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Chemostats with time-dependent inputs and wall growth

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Abstract: Traditional assumptions in the simple chemostat model include fixed availability of the nutrient and its supply rate, and fast flow rate to avoid wall growth. 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. In this paper, we relax these assumptions and study the chemostat models with a variable nutrient supplying rate or a variable input nutrient concentration, with or without wall growth. This leads the models to nonautonomous dynamical systems and requires new concepts of nonautonomous attractors from the recently developed theory of nonautonomous dynamical systems. Our results provide sufficient conditions for existence of nonautonomous attractors and singleton attractors.

Keywords: Chemostat, wall growth, nonautonomous attractor

1 Introduction

A chemostat is associated with a laboratory device which consists of three interconnected vessel and is used to grow microorganisms in a cultured environment. In its basic form, the outlet of the first vessel is the inlet for the second vessel and the outlet of the second vessel is the inlet for the third. The first vessel is called a feed bottle, which contains all the nutrients required to grow the microorganisms. All nutrients are assumed to be abundantly supplied except one, which is called a *limiting nutrient*. The contents of the first vessel are pumped into the second vessel, which is called the culture vessel, at a constant rate. The microorganisms feed on nutrients from the feed bottle and grow in the culture vessel. The culture vessel is continuously stirred so that all the organisms have equal access to the nutrients. The contents of the culture vessel are then pumped into the third vessel, which is call a collection vessel. Naturally it contains nutrients, microorganisms and the products produced by the microorganisms [21].

As the best laboratory idealization of nature for population studies, the chemostat plays an important role in ecological studies [3,5,6,9,24,25,26,28]. With some modifications it is also used as the model for waste-water treatment process [1,14]. The chemostat model can be considered as the starting point for many variations that yield more realistic biological models, e.g., the recombinant problem in genetically altered organisms [22,23] and the model of mammalian large intestine [7, 8]. More literature on the derivation and analysis of chemostat-like models can be found in [17,19,27] and the references therein.

In the simple chemostat model, the availability of the nutrient and its supply rate are assumed to be fixed. However, the availability of a nutrient in a natural system usually depends on the nutrient consumption rate and input nutrient concentration, which may lead to a nonautonomous dynamical system. Another basic assumption in the simple chemostat model is that the flow rate is assumed to be fast enough that it does not allow growth on the cell walls. Yet wall growth does occur when the washout rate is not fast enough and is a problem in bio-reactors. Studies of chemostat models treated as nonautonomous dynamical systems are very limited to date, e.g., Smith and Thieme introduced practical persistence for nonautonomous dynamical system with the simple chemostat as an example in [18] when the washout rate is time-dependent.

In this paper we study the chemostat models with a variable nutrient supplying rate or a variable input nutrient concentration, with or without wall growth. This

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requires new concepts of nonautonomous attractors from the recently developed theory of nonautonomous dynamical systems. The rest of this paper is organized as follow. In section 2 we present the chemostat model and its basic properties. In section 3 we recall some definitions and results from the theory of nonautonomous dynamical systems which will be necessary for our analysis. In section 4 we study the models with a variable nutrient supplying rate with and without wall growth. In section 5 we study the model with variable input nutrient concentration with and without wall growth. A closing remark is given in section 6 and completes the paper.

2 The model

Consider a chemostat model consisting of a microorganism feeding on a single growth-limiting nutrient. Denote by x the growth-limiting nutrient and by y the microorganism feeding on the nutrient x. Assume that all other nutrients, except x, are abundantly available, i.e., we are interested only in the study of the effect of this essential limiting nutrient x on the species y.

Under the standard assumptions of a chemostat, a list of basic parameters and functional relations in the system includes [21]:

– D, the rate at which the nutrient is supplied and also the rate at which the contents of the growth medium are removed.
– I, the input nutrient concentration which describes the quantity of nutrient available with the system at any time.
– a, the maximal consumption rate of the nutrient and also the maximum specific growth rate of microorganisms – a positive constant.
– U, the functional response of the microorganism describing how the nutrient is consumed by the species. It is known in literature as consumption function or uptake function. Basic assumptions on $U : \mathbb{R}^+ \to \mathbb{R}^+$ are given by
  1. $U(0) = 0, \quad U(x) > 0$ for all $x > 0$.
  2. $\lim_{x\to\infty} U(x) = L_1$, where $L_1 < \infty$.
  3. U is continuously differentiable.
  4. U is monotonically increasing.

  Note that conditions 1 and 2 of the uptake function U ensure the existence of a positive constant $L > 0$ such that

$$U(x) \le L \quad \text{for all} \quad x \in [0, \infty). \tag{1}$$

Denote by $x(t)$ and $y(t)$ the concentrations of the nutrient and the microorganism at any specific time t. When I and D are both constants, [21] proposed the following growth equations to describe the limited resource-consumer dynamics:

$$x' = D(I - x) - aU(x(t))y(t), \tag{2}$$

$$y' = -Dy(t) + aU(x(t))y(t). \tag{3}$$

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 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 $r_1 y_1(t)$ and $r_2 y_2(t)$ 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.

When the flow rate is low, the organisms may die naturally before being washed out and thus washout is no longer the only prime factor of death. Denote by $\nu(> 0)$ the collective death rate coefficient of $y(t)$ representing all the aforementioned factors such as diseases, aging, 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.

When I and D are both constants, and there are no time delays in the system, the following model describes the dynamics of chemostats with wall growth. 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 $y_2(t)$. All the parameters are same as those of system (2) - (3), but $0 < c \le a$ replaces a as the growth rate coefficient of the consumer species.

$$\begin{aligned} x'(t) &= D(I - x(t)) - aU(x(t))\,(y_1(t) + y_2(t)) \\ &\quad + b\nu y_1(t), \end{aligned} \tag{4}$$

$$\begin{aligned} y_1'(t) &= -(\nu + D)y_1(t) + cU(x(t))y_1(t) - r_1 y_1(t) \\ &\quad + r_2 y_2(t), \end{aligned} \tag{5}$$

$$\begin{aligned} y_2'(t) &= -\nu y_2(t) + cU(x(t))y_2(t) + r_1 y_1(t) \\ &\quad - r_2 y_2(t). \end{aligned} \tag{6}$$

We are interested in studying the above systems (2) - (3), (4) - (6) with varied input, i.e., when D or I varies in time. We assume here that the consumption function follows the Michaelis-Menten or Holling type-II form:

$$U(x) = \frac{x}{\lambda + x}, \tag{7}$$

where $\lambda > 0$ is the half-saturation constant [21].

3 Nonautonomous dynamical systems

In this section we provide some background information from the theory of nonautonomous dynamical systems [13] that we require in the sequel. Our situation is, in fact, somewhat simpler, but to facilitate the reader's access to the literature we give more general definitions here.

Consider an initial value problem for a nonautonomous ordinary differential equation in $\mathbb{R}^d$,

$$\frac{dx(t)}{dt} = f(t,x), \quad x(t_0) = x_0.$$

The solution usually depends on both the actual time t and the initial time t_0 rather than just on the elapsed time $t - t_0$ as in an autonomous system. The solution mapping $\phi(t,t_0,x_0)$ of an initial value problem for which an existence and uniqueness theorem holds then satisfies the *initial value* property $\phi(t_0,t_0,x_0) = x_0$, the *two-parameter semigroup* evolution property

$$\phi(t_2,t_0,x_0) = \phi(t_2,t_1,\phi(t_1,t_0,x_0)), \quad t_0 \le t_1 \le t_2,$$

as well as the *continuity* property that $(t,t_0,x_0) \mapsto \phi(t,t_0,x_0)$ is continuous on the state space $\mathbb{R}^d$.

