

# STABILITY LOSS DELAY IN THE CHEMOSTAT WITH A SLOWLY VARYING WASHOUT RATE

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**Abstract.** In this paper, we propose to study a model with two competitors competing for a single nutrient in a chemostat with a slowly varying washout rate. We show that the model exhibits the delayed loss of stability phenomenon when the washout rate crosses the bifurcation value at which the growth curves of the two competitors intersect.

## 1 Introduction

Consider the chemostat model with two competitors on a single resource, of concentration  $s(\cdot)$  :

$$\begin{aligned} \frac{ds}{d\tau} &= D(s_{in} - s) - \mu_1(s)x_1 - \mu_2(s)x_2 \\ \frac{dx_i}{d\tau} &= (\mu_i(s) - D)x_i, \quad (i = 1, 2) \end{aligned} \quad (1)$$

The concentrations of the two different micro-organisms in the system are denoted  $x_1(\cdot)$  and  $x_2(\cdot)$ . The concentration of the input nutrient, denoted by  $s_{in}$ , is kept constant. The growth functions  $\mu_i(\cdot)$  are assumed to be strictly monotonic and such that  $\mu_i(0) = 0$ . The term  $D$  is called the *washout rate*. Considering values of  $D$  less than  $\min_i \mu_i(s_{in})$ , we denote by  $\lambda_i$  the break-even concentrations  $\mu_i^{-1}(D)$ . When  $D$  is kept constant, it is well known from the Competitive Exclusion Principle (CEP) that generically at most one competitor survives asymptotically. More precisely, when  $\lambda_1 < \lambda_2$  (resp.  $\lambda_1 > \lambda_2$ ), the CEP claims that  $(s(\tau), x_1(\tau), x_2(\tau))$  converges asymptotically to  $(\lambda_1, s_{in} - \lambda_1, 0)$  (resp.  $(\lambda_2, 0, s_{in} - \lambda_2)$ ) when  $\tau$  tends to infinity (see for instance [9]).

In this paper, we consider growth curves  $\mu_1$  and  $\mu_2$  that intersect in exactly one point  $s^* > 0$ :

$$\mu_1(s^*) = \mu_2(s^*) = D^* < s_{in}$$

with  $\mu_2(s) < \mu_1(s)$  for  $0 < s < s^*$  and  $\mu_2(s) > \mu_1(s)$ , see Figure 3, left. Furthermore, we consider a slow time varying washout rate  $D = D(\varepsilon\tau)$ , that is  $\varepsilon > 0$  is small, that alternatively favors competitor 1 and competitor 2, assuming that there exist numbers

$$a_n < b_n < a_{n+1} < b_{n+1}, \quad n \in I,$$

where  $I$  is a set of indices such that for all  $n \in I$  we have

$$D(a_n) = D(b_n) = D^*, \quad D(t) < D^* \text{ for } a_n < t < b_n, \quad D(t) > D^* \text{ for } b_n < t < a_{n+1}.$$

Let  $\lambda_1(t) = \mu_1^{-1}(D(t))$ , and  $\lambda_2(t) = \mu_2^{-1}(D(t))$ . We have  $\lambda_1(t^*) = \lambda_2(t^*) = s^*$  and

$$\lambda_1(t) < \lambda_2(t) \text{ for } a_n < t < b_n, \quad \lambda_2(t) < \lambda_1(t) \text{ for } b_n < t < a_{n+1}.$$

In real-life bioprocesses, such as waste-water treatments, inputs are often time-varying. Usually the time scale of these variations is faster or about the same than the biological one. This is a motivation for studying the chemostat with time-varying inputs ( $s_{in}$  or  $D$ ) favoring alternatively one of the competitors, as it has already been made in the literature [10, 6, 8, 5, 3, 4]. Then, an asymptotic coexistence has been proved to occur, under particular conditions on the variations of the inputs. Designing periodic inputs is a way to maintain more than one competitor above some thresholds at any time.

On the opposite, in natural ecosystems, such as in mountain lakes for instance, one may expect that the variations of the environment are much slower than the biological time scale. To our knowledge, the model of the chemostat distinguishing two different time scales has not been yet studied. This is the purpose of the present work. We focus here on the transient behavior of the dynamics, and show that when  $D$  crosses the bifurcation value  $D^*$  i.e. gets more favorable to the other species, one may have to wait a large time before observing the density of this later species becoming dominant. This phenomenon is known in slow-fast dynamics as a stability loss delay. Here, we provide also an approximation of this delay.

