

BIOLOGICAL CONTROL OF THE CHEMOSTAT WITH NONMONOTONIC RESPONSE AND DIFFERENT REMOVAL RATES

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ABSTRACT. We show the global stabilization of the chemostat with nonmonotonic growth, adding a new species as a “biological” control, in presence of different removal rates for each species. This result is obtained by an extension of the Competitive Exclusion Principle in the chemostat, for the case of two species with different removal rates and at least one nonmonotonic response.

1. Introduction. Consider the chemostat model with one species, of concentration x_1 , and one limiting resource, of concentration S

$$\begin{aligned} S' &= (S^0 - S)D - \frac{x_1 p_1(S)}{y_1}, \\ x_1' &= x_1(-D_1 + p_1(S)), \end{aligned} \tag{1}$$

where $S(0) \geq 0$ and $x_1(0) > 0$. S^0 and D are respectively the feed concentration and its dilution rate. D_1 is the removal rate of the micro organisms. When the response (or growth) function $p_1(\cdot)$ is such that the set $\{S \geq 0 \mid p_1(S) > D_1\}$ is a nonempty interval (λ_1, μ_1) with $\mu_1 < S^0$, it is well known that dynamics (1) possesses two stable critical points : the *wash-out* $(0, S^0)$ and a positive equilibrium $E_1^* = (\lambda_1, y_1 D(S^0 - \lambda_1)/D_1)$ (see for instance the textbook [6]). This typically occurs for nonmonotonic response functions, such as the Haldane law.

Such situations are well known among micro biologists and control engineers : from certain initial conditions, the dilution rate can lead to the wash-out of the reactor (i.e. the extinction of the species). Several control strategies for manipulating the dilution rate with respect to measurements of the substrate S or biomass x_1 concentrations have been proposed in the literature (see for instance the textbook [1]). The objective is to make E_1^* a globally asymptotically stable equilibrium point of the closed-loop system. However, controlling the dilution rate imposes an upstream tank, which can be penalizing in certain applications such as wastewater

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treatment. In addition, measuring the nutrient concentration in the tank imposes the use of on-line sensors, often costly or unreliable in practice.

In this paper, we study how to globally stabilize trajectories of system (1) about E_1^* with a *biological* control, instead of *physical* ones. The biological control consists in adding at initial time another species, of concentration x_2 , whose growth function $p_2(\cdot)$ fulfills *good* properties. Mathematically, this amounts to consider the chemostat model with two populations of micro organisms in competition on the same substrate and show that the equilibrium $(E_1^*, 0)$ is globally asymptotically stable.

Such a result can be expressed in terms of the competitive exclusion principle, as it is mentioned in the discussion section of the paper [2]. But, in this last reference, the principle is proved under the assumption that the removal rates D_1, D_2 are both equal to D . To the best of our knowledge, the principle has been proved only for nonmonotonic response functions and different removal rates under the assumption $S^0 < \mu_1$ [7, 5] and therefore does not apply to the case under interest in the present paper. Nevertheless, inspired by these former works, we show here that considering conditions from [2] and results from [5] (which we recall in Section 2) leads to an extension of the principle valid when $\mu_1 < S^0$. More precisely, in Section 3, we propose conditions on the growth function of the additional species under which we prove that the principle holds. The biological control is illustrated in Section 4 on an example with Haldane and Monod responses.

2. Modeling and assumptions. Consider the model

$$\begin{aligned} S' &= (S^0 - S)D - x_1 p_1(S)/y_1 - x_2 p_2(S)/y_2, \\ x_1' &= x_1(-D_1 + p_1(S)), \\ x_2' &= x_2(-D_2 + p_2(S)), \end{aligned} \tag{2}$$

where $S(0) \geq 0$ and $x_i(0) > 0$ ($i = 1, 2$). Without loss of generality, we shall assume that the yield factors y_1, y_2 have been chosen equal to one (this amounts to rescaling the concentrations x_i in x_i/y_i).

Remark 1. In chemostats (or bioreactors) with output membranes that selectively remove the biomass, depending on the size of the micro organisms, one usually assumes the removal rates D_i to be less than D . On the contrary, when the mortality of a species is predominant, one may consider its removal rate D_i to be larger than D .

The growth functions $p_i(\cdot)$ fulfill the usual assumption.

Assumption A1. For $i = 1, 2$, the function $p_i(\cdot)$ is nonnegative, with $p_i(0) = 0$, and Lipschitz continuous.

Under this last assumption, one can easily check that solutions of (2) are well defined and remain nonnegative and bounded for any time.

For each species $i = 1, 2$, we define the numbers

$$\bar{D}_i = \max(D, D_i),$$

and the sets

$$Q_i(d_i) = \{S \geq 0 \mid p_i(S) > d_i\},$$

where d_i is equal to D or D_i , and assume that $Q_i(\bar{D}_i)$ are nonempty. As in former works [2, 7, 5], we consider the following assumption that holds for most of the growth functions found in the literature.

Assumption A2. The sets $Q_i(d_i)$, with $d_i \in \{D_i, D\}$, are intervals

$$Q_i(d_i) = (\lambda_i(d_i), \mu_i(d_i)) ,$$

where $\mu_i(d_i)$ is possibly equal to $+\infty$.

Notice that any monotonic functions, such as the Monod law, some nonmonotonic ones, such as the Haldane law, fulfill this last assumption when the numbers \bar{D}_i are not too large.

Let E^* be the critical point of dynamics (2)

$$E^* = (\lambda_1, D(S^0 - \lambda_1)/D_1, 0) ,$$

and recall the result from [5] (Theorem 2.1).