These properties of the solution mapping of nonautonomous ordinary differential equations are one of the main motivations for the *process* formulation of a nonautonomous dynamical system on a state space $\mathbb{R}^d$ (or, more generally, a metric space (X,d)) and time set $\mathbb{R}$ for a continuous-time process. Define

$$\mathbb{R}^2_{\ge} := \{(t,t_0) \in \mathbb{R}^2 \;:\; t \ge t_0\}.$$

Definition 1. *A process ϕ on space $\mathbb{R}^d$ is a family of mappings*

$$\phi(t,t_0,\cdot) : \mathbb{R}^d \to \mathbb{R}^d, \qquad (t,t_0) \in \mathbb{R}^2_{\ge},$$

which satisfies

(i) initial value property: $\phi(t_0,t_0,x) = x$ for all $x \in \mathbb{R}^d$ and any $t_0 \in \mathbb{R}$;
(ii) two-parameter semigroup property: for all $x \in \mathbb{R}^d$ and (t_2,t_1), $(t_1,t_0) \in \mathbb{R}^2_{\ge}$ it holds

$$\phi(t_2,t_0,x) = \phi(t_2,t_1,\phi(t_1,t_0,x)),$$

(iii) continuity property: the mapping $(t,t_0,x) \mapsto \phi(t,t_0,x)$ is continuous on $\mathbb{R}^2_{\ge} \times \mathbb{R}^d$.

Definition 2. *Let ϕ be a process on $\mathbb{R}^d$. A family $\mathscr{B} = \{B(t) : t \in \mathbb{R}\}$ of nonempty subsets of $\mathbb{R}^d$ is said to be ϕ-invariant if $\phi(t,t_0,B(t_0)) = B(t)$ for all $(t,t_0) \in \mathbb{R}^2_{\ge}$ and ϕ- positively invariant if $\phi(t,t_0,B(t_0)) \subseteq B(t)$ for all $(t,t_0) \in \mathbb{R}^2_{\ge}$.*

Definition 3. *Let ϕ be a process on $\mathbb{R}^d$. A ϕ-invariant family $\mathscr{A} = \{A(t) : t \in \mathbb{R}\}$ of nonempty compact subsets of $\mathbb{R}^d$ is called a forward attractor of ϕ if it forward attracts all families $\mathscr{D} = \{D(t) : t \in \mathbb{R}\}$ of nonempty bounded subsets of $\mathbb{R}^d$, i.e.,*

$$\operatorname{dist}(\phi(t,t_0,D(t_0)),A(t)) \to 0 \quad \textit{as } t \to \infty \quad (t_0 \textit{ fixed}), \tag{8}$$

and is called a pullback attractor of ϕ if it pullback attracts all families $\mathscr{D} = \{D(t) : t \in \mathbb{R}\}$ of nonempty bounded subsets of $\mathbb{R}^d$, i.e.,

$$\operatorname{dist}(\phi(t,t_0,D(t_0)),A(t)) \to 0 \quad \textit{as } t_0 \to -\infty \quad (t \textit{ fixed}). \tag{9}$$

The existence of a pullback attractor follows from that of a pullback absorbing family, which is usually more easily determined.

Definition 4. *A family $\mathscr{B} = \{B(t) : t \in \mathbb{R}\}$ of nonempty compact subsets of $\mathbb{R}^d$ is called a pullback absorbing family for a process ϕ if for each $t_1 \in \mathbb{R}$ and every family $\mathscr{D} = \{D(t) : t \in \mathbb{R}\}$ of nonempty bounded subsets of $\mathbb{R}^d$ there exists some $T = T(t_1,\mathscr{D}) \in \mathbb{R}^+$ such that*

$$\phi(t_1,t_0,D(t_0)) \subseteq B(t_1) \quad \textit{for all } t_0 \in \mathbb{R} \textit{ with } t_0 \le t_1 - T.$$

The proof of the following theorem is well known, see e.g., [13].

Theorem 1. *Suppose that a process ϕ on $\mathbb{R}^d$ has a ϕ-positively invariant pullback absorbing family $\mathscr{B} = \{B(t) : t \in \mathbb{R}\}$ of nonempty compact subsets of $\mathbb{R}^d$.*

Then ϕ has a unique global pullback attractor $\mathscr{A} = \{A(t) : t \in \mathbb{R}\}$ with its component sets determined by

$$A(t) = \bigcap_{t_0 \le t} \phi(t,t_0,B(t_0)) \quad \textit{for each } t \in \mathbb{R}. \tag{10}$$

If $\mathscr{B}$ is not ϕ-positively invariant, then

$$A(t) = \bigcap_{s \ge 0} \overline{\bigcup_{t_0 \le t-s} \phi(t,t_0,B(t_0))} \quad \textit{for each } t \in \mathbb{R}.$$

A pullback attractor consists of *entire solutions*, i.e., functions $\xi : \mathbb{R} \to \mathbb{R}$ such that $\xi(t) = \phi(t,t_0,\xi(t_0))$ for all $(t,t_0) \in \mathbb{R}^2_{\ge}$. In special cases it consists of a single entire solution.

Definition 5. *A nonautonomous dynamical system ϕ is said to satisfy a uniform strictly contracting property if for each $R > 0$, there exist positive constants K and α such that*

$$\|\phi(t,t_0,x_0) - \phi(t,t_0,y_0)\|^2 \le K e^{-\alpha(t-t_0)} \cdot \|x_0 - y_0\|^2 \tag{11}$$

for all $(t,t_0) \in \mathbb{R}^2_{\ge}$ and x_0, $y_0 \in \mathbb{B}_R$, where $\mathbb{B}_R$ is the closed ball in $\mathbb{R}^d$ centered at the origin with radius $R > 0$.

This property suffices in combination with a pullback absorbing set to ensure the existence of an attractor in both the forward and pullback sense that consists of singleton sets, i.e., a single entire solution. The proof of the following result involves the construction of an appropriate Cauchy sequence which converges to a unique limit, see [11,12].

Theorem 2. *Suppose that a process ϕ on $\mathbb{R}^d$ is uniform strictly contracting on a ϕ-positively invariant pullback absorbing family $\mathscr{B} = \{B(t) : t \in \mathbb{R}\}$ of nonempty compact subsets of $\mathbb{R}^d$. Then the process ϕ 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.*

4 Variable nutrient supplying rate

In this section we consider the case that the input nutrient concentration is a constant but the nutrient consumption rate is varied. Specifically we assume that D varies continuously in time, e.g., periodically or randomly, in a bounded positive interval $D(t) \in [d_m, d_M]$ for all $t \in \mathbb{R}$.