From the application point of view, this result might be an interpretation of the sudden apparition of a species in ecosystems that are known to be favorable to this species, but when one may think that the species is absent because it hasn't been observed in significant concentrations from a relatively long time.

The paper is organized as follows. In Section 2 we study the delayed loss of stability phenomenon and we compute the *entrance-exit* functions which give the approximation of the delay. In Section 3 we give sufficient conditions for the coexistence of the species in the nonperiodic case. In Section 4 we illustrate our results by numerical simulations.

## 2 Stability Loss Delay in the chemostat

In terms of the slow time  $t = \varepsilon\tau$ , system (1) becomes

$$\begin{aligned} \varepsilon\dot{s} &= D(t)(S_{in} - s) - \mu_1(s)x_1 - \mu_2(s)x_2 \\ \varepsilon\dot{x}_i &= (\mu_i(s) - D(t))x_i, \quad (i = 1, 2) \end{aligned} \tag{2}$$

where the dot designates the derivatives with respect to time  $t$ . This system is a slow-fast system whose slow curve is given by

$$\mathcal{S}_1 = (\lambda_1(t), s_{in} - \lambda_1(t), 0), \quad \mathcal{S}_2 = (\lambda_2(t), 0, s_{in} - \lambda_2(t)).$$

Notice that  $\mathcal{S}_1$  is attracting when  $a_n < t < b_n$  and  $\mathcal{S}_2$  is attracting when  $b_n < t < a_{n+1}$ . Let  $(s_0, x_{10}, x_{20}, t_0)$  be an initial condition such that  $a_n < t_0 < b_n$ . From Tikhonov theory (see [7]) we deduce that the solution  $(s(t), x_1(t), x_2(t))$  of (2) jumps very quickly near the quasi-steady  $(\lambda_1(t_0), s_{in} - \lambda_1(t_0), 0)$  and then remains close the slow curve  $\mathcal{S}_1$  as long as  $t \in ]t_0, b_n[$ , that is

$$s(t) \approx \lambda_1(t), \quad x_1(t) \approx s_{in} - \lambda_1(t), \quad x_2(t) \approx 0, \quad \text{when } t \in ]t_0, b_n[.$$

It seems plausible to expect that when  $t \in ]b_n, a_{n+1}[$  then the solution will be close to the attracting slow curve  $\mathcal{S}_2$  so that we will have the following approximations

$$s(t) \approx \lambda_2(t), \quad x_1(t) \approx 0, \quad x_2(t) \approx s_{in} - \lambda_2(t), \quad \text{when } t \in ]b_n, a_{n+1}[.$$

In fact, due to the delayed loss of stability phenomenon (see [1]), this behavior is not the right one and the solution will stay near the slow curve  $\mathcal{S}_1$ , until  $t$  reaches a value  $t_1 > b_n$ . Since the slow curve  $\mathcal{S}_1$  is not attracting when  $b_n < t < a_{n+1}$ , and the solution remains near this non attracting slow curve for  $b_n < t < t_1$  we say that there there is a *stability loss delay*. The mapping  $H_n : t_0 \mapsto H_n(t_0) = t_1$  is called the *entrance-exit* function along the slow curve  $\mathcal{S}_1$ . We have (see [2] for similar results)

**Theorem 1** *Assume that*

$$\int_{a_n}^{a_{n+1}} [\mu_2(\lambda_1(t)) - D(t)] dt > 0. \tag{3}$$

*The entrance exit function  $H_n : [a_n, b_n] \rightarrow [b_n, a_{n+1}]$  is given by the smallest time  $H_n(t) > t$  such that*

$$\int_t^{H_n(t)} [\mu_2(\lambda_1(u)) - D(u)] du = 0. \tag{4}$$

*Proof.* Without loss of generality we assume that  $0 < x_{20} < 1$ . The change of variable  $X_2 = \varepsilon \ln x_2$  maps the strip  $0 < x_2 < 1$  into the half space  $X_2 < 0$ . This change of variable transforms (2) into

$$\begin{aligned} \varepsilon\dot{s} &= D(t)(S_{in} - s) - \mu_1(s)x_1 - \mu_2(s) \exp(X_2/\varepsilon) \\ \varepsilon\dot{x}_1 &= [\mu_1(s) - D(t)]x_1 \\ \dot{X}_2 &= \mu_2(s) - D(t) \end{aligned} \tag{5}$$

