cdot; t_0, \phi)$ of (4.2) such that $z_{t_0}(\cdot; t_0, \phi) = \phi$, i.e.,

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

Consequently we can construct a nonautonomous dynamical system or process $Z(t, t_0) : \tilde{C}_h \to \tilde{C}_h$ in the phase space $\tilde{C}_h$ defined for any $t \geq t_0$ as

$$Z(t, t_0)\phi = z_t(\cdot; t_0, \phi), \quad \phi \in \tilde{C}_h.$$

In the next subsections we show that all solutions to (4.2) are nonnegative and bounded for all $t \geq t_0$ corresponding to nonnegative and bounded initial conditions (4.1).

**4.1. Positiveness and boundedness of solutions.** Let us start with the nonnegativeness of solutions.

LEMMA 4.1. *For any nonnegative continuous initial conditions* (4.1) *on* $[t_0 - h, t_0]$, *the solutions to* (1.8)–(1.10) *are nonnegative.*

*Proof.* Similar to the proof of Lemma 3.1, we will show that if a solution starts in the octant $\mathbb{R}_+^3 = \{(x, y_1, y_2) : x \geq 0, y_1 \geq 0, y_2 \geq 0\}$ 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 $y_1 \geq 0$, $y_2 \geq 0$, (1.8) reduces to

$$x'(t) = DI + b\gamma y_1(t - \tau_1(t)) > 0,$$

and thus $x(t)$ will bounce back to a positive region once it reaches $x = 0$. 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 nondecreasing at $y_1 = 0$. Similarly, $y_2$ is nondecreasing at $y_2 = 0$. Therefore, $(x(t), y_1(t), y_2(t)) \in \mathbb{R}_+^3$ for any $t$.  □

The boundedness of solutions to (1.8)–(1.10) is stated in the following lemma, which corresponds to Lemma 3.2 in the previous case without wall growth.

LEMMA 4.2. *Assume that $\tau_1'(t) \leq M_1 < 1$. Then solutions to* (1.8)–(1.10) *are bounded for any bounded initial conditions provided that*

$$(4.3) \qquad \mu := \min\{\delta, \gamma - c\} > 0, \quad \text{where} \quad \delta := D - \frac{M_1}{1 - M_1}\gamma - c.$$

*Proof.* Given a solution $(x(t), y_1(t), y_2(t))$ of (1.8)–(1.10), we define the function $\nu(x, y_1, y_2)$ to be

$$\nu(t) := x(t) + b y_1(t) + b y_2(t) + \frac{b\gamma}{1 - M_1} \int_{t - \tau_1(t)}^{t} y_1(s)ds.$$

Then the time derivative of $\nu(t)$ is

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

Since $\tau_1'(t) \leq M_1 < 1$, we have $-\frac{1}{1 - M_1}(1 - \tau_1'(t)) \leq -1$. Also using that the fact that $U(x) \leq 1$ for $x \geq 0$, we have

$$\begin{aligned}
\frac{d\nu(t)}{dt} &\leq DI - Dx(t) - b(\gamma + D)y_1(t) + bc(y_1(t) + y_2(t)) + \frac{b\gamma}{1 - M_1}y_1(t) \\
&\leq DI - Dx(t) - b\delta y_1(t) - b(\gamma - c)y_2(t),
\end{aligned}$$

where $\delta$ is as defined in (4.3).

Now define the region

$$\widetilde{\Omega} := \{(x, y_1, y_2) \in \mathbb{R}_+^3 : Dx + b\delta y_1 + b(\gamma - c)y_2 \leq DI\}.$$

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

$$\nu(x(t), y_1(t), y_2(t)) \leq x(t_0) + by_1(t_0) + by_2(t_0) + \frac{b\gamma}{1 - M_1} \int_{t_0 - \tau_1(t)}^{t_0} y_1(s)ds$$

$$\leq |\phi_1| + b\left(1 + \frac{\gamma h}{1 - M_1}\right)|\phi_{21}| + b|\phi_{22}|,$$

which implies that

(4.4)

$$\|(x(t), y_1(t), y_2(t))\| \leq \frac{1}{b}\nu(x(t), y_1(t), y_2(t)) \leq \frac{1}{b}|\phi_1| + \left(1 + \frac{\gamma h}{1 - M_1}\right)|\phi_{21}| + |\phi_{22}|.$$