4.1 ODE case without a wall

We first study the case without a wall. When I is a positive constant and D varies in time, with U taking the form (7), system (2) - (3) becomes

$$\frac{dx(t)}{dt} = D(t)\,(I - x(t)) - \frac{ax(t)}{\lambda + x(t)} y(t), \tag{12}$$

$$\frac{dy(t)}{dt} = -D(t)y(t) + \frac{ax(t)}{\lambda + x(t)} y(t). \tag{13}$$

Lemma 1. *For any initial time $t_0 \in \mathbb{R}$ and initial conditions x_0, $y_0 \geq 0$, all the solutions of system (12)-(13) are nonnegative and bounded for all $t \geq t_0$.*

Proof. The coefficients are continuously differentiable for x, $y \geq 0$. In particular, the nonlinear term

$$\frac{axy}{\lambda + x} = ay\left(1 - \frac{\lambda}{\lambda + x}\right)$$

is nonnegative and bounded above by the linear function ay on the positive quadrant. This ensures the existence and uniqueness of solutions as long as they stay within the positive quadrant. By continuity of solutions, with initial condition $x(t_0) = x_0 > 0$, $x(t)$ has to take value 0 before it becomes negative. Since

$$\left.\frac{dx}{dt}\right|_{x=0} = D(t)I > 0,$$

$x(t)$ cannot become negative. With the initial condition $y(t_0) = y_0 > 0$, there exists $t_1 > t_0$ such that $y(t) > 0$ on $[t_0, t_1]$. Therefore

$$y(t) = y_0 e^{\int_{t_0}^{t}\left(-D(s) + \frac{ax(s)}{\lambda + x(s)}\right)ds}$$

for $t \in [t_0, t_1]$. By uniqueness of solutions this expression holds for all $t \geq t_0$, thus $y(t)$ is nonnegative.

Summing (12) and (13) gives

$$\frac{d\,(x(t) + y(t))}{dt} = -D(t)\,(x(t) + y(t) - I)$$

and yields immediately that when $x(t) + y(t) > I$, we have $I \leq x(t) + y(t) \leq x_0 + y_0$. Similarly, when $x(t) + y(t) < I$ we have $0 \leq x(t) + y(t) \leq I$. Therefore $0 \leq x(t) + y(t) \leq \max\{I, x_0 + y_0\}$, which implies that $x(t)$ and $y(t)$ are bounded. □

We next study the long term behavior of solutions to (12)-(13). More specifically, we will provide conditions under which the system has a pullback attractor, and the conditions under which the attractor is a single entire solution or a single point. Note that $(I, 0)$ is the only steady state solution for all parameters values. Other attracting solutions will not be steady states.

Theorem 3. *Assume that $D : \mathbb{R} \to [d_m, d_M]$, where $0 < d_m < d_M < \infty$, is continuous. Then the system (12)-(13) has a pullback attractor $\mathscr{A} = \{A(t) : t \in \mathbb{R}\}$ inside the nonnegative quadrant $\mathbb{R}^2_+ := \{(x,y) \in \mathbb{R}^2 : x \geq 0, y \geq 0\}$. Moreover,*

(i) when $a < d_m$ the axial steady state solution $(I, 0)$ is asymptotically stable in the nonnegative 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

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

for $t \in \mathbb{R}$.

Proof. Define $w(t) := x(t) + y(t)$. Then summing (12) and (13) above gives

$$\frac{dw(t)}{dt} = D(t)(I - w(t)).$$

This has a steady state solution $w^* = I$, even when $D(t)$ is not a constant. One can show that it is both pullback and forward attracting, see e.g., [13]. Let $w_0 := w(t_0) = x(t_0) + y(t_0)$. Then

$$w(t) = w_0 e^{-\int_{t_0}^t D(s)\,ds} + I e^{-\int_{t_0}^t D(s)\,ds} \int_{t_0}^t D(s) e^{\int_{t_0}^s D(r)\,dr}\,ds$$

$$= w_0 e^{-\int_{t_0}^t D(s)\,ds} + I e^{-\int_{t_0}^t D(s)\,ds} \int_{t_0}^t \frac{d}{ds}\left[e^{\int_{t_0}^s D(r)\,dr}\right] ds$$

$$= w_0 e^{-\int_{t_0}^t D(s)\,ds} + I e^{-\int_{t_0}^t D(s)\,ds} e^{\int_{t_0}^t D(r)\,dr}$$

$$= w_0 e^{-\int_{t_0}^t D(s)\,ds} + I - I e^{-\int_{t_0}^t D(s)\,ds},$$

which converges to I as either $t_0 \to -\infty$ with t fixed or as $t \to \infty$ with t_0 fixed, since

$$0 \le e^{-\int_{t_0}^t D(s)\,ds} \le e^{-d_m(t-t_0)} \to 0$$

in both cases.

From this and Lemma 1 it follows that for every $\varepsilon > 0$, the nonempty compact set

$$B_\varepsilon := \left\{(x,y) \in \mathbb{R}_+^2 : x + y \le I + \varepsilon\right\}$$

is positively invariant and absorbing in the $\mathbb{R}_+^2$. The nonautonomous dynamical system on $\mathbb{R}_+^2$ generated by the ODE system (12)-(13) thus has a pullback attractor $\mathscr{A} = \{A(t) : t \in \mathbb{R}\}$ consisting of non-empty compact subsets of $\mathbb{R}_+^2$.

The various cases in the theorem provide us with more information about the internal structure of the pullback attractor.

(i) Since $w(t) = x(t) + y(t)$ approaches I as $t \to \infty$ in the positive quadrant it suffices to consider points (x,y) on the line $x + y = I$ in the positive quadrant. Since $x(t)$ satisfies (12) with $y(t) = I - x(t) > 0$, we have

$$\frac{dx(t)}{dt} = (I - x(t))\left(D(t) - \frac{ax(t)}{\lambda + x(t)}\right). \tag{14}$$

If $d_m > a$, then

$$\frac{dx(t)}{dt} \ge (d_m - a)(I - x(t)) > 0 \tag{15}$$

as long as $x(t) \ne I$. Since $\lambda > 0$ and

$$\frac{ax}{\lambda + x} < a$$

for $x \ge 0$, then $x(t)$ increases to I and $y(t)$ decreases to 0 along this line. This means all solutions in the nonnegative quadrant approach $(I,0)$ asymptotically. Now, to prove the additional statement on the structure of the pullback attractor, i.e. that the solutions in then nonnegative quadrant pullback converge to $(I,0)$, we need to integrate the previous differential inequality (15) and take limits in the pullback sense. Indeed, (15) can be rewritten as

$$\frac{dx(t)}{dt} + (d_m - a)x(t) \ge (d_m - a)I,$$

and, consequently,

$$\frac{d}{dt}\left[e^{(d_m-a)t}x(t)\right] \ge (d_m - a)Ie^{(d_m-a)t}.$$

Integrating this inequality in the interval $[t_0, t]$, we obtain

$$x(t) \ge e^{-(d_m-a)(t-t_0)} + I\left(1 - e^{-(d_m-a)(t-t_0)}\right), \tag{16}$$

and taking limits now when $t_0 \to -\infty$, we deduce that $x(t) \ge I$, what yields our result. In summary, we have proved that the pullback attractor consists of singleton component subsets $A(t) = \{(I,0)\}$ and is also forward asymptotically stable as well as pullback attracting.