The initial condition becomes  $X_2(t_0) = \varepsilon \ln x_{20}$ . System (5) is a slow and fast system, with  $X_2$  and  $t$  as the slow variables and  $s$  and  $x_1$  as the fast variables. We have  $\lim_{\varepsilon \rightarrow 0} \exp(X_2/\varepsilon) = 0$ . Thus, the fast equation is written as

$$\begin{aligned} s' &= D(t)(S_{in} - s) - \mu_1(s)x_1 \\ x_1' &= [\mu_1(s) - D(t)]x_1 \end{aligned} \tag{6}$$

where  $t$  is considered as a parameter. The equilibrium

$$s = \lambda_1(t), \quad x_1 = S_{in} - \lambda_1(t) \tag{7}$$

of (6) is attracting for all  $t \in [a_n, b_n]$ . Thus, on the slow surface  $\Sigma$  of (5) defined by equations (7), the slow equation is

$$\dot{X}_2 = \mu_2(\lambda_1(t)) - D(t) \tag{8}$$

According to Tikhonov’s theory, the trajectory goes very quickly towards the slow surface  $\Sigma$ . Then a slow transition develops near  $\Sigma$ . This slow transition is approximated by the solution of (8) with initial condition  $X_2(0) = 0$ . This solution is given by

$$X_2(t) = \int_{t_0}^t [\mu_2(\lambda_1(u)) - D(u)] du. \tag{9}$$

Thus, according to (4), we have again  $X_2 = 0$  for  $t_1 = H_n(t_0)$ . Returning to the original variables, we see that the trajectory  $\gamma(t, \varepsilon)$  crosses again the set  $x_2 = x_{20}$  when  $t$  is asymptotically equal to  $t_1 = H_n(t_0)$ . Since (3) holds, we have  $t_1 \in ]b_n, a_{n+1}[$ . Since for all  $t \in ]b_n, a_{n+1}[$ , the slow curve  $\mathcal{S}_2$  is attracting, Tikhonov’s theory predicts that the trajectory  $\gamma(t, \varepsilon)$  will jump quickly near the slow curve  $\mathcal{S}_2$  and then move near this slow curve, with increasing  $t$ .  $\square$

At time  $t_1$  the solution jumps from the neighborhood of the the quasi-steady  $(\lambda_1(t_1), s_{in} - \lambda_1(t_1), 0)$  to the neighborhood of the quasi-steady  $(\lambda_2(t_1), 0, s_{in} - \lambda_2(t_1))$  and then remains close the attracting slow curve  $\mathcal{S}_2$ , as long as  $t \in ]t_1, t_2[$ , where  $t_2 = G_n(t_1)$  and.  $G_n$  is the *entrance-exit* function along the slow curve  $\mathcal{S}_2$ . Similarly we have

**Theorem 2** *Assume that*

$$\int_{b_n}^{b_{n+1}} [\mu_1(\lambda_2(t)) - D(t)] dt > 0. \tag{10}$$

The entrance exit function  $G_n : [b_n, a_{n+1}] \rightarrow [a_{n+1}, b_{n+1}]$  is given by the smallest time  $G_n(t) > t$  such that

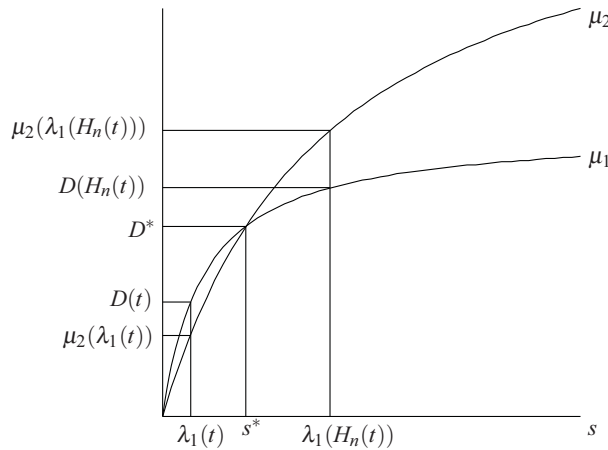
$$\int_t^{G_n(t)} [\mu_1(\lambda_2(u)) - D(u)] du = 0. \tag{11}$$

### 3 Coexistence

For a  $T$ -periodic  $D(\cdot)$  the conditions (3) and (10) reduce simply to the following conditions

$$\int_0^T [\mu_2(\lambda_1(t)) - D(t)] dt > 0 \quad \int_0^T [\mu_1(\lambda_1(t)) - D(t)] dt > 0.$$

These condition are sufficient for the existence of periodic solutions [9]. In this section we show that in the general nonperiodic case conditions (3) and (10) are sufficient for the the coexistence of the species.