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

(4.5)          $$\|(x(t), y_1(t), y_2(t))\| \leq \frac{D}{b\mu}x(t) + \frac{\delta}{\mu}y_1(t) + \frac{\gamma - c}{\mu}y_2(t) \leq \frac{DI}{b\mu}.$$

If a trajectory starts from, enters, or reenters the region $\widetilde{\Omega}$ at times $t_{2i-1} \geq t_0$ and exits at time $t_{2i}$, $(i = 1, 2, \ldots)$, then (4.4) holds for all times $(t_{2i}, t_{2i+1})$ and (4.5) holds for all times $(t_{2i-1}, t_{2i})$.

In summary for any $t > t_0$, we have

$$\|(x_t, y_{1t}, y_{2t})\| = x(t + \theta) + y_1(t + \theta) + y_2(t + \theta)$$

$$\leq \max\left\{\frac{|\phi_1|}{b} + \left(1 + \frac{\gamma h}{1 - M_1}\right)|\phi_{21}| + |\phi_{22}|, \frac{DI}{b\mu}\right\}.$$

Therefore given any $(\phi_1, \phi_{11}, \phi_{21}) \in \tilde{C}_h$ with $|\phi_1| + |\phi_{11}| + |\phi_{21}| \leq d$ we have $(x_t, y_{1t}, y_{2t}) \in \mathcal{B}_{\tilde{C}_h}(0, R_2)$ for $t \geq t_0$, where

$$R_2 := \max\left\{\frac{d}{b}, d\left(1 + \frac{\gamma h}{1 - M_1}\right), \frac{DI}{b\mu}\right\}. \qquad \square$$

In the next section we will study the stability of positive equilibria, which are of most biological interest.

**4.2. Stability analysis.** Note that any equilibrium solution $(x, y_1, y_2)$ to system (1.8)–(1.10) should satisfy the following algebraic equations:

$$D(I - x) - aU(x)(y_1 + y_2) + b\gamma y_1 = 0,$$
$$-(\gamma + D)y_1 + cU(x)y_1 - r_1 y_1 + r_2 y_2 = 0,$$
$$-\gamma y_2 + cU(x)y_2 + r_1 y_1 - r_2 y_2 = 0.$$

Clearly $(x, y_1, y_2) = (I, 0, 0)$ is an equilibrium, which is asymptotically stable when $\gamma \geq c$. In fact, when $\gamma \geq c$,

$$\frac{d(y_1(t) + y_2(t))}{dt} = -(\gamma + D)y_1(t) - \gamma y_2(t) + cU(x(t - \tau_2(t))(y_1(t) + y_2(t))$$

$$< -(\gamma - c)(y_1(t) + y_2(t)) \leq 0.$$

To study the stability of nontrival equilibrium solutions to system (1.8)–(1.10), we first make the following change of variables:

$$\eta(t) = y_1(t) + y_2(t), \quad \beta(t) = \frac{y_1(t)}{\eta(t)}.$$

Equations (1.8)–(1.10) then become

$$(4.6) \qquad \frac{dx(t)}{dt} = D(I - x(t)) - aU(x(t))\eta(t) + b\gamma\beta(t - \tau_1(t))\eta(t - \tau_1(t)),$$

$$(4.7) \qquad \frac{d\eta(t)}{dt} = -\gamma\eta(t) - D\beta(t)\eta(t) + cU(x(t - \tau_2(t)))\eta(t),$$

$$(4.8) \qquad \frac{d\beta(t)}{dt} = -D\beta(t)(1 - \beta(t)) - r_1\beta(t) + r_2(1 - \beta(t)).$$