(ii) For $0 < \varepsilon_1 < I$ sufficiently small we always have

$$\frac{a\varepsilon_1}{\lambda + \varepsilon_1} < d_m,$$

and from equation (12)

$$\left.\frac{dx(t)}{dt}\right|_{x=\varepsilon_1} = \left(D(t) - \frac{a\varepsilon_1}{\lambda + \varepsilon_1}\right)(I - \varepsilon_1)$$

$$\ge \left(d_m - \frac{a\varepsilon_1}{\lambda + \varepsilon_1}\right)(I - \varepsilon_1) > 0$$

In addition, from equation (13)

$$\left.\frac{dy(t)}{dt}\right|_{y=I-\varepsilon_1} = -\left(D(t) - \frac{a\varepsilon_1}{\lambda + \varepsilon_1}\right)(I - \varepsilon_1)$$

$$\le \left(\frac{a\varepsilon_1}{\lambda + \varepsilon_1} - d_m\right)(I - \varepsilon_1) < 0$$

Similarly, by the assumption in Assertion (2), which implies that $d_M < a$, for $0 < \varepsilon_2 < I - \varepsilon_1$ sufficiently small we have

$$\frac{a(I - \varepsilon_2)}{\lambda + I - \varepsilon_2} > d_M.$$

Then from equation (12)

$$\left.\frac{dx}{dt}\right|_{x=I-\varepsilon_2} = \left(D(t) - \frac{a(I - \varepsilon_2)}{\lambda + I - \varepsilon_2}\right)\varepsilon_2$$

$$\le \left(d_M - \frac{a(I - \varepsilon_2)}{\lambda + I - \varepsilon_2}\right)\varepsilon_2 < 0$$

and from equation (13)

$$\left.\frac{dy}{dt}\right|_{y=\varepsilon_2} = -\left(D(t) - \frac{a(I - \varepsilon_2)}{\lambda + I - \varepsilon_2}\right)\varepsilon_2$$

$$\ge \left(\frac{a(I - \varepsilon_2)}{\lambda + I - \varepsilon_2} - d_M\right)\varepsilon_2 > 0.$$

Combining these results, we see that the compact subset

$$\mathscr{B}_{\varepsilon_1,\varepsilon_2} := \left\{(x,y) \in \mathbb{R}_+^2 : x+y = I, \varepsilon_1 \le x \le I-\varepsilon_2\right\}$$

is positively invariant and this implies the result.

(iii) All the solutions to (14) with $0 \le x \le I$ satisfy

$$d_m I - d_M x(t) - aI \le \frac{dx(t)}{dt} \le d_M I - d_m x(t). \qquad (17)$$

The first inequality follows from the fact that

$$\begin{aligned}\frac{dx(t)}{dt} &= (I-x(t))\left(D(t) - \frac{ax(t)}{\lambda + x(t)}\right)\\ &\ge d_m I - d_M x(t) - a\left(1 - \frac{\lambda}{\lambda + x(t)}\right)(I - x(t))\\ &\ge d_m I - d_M x(t) - a(I - x(t))\\ &\ge d_m I - d_M x(t) - aI\end{aligned}$$

and the second from

$$\begin{aligned}\frac{dx(t)}{dt} &= (I-x(t))\left(D(t) - \frac{ax(t)}{\lambda + x(t)}\right)\\ &\le (I-x(t))D(t)\\ &\le d_M I - d_m x(t).\end{aligned}$$

These imply that

$$\frac{(d_m - a)I}{d_M} \le x(t) \le \frac{d_M I}{d_m}. \qquad (18)$$

And, on the other hand, we have

$$d_M I - d_m x(t) = d_M(I - x(t)) + (d_M - d_m)x(t) > 0.$$

Then for any two solutions $x_1(t)$ and $x_2(t)$ to (14), $\Delta(t) := x_1(t) - x_2(t)$ satisfies

$$\begin{aligned}\frac{d\Delta(t)}{dt} &= -D(t)\Delta(t) - (I - x_1(t))\frac{ax_1(t)}{\lambda + x_1(t)}\\ &\quad + (I - x_2(t))\frac{ax_2(t)}{\lambda + x_2(t)}\\ &= -D(t)\Delta(t) - \frac{a\lambda I}{(\lambda + x_1)(\lambda + x_2)}\Delta(t)\\ &\quad + a\frac{\lambda(x_1 + x_2) + x_1 x_2}{(\lambda + x_1)(\lambda + x_2)}\Delta(t).\end{aligned} \qquad (19)$$

By the inequalities (18) we obtain

$$\frac{d\Delta(t)}{dt} < -d_m\Delta(t) - \frac{a\lambda I}{\left(\lambda + \frac{d_M I}{d_m}\right)^2}\Delta(t) + a\Delta(t).$$

Hence $\Delta(t) \to 0$ as $t \to \infty$ when

$$d_m + \frac{a\lambda I}{\left(\lambda + \frac{d_M I}{d_m}\right)^2} > a,$$

i.e., when

$$a < \frac{d_m(\lambda d_m + d_M I)^2}{(\lambda d_m + d_M I)^2 - \lambda I d_m^2}$$

This holds if $a < d_m$ as in case (1). However, it can also hold if a is slightly larger than d_m. In this case the pullback limit for strictly positive initial conditions of the scalar system (14) is uniform strictly contracting [11,12] in $(0,I)$ and there exists a single entire solution $\xi^*(t) \in (0,I)$, which is also forward asymptotically stable in the usual forward sense. The corresponding pullback attractor $\mathscr{A}_1$ of this system on $[0,I]$ includes the steady state solution I and has component sets $A_1(t) = [\xi^*(t), I]$ for each $t \in \mathbb{R}$, i.e., it includes the heteroclinic trajectories joining the two "equilibrium" solutions $\xi^*(t)$ and I. For the two-dimensional system (12)–(13) the pullback attractor $\mathscr{A}$ has component sets

$$A(t) = \{(x,y) : x + y = I; \xi^*(t) \le x \le I\}$$

in $\mathbb{R}_+^2$ for $t \in \mathbb{R}$. □

4.2 ODE with a wall

Pilyugin and Waltman introduced the idea of a chemostat with a wall in [15], see also [20] for the case with delays and the book [21]. This corresponds to part of the population that lives near the wall (e.g., the bank of a lake or boundary layer of the intestines), and behaves differently. Here we follow Chapter 5 of the book [21], in particular equation (5.1) on page 176. When I is a constant, D varies in time and there are no delays in time, the system (4) - (6) with U taking the form (7) becomes

$$\begin{aligned}x'(t) &= D(t)(I - x(t)) - a\frac{x(t)}{\lambda + x(t)}(y_1(t) + y_2(t))\\ &\quad + b\nu y_1(t),\end{aligned} \qquad (20)$$

$$\begin{aligned}y_1'(t) &= -(\nu + D(t))y_1(t) + c\frac{x(t)}{\lambda + x(t)}y_1(t)\\ &\quad - r_1 y_1(t) + r_2 y_2(t),\end{aligned} \qquad (21)$$

$$\begin{aligned}y_2'(t) &= -\nu y_2(t) + c\frac{x(t)}{\lambda + x(t)}y_2(t)\\ &\quad + r_1 y_1(t) - r_2 y_2(t),\end{aligned} \qquad (22)$$

where a represents the maximum specific growth rate, c represents the growth rate coefficient of the consumer species, so $a \ge c$; m is the half-saturation constant of the consumption; r_1, r_2 represent the rates at which the species stick on to and shear off from the walls; ν denotes the collective death rate coefficient of y; b describes the fraction of dead biomass that is recycled.

Since the variables x, y_1, and y_2 represent concentrations, we assume nonnegative initial conditions:

$$x(t_0) = x_0; \quad y_1(t_0) = y_{1,0}; \quad y_2(t_0) = y_{2,0}.$$

Lemma 2. *Suppose that* $(x_0, y_{1,0}, y_{2,0}) \in \mathbb{R}^3_+ := \{(x, y_1, y_2) \in \mathbb{R}^3 : x \geq 0, y_1 \geq 0, y_2 \geq 0\}$. *Then all the solutions to system* (20)–(22) *corresponding to initial data in* $\mathbb{R}^3_+$ *are*

(i) nonnegative for all $t > t_0$;
(ii) uniformly bounded in $\mathbb{R}^3_+$.