**Figure 1:** The functions  $\mu_i$  and the relative positions of  $D(t)$  and  $D(H_n(t))$  when  $t \in [a_n, b_n]$ .

From (3) we deduce that  $c_n = H_n(a_n) < a_{n+1}$ . From (4) and the implicit function theorem we have

$$H'_n(t) = \frac{\mu_2(\lambda_1(t)) - D(t)}{\mu_2(\lambda_1(H_n(t))) - D(H_n(t))}.$$

Since  $t \in [a_n, b_n]$  and  $H_n(t) \in [b_n, a_{n+1}]$ , we have, see Fig. 1:

$$\mu_2(\lambda_1(t)) < D(t), \quad \mu_2(\lambda_1(H_n(t))) > D(H_n(t))$$

Thus  $H'_n(t) < 0$  and  $H_n$  is decreasing from  $[a_n, b_n]$  into  $[b_n, c_n]$ . Similarly  $G_n$  is decreasing from  $[b_n, a_{n+1}]$  into  $[a_{n+1}, b_n^0]$ , where, from (10),  $b_n^0 = G_n(b_n) < b_{n+1}$ . Let  $a_n^0 = G_n(c_n) > a_{n+1}$ . The mapping

$$T_n = G_n \circ H_n : [a_n, b_n] \longrightarrow [a_n^0, b_n^0]$$

is increasing, we have  $T_n(a_n) = a_n^0$ ,  $T_n(b_n) = b_n^0$  and, see Fig. 2:

$$a_{n+1} < a_n^0 < b_n^0 < b_{n+1}.$$

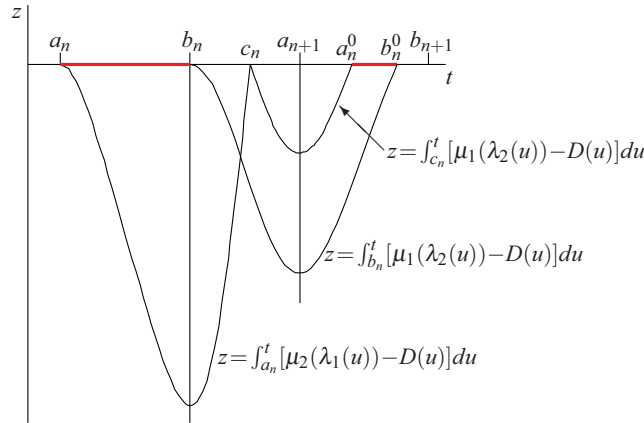


Figure 2: The mapping  $T_n = G_n \circ H_n$  from  $[a_n, b_n]$  into  $[a_n^0, b_n^0]$ .

From Theorems 1 and 2 we obtain the following approximations

**Proposition 3** *Assume that  $s_{in} > \max_t(\lambda_1(t), \lambda_2(t))$  and conditions (3) and (10) are satisfied. Let  $(s_0, x_{10}, x_{20}, t_0)$  be an initial condition such that  $a_n < t_0 < b_n$ . Let  $t_1 = H_n(t_0)$  and  $t_2 = G_n(t_1) = T_n(t_0)$ . Then the solution  $(s(t), x_1(t), x_2(t))$  of (2) satisfies the following approximation*

$$(s(t), x_1(t), x_2(t)) \approx \begin{cases} (\lambda_1(t), s_{in} - \lambda_1(t), 0) & \text{when } t \in ]t_0, t_1[ \\ (\lambda_2(t), 0, s_{in} - \lambda_2(t)) & \text{when } t \in ]t_1, t_2[ \end{cases} \quad (12)$$

We assume that the sequences  $a_n$  and  $b_n$  are indexed by  $\mathbb{N}$  and satisfy

$$A \leq b_n - a_n \leq B \quad \text{and} \quad A \leq a_{n+1} - b_n \leq B,$$

with  $B \geq A > 0$ . We assume that conditions (3) and (10) hold for any  $n \in \mathbb{N}$ . Let  $m > 0$  such that  $m < s_{in} - \max_t(\lambda_1(t), \lambda_2(t))$ . Let  $t_0 \in [a_0, b_0]$ . Let  $(s(t), x_1(t), x_2(t))$  the solution of (2) with initial condition satisfying  $x_1(t_0) > m$  and  $x_2(t_0) > m$ . From Proposition 3 we deduce that for any  $n \geq 1$  there exists  $\theta_n \in [a_n, b_n]$  such that  $x_1(\theta_n) > m$ . Similarly for any  $n \geq 1$  there exist  $\sigma_n \in [a_n, b_n]$  such that  $x_2(\sigma_n) > m$ . Hence both species are observed in significant concentrations for arbitrarily large times.