The equation for $\beta(t)$ is decoupled from equations for $x(t)$ and $\eta(t)$. Solving the algebraic equation

$$-D\beta(1 - \beta) - r_1\beta + r_2(1 - \beta) = 0$$

gives

$$\beta = \frac{D + r_1 + r_2 \pm \sqrt{(D + r_1 + r_2)^2 - 4Dr_2}}{2D}.$$

Note that $\beta(t) \in (0, 1)$ for any positive solutions $y_1(t) > 0$ and $y_2(t) > 0$ of (1.8)–(1.10). In addition, since $\beta'(0) = r_2 > 0$ and $\beta'(1) = -r_1 < 0$, the interval $(0, 1)$ is positively invariant for $\beta(t)$ and is the region of biological interest. Therefore the equilibrium of (4.8) is given by

$$(4.9) \qquad \beta^* = \frac{D + r_1 + r_2 - \sqrt{(D + r_1 + r_2)^2 - 4Dr_2}}{2D}.$$

LEMMA 4.3. $\beta^*$ *as defined in* (4.9) *is an asymptotically stable equilibrium of ODE* (4.8).

*Proof.* Define $\Delta(t) := \beta(t) - \beta^*$; then $\Delta(t)$ satisfies the following ODE:

$$\frac{d\Delta(t)}{dt} = D\Delta(t)\left(\Delta(t) + 2\beta^* - 1 - \frac{r_1 + r_2}{D}\right),$$

i.e.,

$$(4.10) \qquad \frac{d\Delta(t)}{dt} = D\Delta(t)\left(\Delta(t) - \frac{\sqrt{(D + r_1 + r_2)^2 - 4Dr_2}}{D}\right). \qquad \square$$

Solving (4.10) with any initial condition $\Delta(t_0) = \Delta_0$ gives

$$\Delta(t) = \frac{\Delta_0\sqrt{(D + r_1 + r_2)^2 - 4Dr_2}}{\Delta_0 - (\Delta_0 - \sqrt{(D + r_1 + r_2)^2 - 4Dr_2})e^{\sqrt{(D+r_1+r_2)^2-4Dr_2}\cdot(t-t_0)}} \longrightarrow 0$$

as $t \to \infty$ or $t_0 \to -\infty$, which implies that $\beta^*$ is both forward asymptotically stable and pullback attracting. $\quad\square$

For sufficiently large time $t$, replacing $\beta(t)$ by $\beta^*$ in (4.6) and (4.8) gives

$$(4.11) \qquad \frac{dx(t)}{dt} = D(I - x(t)) - aU(x(t))\eta(t) + b\gamma\beta^*\eta(t - \tau_1(t)),$$

$$(4.12) \qquad \frac{d\eta(t)}{dt} = -\gamma\eta(t) - D\beta^*\eta(t) + cU(x(t - \tau_2(t)))\eta(t).$$

Any nontrivial equilibrium of (4.11)–(4.12) should satisfy the algebraic equations

$$D(I - x^*) - aU(x^*)\eta^* + b\gamma\beta^*\eta^* = 0,$$
$$-\gamma - D\beta^* + cU(x^*) = 0.$$

Applying $U(x) = \frac{x}{\lambda + x}$, and assuming that

$$c > \gamma + D\beta^* \quad \text{and} \quad (I(c - \gamma - D\beta^*) - \lambda(\gamma + D\beta^*))(a(\gamma + D\beta^*) - bc\gamma\beta^*) > 0,$$

we obtain a positive equilibrium:

$$x^* = \frac{\lambda(\gamma + D\beta^*)}{c - \gamma - D\beta^*}, \quad \eta^* = \frac{cD(I - x^*)}{a(\gamma + D\beta^*) - bc\gamma\beta^*}.$$

We next establish the asymptotic stability of $(x^*, \eta^*)$ in the following theorem.

THEOREM 4.4. *Assume that $\tau_1(\cdot), \tau_2(\cdot) : \mathbb{R}_+ \to [0, h]$ and $\tau_1'(t) \leq M_1 < 1$. Then the equilibrium solution $(x^*, \eta^*)$ for system (4.11)–(4.12) is asymptotically stable provided*

$$\frac{1}{D + \gamma}\left(e^{(D+\gamma)h} - 1\right) + \frac{1}{1 - M_1}h < \frac{2a}{bc\gamma\beta^*}.$$