Moreover, the nonautonomous dynamical system on $\mathbb{R}^3_+$ *generated by the system of ODEs* (20)–(22) *has a pullback attractor* $\mathscr{A} = \{A(t) : t \in \mathbb{R}\}$ *in* $\mathbb{R}^3_+$.

Proof. (i) By continuity each solution has to take value 0 before it reaches a negative value. With $x = 0$ and $y_1 \geq 0$, $y_2 \geq 0$, the ODE for $x(t)$ reduces to

$$x' = D(t)I + b\nu y_1,$$

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

$$y_1' = r_2 y_2 \geq 0,$$

thus $y_1(t)$ 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.

(ii) Define $\|X(t)\|_1 := x(t) + y_1(t) + y_2(t)$ for $X(t) = (x(t), y_1(t), y_2(t)) \in \mathbb{R}^3_+$. Then $\|X(t)\|_1 \leq S(t) \leq \frac{a}{c}\|X(t)\|_1$, where

$$S(t) = x(t) + \frac{a}{c}(y_1(t) + y_2(t)).$$

The time derivative of $S(t)$ along solutions to (20)–(22) satisfies

$$\begin{aligned}\frac{dS(t)}{dt} &= D(t)[I - x(t)] - \left[\frac{a}{c}(\nu + D(t)) - b\nu\right] y_1(t) \\ &\quad - \frac{a}{c}\nu y_2(t) \\ &\leq d_M I - d_m x(t) - \left[\frac{a}{c}(\nu + d_m) - b\nu\right] y_1(t) \\ &\quad - \frac{a}{c}\nu y_2(t) \qquad (23)\end{aligned}$$

Note that $\frac{a}{c}(\nu + d_m) - b\nu > \frac{a}{c} d_m$ since $a \geq c$ and $0 < b < 1$. Let $\mu := \min\{d_m, \nu\}$, then

$$\frac{dS(t)}{dt} \leq d_M I - \mu S(t). \qquad (24)$$

If $S(t_0) < \frac{d_M I}{\mu}$, then $S(t) \leq \frac{d_M I}{\mu}$ for all $t \geq t_0$. On the other hand, if $S(t_0) \geq \frac{d_M I}{\mu}$, then $S(t)$ will be non-increasing for all $t \geq t_0$ and thus $S(t) \leq S(t_0)$. These imply that $\|X(t)\|_1$ is bounded above, i.e.,

$$\|X(t)\|_1 \leq \max\left\{\frac{d_M I}{\mu}, x(t_0) + \frac{a}{c}(y_1(t_0) + y_2(t_0))\right\},$$

for all $t \geq t_0$.

It follows that for every $\varepsilon > 0$ the nonempty compact set

$$B_\varepsilon := \left\{(x, y_1, y_2) \in \mathbb{R}^3_+ : x + \frac{a}{c}(y_1 + y_2) \leq \frac{d_M I}{\mu} + \varepsilon\right\}$$

is positively invariant and absorbing in $\mathbb{R}^3_+$. The nonautonomous dynamical system on $\mathbb{R}^3_+$ generated by the ODE system (20)–(22) thus has a pullback attractor $\mathscr{A} = \{A(t) : t \in \mathbb{R}\}$, consisting of nonempty compact subsets of $\mathbb{R}^3_+$ that are contained in B_ε. □

To obtain more information about the internal structure of the pullback attractor of the nonautonomous dynamical system generated by the ODE system (20) - (22), we make the following change of variables:

$$\alpha(t) = \frac{y_1(t)}{y_1(t) + y_2(t)}, \qquad z(t) = y_1(t) + y_2(t). \qquad (25)$$

System (20) - (22) then assumes the form

$$x'(t) = D(t)(I - x(t)) - \frac{ax(t)}{\lambda + x(t)} z(t) + b\nu\alpha(t)z(t), \quad (26)$$

$$z'(t) = -\nu z(t) - D(t)\alpha(t)z(t) + \frac{cx(t)}{\lambda + x(t)} z(t), \qquad (27)$$

$$\begin{aligned}\alpha'(t) &= -D(t)\alpha(t)(1 - \alpha(t)) - r_1\alpha(t) \\ &\quad + r_2(1 - \alpha(t)). \qquad (28)\end{aligned}$$

Note that the steady state solution $(I, 0, 0)$ of system (20) - (22) has no counterpart for system (26)–(28), since α is not defined for it. On the other hand, $(I, 0)$ is a steady state solution for the subsystem (26)–(27).

4.2.1 Global dynamics of $\alpha(t)$

Observe that the dynamics of $\alpha(t) = \alpha(t, t_0, \alpha_0)$ are uncoupled from $x(t)$ and $z(t)$ and satisfy the Ricatti equation (28). 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 is a constant, there is a unique asymptotically stable steady state $\alpha^* \in (0, 1)$ given by (see [21], page 180)

$$\alpha^* := \frac{D + r_1 + r_2 - \sqrt{(D + r_1 + r_2)^2 - 4Dr_2}}{2D}. \qquad (29)$$

We want to investigate the case that D varies in time, randomly or, say, almost periodically in a bounded positive interval $D(t) \in [d_m, d_M]$ for all $t \in \mathbb{R}$. In this case we need to talk about a random or deterministic pullback attractor $\mathscr{A}_\alpha = \{A_\alpha(t) : t \in \mathbb{R}\}$ in the interval $(0, 1)$. Such an attractor exists since the unit interval is positively invariant (see e.g., [13]), so its component subsets are given by

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

These component subsets have the form

$$A_\alpha = [\alpha_l^*(t), \alpha_u^*(t)],$$

where $\alpha_l^*(t)$ and $\alpha_u^*(t)$ are entire bounded solutions of the Ricatti equation. The other bounded entire solutions of the Ricatti equation lie between these ones.

We can use differential inequalities to obtain bounds on these entire solutions. Let us rewrite the Ricatti equation (28) in the form

$$\alpha'(t) = D(t)(\alpha^2(t) - \alpha(t)) - (r_1+r_2)\alpha(t) + r_2. \qquad (30)$$

Since $\alpha(t) < 1$ and $D(t) > 0$, we have

$$\alpha'(t) \le -(r_1+r_2)\alpha(t) + r_2.$$

Hence $\alpha(t) \le \beta(t)$ with $\alpha(t_0) = \beta(t_0)$, where

$$\beta'(t) = -(r_1+r_2)\beta(t) + r_2$$

This ODE has an asymptotically stable steady state solution

$$\beta^* = \frac{r_2}{r_1+r_2},$$

so the entire solutions of the Ricatti equation (28) lie (minus an infinitesimal) below it, i.e., $\alpha_u^*(t) \le \beta^*$ for all $t \in \mathbb{R}$. This provides an upper bound. On the other hand,

$$\alpha'(t) = D(t)\alpha^2(t) - (D(t)+r_1+r_2)\alpha(t) + r_2$$
$$\ge -(d_M+r_1+r_2)\alpha(t) + r_2$$

Hence $\alpha(t) \ge \gamma(t)$ with $\alpha(t_0) = \gamma(t_0)$, where

$$\gamma'(t) = -(d_M+r_1+r_2)\gamma(t) + r_2.$$

This ODE has an asymptotically stable steady state solution

$$\gamma^* = \frac{r_2}{r_1+r_2+d_M}.$$

In this case we obtain a lower bound $\alpha_l^*(t) \ge \gamma^*$ for all $t \in \mathbb{R}$. In summary,

$$\mathscr{A}(t) = [\alpha_l^*(t), \alpha_u^*(t)] \subset [\gamma^*, \beta^*].$$

To investigate the case where the pullback attractor consists of a single entire solution, we need to find conditions under which

$$\alpha_l^*(t) \equiv \alpha_u^*(t), \qquad t \in \mathbb{R}.$$

Suppose that they are not equal and consider their difference $\Delta_\alpha(t) = \alpha_u^*(t) - \alpha_l^*(t)$. Then

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

Thus

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

(as well as when $t_0 \to -\infty$) provided

$$\frac{2d_M r_2}{r_1+r_2} - d_m - r_1 - r_2 < 0,$$

which is equivalent to $2d_M r_2 < d_m(r_1+r_2) + (r_1+r_2)^2$. 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.