## 4 Simulation

We have considered the following growth functions

$$\mu_1(s) = \frac{4s}{1+s}, \quad \mu_2(s) = \frac{s}{0.5+s} + s^2$$

that take the value  $D^* \simeq 2.2$  at the intersection of their graph away from zero (see Figure 3, left).

The washout rate  $D(\cdot)$  has been chosen periodic (for simplicity)

$$D(\varepsilon\tau) = D^*(1 + 0.2 \cos(\varepsilon\tau)), \quad \varepsilon = 0.05$$

The values  $a_n, b_n$  are given by

$$a_n = \frac{\pi}{2} + 2n\pi, \quad b_n = \frac{3\pi}{2} + 2n\pi, \quad n \in \mathbb{Z}.$$

Bifurcations occur in time  $\tau$  at  $\alpha_0 = a_0/\varepsilon = 10\pi \simeq 31.4$  and  $\beta_0 = b_0/\varepsilon = 30\pi \simeq 94.2$ , while the change of dominance of species is observed at times  $\tau_* \simeq 64 > \alpha_0$  and  $\tau_{**} \simeq 116 > \beta_0$  on the simulation (see Figure 3, right and Figure 4). We have computed numerically the time  $\tau_1 = t_1/\varepsilon \simeq 65$  where  $t_1 = H_2(0)$  is given by (11) and the time  $\tau_2 = t_2/\varepsilon \simeq 113$  where  $t_2 = H_1(t_1)$  is given by (4). In accordance with Theorems 1 and 2, one can check that times  $\tau_1, \tau_2$  are good approximations of times  $\tau_*, \tau_{**}$ .

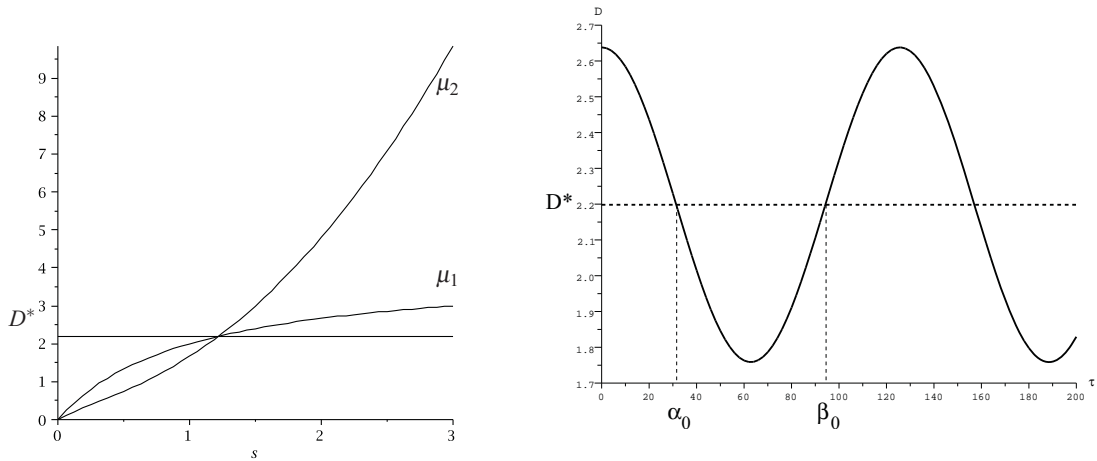


Figure 3: On the left, the growth functions  $\mu_i(\cdot)$ . On the left, the washout  $D(\cdot)$  with respect to time  $\tau$ .

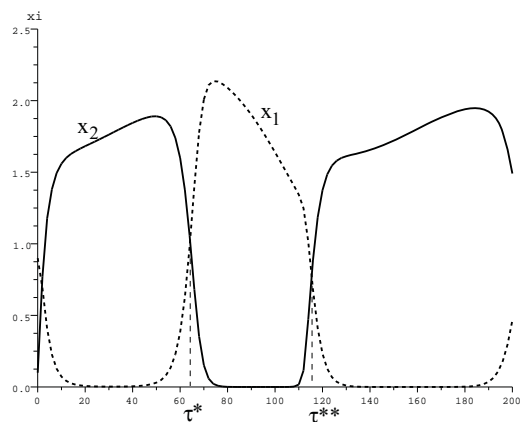


Figure 4: Competitors concentrations with respect to time  $\tau$ .

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