*Proof.* The proof is similar to that of Theorem 3.3, hence we will keep only the estimates that are different and omit the rest. Let

$$\tilde{x}(t) := x(t) - x^*, \qquad \tilde{\eta}(t) : \ln\frac{\eta(t)}{\eta^*}, \qquad \widetilde{U}(\cdot) := U(\cdot + x^*) - U(x^*).$$

Equations (4.11)–(4.12) can then be transformed into

$$\frac{d\tilde{x}(t)}{dt} = -D\tilde{x}(t) - a\widetilde{U}(\tilde{x}(t))\eta^* e^{\tilde{\eta}(t)} - aU(x^*)\eta^*(e^{\tilde{\eta}(t)} - 1) + b\gamma\beta^*\eta^*(e^{\tilde{\eta}(t - \tau_1(t))} - 1)$$
$$\frac{d\tilde{\eta}(t)}{dt} = c\widetilde{U}(\tilde{x}(t - \tau_2(t))).$$

Define the function

$$V(t) = V(\tilde{x}(t), \tilde{\eta}(t)) = \int_0^{\tilde{x}(t)} \widetilde{U}(\tilde{x}(s))ds + \frac{(aU(x^*) - b\gamma\beta^*)\eta^*}{c}\int_0^{\tilde{\eta}(t)}(e^s - 1)ds$$
$$+ \frac{bc\gamma\beta^*\eta^*}{2(1 - M_1)}\int_{t - \tau_1(t)}^t \int_v^t e^{\tilde{\eta}(s)}\widetilde{U}^2(\tilde{x}(s - \tau_2(s)))dsdv$$

Clearly $V(0, 0) = 0$. Also since $U(x)$ is increasing with respect $x$, $\widetilde{U}(t)\tilde{x}(t) \geq 0$ and thus $V(t) > 0$ for any $(\tilde{x}(t), \tilde{\eta}(t)) \in \mathbb{R}_+^2/(0, 0)$. The time derivative of $V(t)$ in solutions

to (4.11)–(4.12) thus satisfies

$$
\begin{aligned}
\frac{dV(t)}{dt} \leq\ & -D\tilde{x}(t-\tau_2(t))\widetilde{U}(\tilde{x}(t-\tau_2(t))) \\
& -\left\{a - \frac{1}{2}bc\gamma\beta^*\left[\frac{1}{D+\gamma}\left(e^{(D+\gamma)\tau_1(t)}-1\right)+\frac{1}{1-M_1}\tau_2(t)\right]\right\} \\
& \quad \eta(t)\widetilde{U}^2(\tilde{x}(t-\tau_2(t))) \\
\leq\ & -\left\{a - \frac{1}{2}bc\gamma\beta^*\left[\frac{1}{D+\gamma}\left(e^{(D+\gamma)h}-1\right)+\frac{1}{1-M_1}h\right]\right\}\eta(t)\widetilde{U}^2(\tilde{x}(t-\tau_2(t))) \\
\leq\ & 0.
\end{aligned}
$$

Therefore $V(t)$ is the required Laypunov function, which ensures the global stability of equilibrium $(x^*,\eta^*)$ by the Lyapunov method. $\quad\square$

In the next subsection we will study the system (1.8)–(1.10) from the perspective of pullback attraction, as we did in the case without wall growth.

**4.3. Pullback attractors.** In order to prove the existence of a pullback absorbing set we will again use the Razumikhin technique.

LEMMA 4.5. *There exist bounded pullback absorbing sets for the nonautonomous dynamical system generated by* (1.8)–(1.10) *provided that*

$$
\min\{D,\gamma-c\} > b\gamma.
$$

*Proof.* As the proof parallels that of Lemma 3.6 we will not provide all the details.

Consider $V(t,x,y_1,y_2) := |x| + |y_1| + |y_2|$ for all $t,\,x,\,y_1,\,y_2 \in \mathbb{R}$. This satisfies $V(t,x,y_1,y_2) = \|(x,y_1,y_2)\| := x + y_1 + y_2$ in the nonnegative octant.