4.2.2 Global Dynamics of $x(t)$ and $z(t)$

Suppose that $\alpha^*(t)$ is the unique entire solution in the pullback attractor of the Ricatti ODE (28). Then $\alpha^*(t) \in [\gamma^*, \beta^*] \subset (0,1)$ for all $t \in \mathbb{R}$. Moreover, for t sufficiently large, $x(t)$ and $z(t)$ components of the system (26)–(28) satisfy

$$x'(t) = D(t)(I - x(t)) - \frac{ax(t)}{\lambda + x(t)}z(t) + b\nu\alpha^*(t)z(t), \quad (31)$$

$$z'(t) = -\nu z(t) - D(t)\alpha^*(t)z(t) + \frac{cx(t)}{\lambda + x(t)}z(t). \qquad (32)$$

The system (31)–(32) has a steady state equilibrium $(I,0)$. Hence $(I,0,\alpha^*(t))$ is a nonautonomous "equilibrium" solution of the system (26)–(28).

Theorem 4. *Assume that $D : \mathbb{R} \to [d_m, d_M]$, with $0 < d_m < d_M < \infty$, is continuous, $a \ge c$, $b \in (0,1)$ and $\nu > 0$. Then, the system (31) - (32) has a pullback attractor $\mathscr{A} = \{A(t) : t \in \mathbb{R}\}$ inside the nonnegative quadrant. Moreover,*

(i) When

$$\nu + d_m\gamma^* > c,$$

the axial steady state solution $(I,0)$ is asymptotically stable in the nonnegative quadrant and the pullback attractor $\mathscr{A}$ has a singleton component subset $A(t) = \{(I,0)\}$ for all $t \in \mathbb{R}$.

(ii) When

$$v + d_M\beta^* < \frac{cd_mI}{\lambda(a-c+v+d_M-bv\beta^*)+d_mI}$$

the pullback attractor $\mathscr{A}$ *also contains points strictly inside the positive quadrant in addition to the point* $\{(I,0)\}$.

Proof. (i) When $v+d_m\gamma^* \geq c$, $z(t)$ satisfies

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

where

$$v+D(t)\alpha^*(t) - \frac{cx(t)}{\lambda+x(t)} > v+d_m\gamma^* - c \geq 0.$$

Thus $z(t)$ decreases to 0 as t approaches ∞. As a consequence, $x(t)$ satisfies

$$x'(t) = D(t)(I-x(t)).$$

Then

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

and converges to I as $t\to\infty$ or $t_0\to-\infty$. Note that in view of the definition of the transformation α it is, however, not possible to take $z=0$, when transforming from the original system (31)–(32), although this system has an analogous steady state $(I,0,0)$ in its (x,y_1,y_2) variables.

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

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

On the one hand,

$$\begin{aligned} u'(t) &\leq D(t)(I-x(t)) \\ &\quad -(v+D(t)\alpha^*(t) - bv\alpha^*(t))z(t) \\ &< D(t)I - D(t)x(t) - D(t)\alpha^*(t)z(t) \\ &< D(t)I - D(t)\alpha^*(t)u(t) \\ &\leq d_MI - d_m\gamma^*u(t). \end{aligned}$$

On the other hand,

$$\begin{aligned} u'(t) &\geq D(t)(I-x(t)) \\ &\quad -(a-c+v+D(t)\alpha^*(t) - bv\alpha^*(t))z(t) \\ &\geq D(t)I - D(t)x(t) - (a-c+v+D(t)-bv\beta^*)z(t) \\ &> D(t)I - (a-c+v+D(t)-bv\beta^*)u(t) \\ &\geq d_mI - (a-c+v+d_M-bv\beta^*)u(t). \end{aligned}$$

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

$$q_1I := \frac{d_mI}{a-c+v+d_M-bv\beta^*} < u(t) < \frac{d_MI}{d_m\gamma^*} =: q_2I, \tag{33}$$

where $q_1<1$ and $q_2>1$. For $\varepsilon>0$ small, define T_ε to be the trapezoid

$$T_\varepsilon := \{(x,z)\in\mathbb{R}^2_+ : x\geq\varepsilon,\ z\geq\varepsilon,\ q_1I\leq x+z\leq q_2I\},$$

which is a subset of the positive quadrant defined as

$$\{(x,z)\in\mathbb{R}^2_+ : x\geq\varepsilon,\ z\geq\varepsilon\}.$$

If we restrict our non-autonomous dynamical system to this set, then T_ε is absorbing here. We next show that T_ε is invariant for this restriction what will give the existence of a pullback attractor $\mathscr{A}^\varepsilon$ and the result easily follows.

First, noting that function $f(x) = \frac{ax}{\lambda+x}$ is increasing on $[0,\infty)$, for ε small enough, we have $\frac{a\varepsilon}{\lambda+\varepsilon} < bv\gamma^*$ and

$$\left.\frac{dx(t)}{dt}\right|_{x=\varepsilon} = D(t)(I-\varepsilon) + \left(bv\alpha^*(t) - \frac{a\varepsilon}{\lambda+\varepsilon}\right)z(t) > 0. \tag{34}$$

Second, the condition

$$v+d_M\beta^* < \frac{cd_mI}{\lambda(a-c+v+d_M-bv\beta^*)+d_mI}$$

is equivalent to $v+d_M\beta^* < \frac{cq_1I}{\lambda+q_1I}$, and thus for ε small enough

$$\begin{aligned} \left.\frac{dz(t)}{dt}\right|_{z=\varepsilon} &= \left(-v-D(t)\alpha^*(t) + \frac{cx(t)}{\lambda+x(t)}\right)\varepsilon \\ &> \left(-v-d_M\beta^* + \frac{c(q_1I-\varepsilon)}{\lambda+q_1I-\varepsilon}\right)\varepsilon > 0. \end{aligned} \tag{35}$$

Inequalities (34), (35), together with

$$\left.\frac{d(x(t)+z(t))}{dt}\right|_{x+z=q_1I} > 0$$

and

$$\left.\frac{d(x(t)+z(t))}{dt}\right|_{x+z=q_2I} < 0,$$

ensure the positive invariance of the compact set T_ε and the existence of a pullback attractor $\mathscr{A}^\varepsilon = \{A^\varepsilon(t) : t\in\mathbb{R}\}$ in T_ε. □

Unfortunately at this point we are not able to obtain the existence of a stable single entire solution that attracts all strictly positive entire solutions as in the case without wall growth.

5 Variable nutrition input rate

Here we assume that the nutrition input value I can vary continuously with time, and henceforth denote it by $I(t)$, while the consumption rate D is a constant. Similarly we assume that I is bounded with positive values, in particular, $I(t)\in[i_m,i_M]$ for all $t\in\mathbb{R}$, where $0<i_m\leq i_M<\infty$.

5.1 ODE without a wall

We now consider the case without a wall, in which case the ODE system (2)–(3) becomes

$$\frac{dx(t)}{dt} = D(I(t) - x(t)) - \frac{ax(t)}{\lambda + x(t)}y(t), \tag{36}$$

$$\frac{dy(t)}{dt} = -Dy(t) + \frac{ax(t)}{\lambda + x(t)}y(t). \tag{37}$$

Let $w(t) := x(t) + y(t)$. Then

$$\frac{dw(t)}{dt} = D(I(t) - w). \tag{38}$$

This does not have a steady state when $I(t)$ is not a constant, but it has a nontrivial nonautonomous "equilibrium" solution that is both pullback and forward attracting:

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

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

which converges to

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

as either $t_0 \to -\infty$ or $t \to \infty$, i.e.,

$$\lim_{t\to\infty} |w(t) - w^*(t)| = \lim_{t_0\to-\infty} |w(t) - w^*(t)| = 0.$$

Note that $w^*(t) \in [i_m, i_M]$ for all $t \in \mathbb{R}$ due to the bounds on I.

Lemma 3. *For any initial time $t_0 \in \mathbb{R}$ and initial conditions x_0, $y_0 \geq 0$, all the solutions of system (36)–(37) are nonnegative and bounded for any $t \geq t_0$.*

The proof is similar to that of Lemma 1 so will be omitted, while the proof of the following theorem is similar to that of Theorem 3, so not all details will be given here.

Theorem 5. *The nonautonomous dynamical system generated by the system of ODEs (36)–(37) 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.

Proof. From Lemma 2 and the fact that $w^*(t) \in [i_m, i_M]$, the nonempty compact set

$$B := \left\{(x, y) \in \mathbb{R}^2_+ \, : \, i_m \leq x + y \leq i_M\right\}$$

is positively invariant and absorbing in $\mathbb{R}^2_+$ for the ODE (38). The nonautonomous dynamical system on $\mathbb{R}^2_+$ generated by the ODE system (36)-(37) thus has a pullback attractor $\mathscr{A} = \{A(t) : t \in \mathbb{R}\}$ consisting of non-empty compact subsets of B. Then $(w^*(t), 0) \in A(t)$ for every $t \in \mathbb{R}$ since the pullback attractor contains all bounded entire solutions.

To prove assertion (i) note that equation (36) can be bounded from above as

$$\frac{dy(t)}{dt} = -\left(D - \frac{ax(t)}{\lambda + x(t)}\right)y(t) \leq -(D - a)y(t),$$

from which it follows immediately that $y(t) \to 0$ as $t \to \infty$ when $D > a$.

(ii) From the positive sign of the derivative of equation (37) $x(t)$ is increasing on the $x = 0$ face of the above absorbing set B. The face $y = 0$ is invariant, but for $y = \varepsilon \ll i_m$ and $i_m \leq x \leq i_M$, equation (36) gives

$$\frac{dy(t)}{dt} = \left(\frac{ax(t)}{\lambda + x(t)} - D\right)y(t)$$

$$\geq \left(\frac{ai_m}{\lambda + i_M} - D\right)y(t) > 0$$

when $ai_m > D(\lambda + i_M)$. This means that the positive interior of the absorbing set also contains points of the pullback attractor.

(iii) Next we consider ODE (36) restricted to the stable manifold $x(t) + y(t) = w^*(t)$ on which it takes the form

$$\frac{dx(t)}{dt} = D(I(t) - x(t)) - \frac{ax(t)}{\lambda + x(t)}(w^*(t) - x(t)). \tag{39}$$

For any two solutions $x_1(t)$ and $x_2(t)$ to (39), define $\Delta_x(t) := x_1(t) - x_2(t)$. Then Δ_x satisfies

$$\frac{d\Delta_x(t)}{dt} = -D\Delta_x(t) - (w^*(t) - x_1(t))\frac{ax_1(t)}{\lambda + x_1(t)}$$

$$+(w^*(t) - x_2(t))\frac{ax_2(t)}{\lambda + x_2(t)}$$

$$= -D\Delta_x(t) - \frac{a\lambda w^*(t)}{(\lambda + x_1)(\lambda + x_2)}\Delta_x(t)$$

$$+a\frac{\lambda(x_1 + x_2) + x_1x_2}{(\lambda + x_1)(\lambda + x_2)}\Delta_x(t).$$

Since $0 \leq x(t) \leq w^*(t) \leq i_M$ and $w^*(t) \geq i_m$ we have

$$\frac{d\Delta_x(t)}{dt} < -D\Delta_x(t) - \frac{a\lambda i_m}{(\lambda+i_M)^2}\Delta_x(t) + a\Delta_x(t).$$

Hence $\Delta_x(t) \to 0$ as $t \to \infty$ when

$$D + \frac{a\lambda i_m}{(\lambda+i_M)^2} > a,$$

i.e., when

$$a\left(\lambda^2 + \lambda(2i_M - i_m) + i_M^2\right) < D(\lambda+i_M)^2.$$

This always holds if $a < D$, in which case we have scenario (i) of the Theorem. It can, however, still hold if a is slightly larger since $\left(\lambda^2+\lambda(2i_M-i_m)+i_M^2\right) < (\lambda+i_M)^2$, in which case the above estimates with neither $x_1(t)$ or $x_2(t)$ equal to $w^*(t)$, the system is strict uniformly contracting [11,12] in the positive quadrant and thus has a unique entire solution as its pullback attractor in the positive quadrant. □

5.2 ODE case with a wall

Last we study the case where the nutrition input I varies and wall growth is considered. When D is a constant, I varies in time and there are no delays in time, the system (4) - (6) with U taking the form (7) becomes

$$x'(t) = D(I(t)-x(t)) - \frac{ax(t)}{\lambda+x(t)}(y_1+y_2) + bvy_1(t), \quad (40)$$

$$y_1'(t) = -(v+D)y_1(t) + \frac{cx(t)}{\lambda+x(t)}y_1(t) - r_1y_1(t) + r_2y_2(t), \quad (41)$$

$$y_2'(t) = -vy_2(t) + \frac{cx(t)}{\lambda+x(t)}y_2(t) + r_1y_1(t) - r_2y_2(t). \quad (42)$$

Lemma 4. *Suppose that $(x_0, y_{1,0}, y_{2,0}) \in \mathbb{R}^3_+$. Then, all solutions to the system (40)–(42) with initial value $(x(t_0), y_1(t_0), y_2(t_0)) = (x_0, y_{1,0}, y_{2,0})$ are*

(i) nonnegative for all $t > t_0$;
(ii) uniformly bounded in $\mathbb{R}^3_+$.

Moreover, the nonautonomous dynamical system on $\mathbb{R}^3_+$ generated by the system of ODES (40)–(42) has a pullback attractor $\mathscr{A} = \{A(t) : t \in \mathbb{R}\}$ in $\mathbb{R}^3_+$.