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

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

Second, the time derivative of $V$ along the solutions of (1.8)–(1.10) through $(t,\phi)$ satisfies (using the same notation as in the proof of Lemma 3.6)

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

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,

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

where

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

Fix $q = 1 + \epsilon$. Then $G_q > 0$ when $\epsilon$ is small enough and $\min\{D, \gamma - c\} > b\gamma$. Let

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

Then $\dot{V}(t, \phi(0)) \leq -w(\|\phi(0)\|)$ for any $\|\phi(0)\| \geq 0$. It follows immediately from Theorem 4.3 on p. 159 in [22] that the solutions to (1.8)–(1.10) 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 indepedent of $t$, such that

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

This implies that the absorbing sets exist, in both the pullback and forward senses.  □

Similar to the chemostat without wall growth in section 3, the following theorem follows immediately from Lemma 4.2, Lemma 4.5, and Theorem 2.4.

THEOREM 4.6. *Assume that $\tau_1'(t) \leq M_1 < 1$. Then the nonautonomous dynamical system generated by* (1.8)–(1.10) *possesses a pullback attractor in $\tilde{C}_h$ provided that*

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

**5. Closing remarks.** In this paper we studied the asymptotic behavior of chemostat models with variable delays, with or without wall growth. Different from existing works in the literature, we considered time-dependent delays instead of constant delays, not only in the growth response but also in material recycling. The time-dependence of delays makes the models nonautonomous, which requires techniques from the theory of nonautonomous dynamical systems. Moreover, we assume that the delay in the growth response ($\tau_2(t)$) is different from that in the material recycling ($\tau_1(t)$), which results in a more realistic model. This assumption also provides more precise analytical results, as the conditions required for $\tau_1(t)$ and $\tau_2(t)$ are different.

For both models with and without wall growth, we first provided sufficient conditions for solutions to be nonnegative and to be bounded, which eventually imply the existence of a nonautonomous pullback attractor. Note that for all our analysis to hold, an upper bound $M_1 < 1$ is required for the time derivative of material recycling delay function $\tau_1'(t)$, i.e., $\tau_1'(t) \leq M_1 < 1$ for all $t$. But no specific condition on the growth response delay $\tau_2(t)$ is required except the one needed for stability of equilibria.

We also provided sufficient conditions on stability of positive equilibria by constructing appropriate Laypunov functions. These sufficient conditions essentially put restrictions on both variable delay terms. It is worth mentioning that the sufficient conditions that we provide in Theorems 3.3 and 4.4 are stronger than needed. In fact the stability of positive equilibria still holds if the term

$$\frac{1}{D + \gamma}\left(e^{(D+\gamma)h} - 1\right) + \frac{1}{1 - M_1}h$$

in both Theorems 3.3 and 4.4 is changed to

$$\frac{1}{D + \gamma}\left(e^{(D+\gamma)\tau_1(t)} - 1\right) + \frac{1}{1 - M_1}\tau_2(t).$$

It is only until recently that mathematicians started to study biological/ecological systems under time-varying environments by using the theory of nonautonomous dynamical systems. The fluctuation of environments can usually be handled by introducing time-dependent coefficients (e.g., due to time-varying inputs of the system) and time-dependent delays (e.g., due to seasonal effects), resulting in nonautonomous dynamical systems. In [7] we investigated the chemostat model with time-dependent coefficients by using the theory of nonautonomous dynamical systems and obtained the existence of attractors along with some geometric details. It is worth mentioning that although the underlying theoretical framework that we use here is the same, the techniques employed are different. Different from [7], we consider the system in a functional differential equation setting instead of an ODE setting, we use the Razumikhin method to prove the existence of a pullback absorbing set, and we provide stability analysis by using Lyapunov functions in addition to the existence of a pullback attractor.

**5.1. Extension to random delays.** The analysis carried out in this paper can be extended to consider random delays instead of deterministic variable delays. However, this extension requires the skew-product flow formulation of random dynamical systems [2] rather than two-parameter semigroups. The equilibria are no longer constants but time-dependent stochastic processes. In general, the sample paths of the stochastic process driving the random delay are Hölder continuous but not differentiable, but the Razumikhin method nevertheless allows the existence of pathwise pullback random attractors to be established. These are also forward attractors in the weaker sense of convergence in probability. See, e.g., [9] for a random differential equation with random delays.

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