Proof. Similar to that of Lemma 2. □

Using the new variables $z(t)$ and $\alpha(t)$ defined as in (25), equations (40)–(42) become

$$x'(t) = D(I(t)-x(t)) - \frac{ax(t)}{\lambda+x(t)}z(t) + bv\alpha(t)z(t), \quad (43)$$

$$z'(t) = -vz(t) - D\alpha(t)z(t) + \frac{cx(t)}{\lambda+x(t)}z(t), \quad (44)$$

$$\alpha'(t) = -D\alpha(t)(1-\alpha(t)) - r_1\alpha(t) + r_2(1-\alpha(t)). \quad (45)$$

Equation (45) has a unique steady state solution

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

which is asymptotically stable on $(0,1)$. Hence when $t \to \infty$, replacing $\alpha(t)$ by α^* in equations (43) and (44) we have

$$\frac{dx(t)}{dt} = D(I(t)-x(t)) - \frac{ax(t)}{\lambda+x(t)}z(t) + bv\alpha^*z(t) \quad (46)$$

$$\frac{dz(t)}{dt} = -vz(t) - D\alpha^*z(t) + \frac{cx(t)}{\lambda+x(t)}z(t). \quad (47)$$

For more details of the long term dynamics of the solutions to (46) - (47) we establish the following theorem.

Theorem 6. *Assume that $I : \mathbb{R} \to [i_m, i_M]$, with $0 < i_m < i_M < \infty$, is continuous, $a \geq c$, $b \in (0,1)$ and $v > 0$. Then system (46) - (47) has a pullback attractor $\mathscr{A} = \{A(t) : t \in \mathbb{R}\}$ inside the nonnegative quadrant. Moreover,*

(i) when $v + D\alpha^* > c$, the entire solution $(w^*(t), 0)$ is asymptotically stable 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 $t \in \mathbb{R}$,
(ii) when

$$v + D\alpha^* < \frac{cDi_M}{\lambda(a-c+v-bv\alpha^*+D)+Di_M}$$

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

Proof. Here we omit some detailed calculations when similar to previous cases.

(i) When $v + D\alpha^* > c$,

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

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

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

On the one hand,

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

On the other hand,

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

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

$$l := \frac{Di_M}{a - c + \nu - b\nu\alpha^* + D} < u(t) < \frac{i_M}{\alpha^*}. \tag{48}$$

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

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

then T_ε is absorbing. We next show that T_ε is invariant.

Similar to the proof of Theorem 5, when ε is small enough, we have the following inequalities satisfied on the boundaries of T_ε:

$$x\, z'(t)\big|_{z=\varepsilon} > \left(-\nu + D\alpha^* + \frac{c(l-\varepsilon)}{\lambda + l - \varepsilon}\right)\varepsilon > 0,$$

$$(x(t)+z(t))'\big|_{x+z=i_M/\alpha^*} < 0,$$

$$(x(t)+z(t))'\big|_{x+z=l} > 0.$$

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. □

6 Capturing the time-variation of the inputs

The properties of the solution mapping $\phi(t;t_0,x_0)$ of a nonautonomous systems of ODEs of the form

$$\frac{dx}{dt} = f(x,t), \quad x(t_0) = x_0,$$

in $\mathbb{R}^d$ motivated the *process* or 2-parameter semigroup formalism of abstract nonautonomous dynamical systems. This intuitive formalism, however, does not always allow the whole asymptotic behaviour to be revealed without additional assumptions, in contrast to the more complicated *skew product flow* formalism that already contains more built-in information in terms of what is called a driving system. See [13].

Let (X,d_X) and (P,d_P) be metric spaces. A *skew product flow* (θ,φ) is defined in terms of a cocycle mapping φ on a state space X which is driven by an autonomous dynamical system θ acting on a base or parameter space P and the time set $\mathbb{R}$. Specifically, the driving system θ on P is a group of homeomorphisms $(\theta_t)_{t\in\mathbb{R}}$ under composition on P (i.e., with the properties that (i) $\theta_0(p) = p$ for all $p \in P$; (ii) $\theta_{s+t} = \theta_s(\theta_t(p))$ for all $s,\ t \in \mathbb{R}$; (iii) the mapping $(t,p) \mapsto \theta_t(p)$ is continuous) and a *cocycle mapping* $\varphi : \mathbb{R}^+_0 \times P \times X \to X$ satisfies

(i) $\varphi(0,p,x) = x$ for all $(p,x) \in P \times X$,
(ii) $\varphi(t+s,p,x) = \varphi(t,\theta_s(p),\varphi(s,p,x))$ for all $s,t \in \mathbb{R}^+_0$, $(p,x) \in P \times X$,
(iii) the mapping $(t,p,x) \mapsto \varphi(t,p,x)$ is continuous.

A φ-invariant family of nonempty compact subsets $\mathscr{A} = \{A_p :\ p \in P\}$ of X, i.e., with $\varphi(t,p,A_p) = A_{\theta_t(p)}$ for all $t \in \mathbb{R}^+_0$ and $p \in P$, is called a *pullback attractor* of a skew product flow (θ,φ) if the *pullback convergence*

$$\lim_{t\to\infty} \text{dist}_X\left(\varphi(t,\theta_{-t}(p),D),A_p\right) = 0 \quad (p \text{ fixed})$$

holds for every nonempty bounded subset D of X and $p \in P$, and a *forward attractor* if the *forward convergence*

$$\lim_{t\to\infty} \text{dist}_X\left(\varphi(t,p,D),A_{\theta_t(p)}\right) = 0$$

holds for every nonempty bounded subset D of X and $p \in P$. Counterparts to the theorems for the existence of a pullback attractors for a process hold for skew product flows [13].

In terms of the chemostat systems above, $\varphi(t,p,x)$ is the unique solution for $t \in \mathbb{R}^+_0$ of an initial value problem

$$\frac{dx}{dt} = f(x,\theta_t(p)) \tag{49}$$

in $\mathbb{R}^d$ for $d = 1$, 2 or 3 with the initial value $x(0) = x_0$ for the driving system starting at p. Here P can be taken as the *hull* of a time-dependent term $q : \mathbb{R} \to \mathbb{R}$ (either $D(t)$ or $I(t)$ above) in the space $C(\mathbb{R},\mathbb{R})$, i.e.,

$$P = \overline{\{q(t+\cdot) : t \in \mathbb{R})\}}^{C(\mathbb{R},\mathbb{R})},$$

and θ_t is the shift operator defined by $\theta_t(q(\cdot)) = q(t+\cdot)$. The advantage is that when q is periodic or almost periodic then P is a compact metric space. Note that a process can be represented a skew product flow with the parameter set $P = \mathbb{R}$, $p = t_0$ the initial time and the shift operator $\theta_t(t_0) = t + t_0$.

The skew product representation of the chemostat dynamics provides more insight into how the pullback attractor component subsets may vary in time. For example, with periodic time-dependent inputs $D(t)$ or $I(t)$ of period T, the driving system θ_t is periodic with period T, so by φ-invariance, the pullback attractor component sets are also T periodic, since

$$\varphi(T,p,A_p) = A_{\theta_T(p)} = A_{\theta_0(p)} = A_p.$$

If the pullback attactor consists of singleton components sets, i.e., is formed by an entire solution, then this entire solution is also periodic with period T. This is also true for the entire solution in the uniformly contracting cases (iii) of Theorems 3 and 5. Analogous results also hold in almost periodic and asymptotically autonomous cases.

A similar analysis is possible for the random attractors of chemostat systems with randomly varying imputs. Random dynamical systems are defined analogously, but with the metric space P replaced by the sample space Ω of a probability space $(\Omega,\mathscr{F},\mathbb{P})$ and the continuity of $p \to \theta_t(p)$ by the measurability of $\omega \to \theta_t(\omega)$. In this case the ordinary differential equation (49) becomes a random ordinary differential equation. Random dynamical systems are also generated by the solutions of Itô stochastic differential equations.

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