Theorem 2.1. *If $\lambda_1(D_1) < S^0 < \mu_1(D_1)$ and*

$$\frac{DS^0}{\min(D, D_1, D_2)} - \frac{DS^0}{\max(D, D_1, D_2)} < \lambda_2(D_2) - \lambda_1(D_1) \tag{3}$$

then all solutions of (2) satisfy

$$\lim_{t \rightarrow +\infty} (S(t), x_1(t), x_2(t)) = E^* .$$

Notice that the condition $\lambda_1(D_1) < S^0 < \mu_1(D_1)$ of Theorem 1 imposes $E_1^* = (\lambda_1, D(S^0 - \lambda_1)/D_1)$ to be a globally attractive equilibrium of system (1).

We recall also the result from [2] (Corollary 3.5) for the particular case of $D_1 = D_2 = D$.

Theorem 2.2. *Assume $\lambda_1(D) < \lambda_2(D)$. If $Q = Q_1(D) \cup Q_2(D)$ is connected and $S^0 \in Q$, then the critical point E^* is globally asymptotically stable.*

3. An extension of the Competitive Exclusion Principle. Define the number $\bar{D} = \max(\bar{D}_1, \bar{D}_2)$ and the quantity

$$\underline{S}^0 = \frac{D}{\bar{D}} S^0 \leq S^0 .$$

We consider the following set of hypotheses on the response functions $p_i(\cdot)$.

Assumption A3. The following inequalities are fulfilled.

$$\mu_1(D_1) \leq \underline{S}^0 , \tag{4}$$

$$\lambda_1(\bar{D}_1) < \lambda_2(\bar{D}_2) < \mu_1(\bar{D}_1) \text{ and } S^0 < \mu_2(\bar{D}_2) . \tag{5}$$

$$\tag{6}$$

Condition (4) allows us to consider dynamics (1) for which the wash-out equilibrium $(0, S^0)$ is attractive. Condition (5) somehow replaces the condition $\lambda_1(D_1) < S^0 < \mu_1(D_1)$ of Theorem 2.1 for the global attractivity of E^* . Notice that this

condition coincides with the one required by Theorem 2.2 when $D_1 = D_2 = D$.

Consider the functions

$$\bar{p}_i(S) = p_i(S) - \bar{D}_i, \quad (i = 1, 2) .$$

Then, condition (5) implies that the graphs of the functions $\bar{p}_1(\cdot)$ and $\bar{p}_2(\cdot)$ cross on the interval $(\lambda_2(\bar{D}_2), \mu_1(\bar{D}_1))$. Define the number

$$\bar{S} = \min \{ S \in (\lambda_2(\bar{D}_2), \mu_1(\bar{D}_1)) \mid \bar{p}_1(S) = \bar{p}_2(S) \}$$

(for an illustration, see Figure 1).

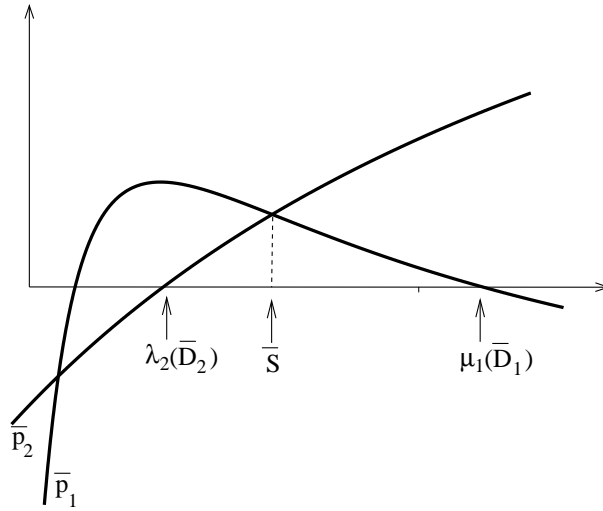


FIGURE 1. Typical graphs of functions $\bar{p}_1(\cdot), \bar{p}_2(\cdot)$.

At this concentration \bar{S} , we require the growths $p_i(\bar{S})$ to be sufficiently above their respective removal rate D_i .

Assumption A4. The following property is fulfilled.

$$p_1(\bar{S}) - \bar{D}_1 = p_2(\bar{S}) - \bar{D}_2 > \frac{S^0 - \underline{S}^0}{\underline{S}^0 - \bar{S}} D . \tag{7}$$

Notice that this last condition is always fulfilled when $D_1 \leq D$ and $D_2 \leq D$.

Proposition 1. *Under Assumptions A1-A2-A3-A4, the condition (3) ensures that any solution of (2) converges asymptotically toward E^* .*

Proof. Fix an initial condition of (2) with $S(0) \geq 0$, $x_1(0) > 0$ and $x_2(0) > 0$.

We first show that there exists $T_1 < +\infty$ such that $S(t) < S^0$ for any $t > T_1$. Notice first that one has $S'(t) \leq D(S^0 - S(t))$ at any time $t \geq 0$. If the trajectory never enters the domain $\mathcal{D}_1 = \{S < S^0\}$ (i.e., $S(t) \geq S^0$ for any $t \geq 0$), $S(\cdot)$ is

decreasing and one should have $p_2(S(t)) \geq \bar{D}_2 \geq D_2$ for any time t larger than T , defined as

$$T = \max \left(0, \frac{1}{D} \log \left(\frac{S(0) - S^0}{\mu_2(\bar{D}_2) - S^0} \right) \right) .$$

This implies $x_2'(t) \geq 0$ at any time $t \geq T$, and then the inequality $S'(t) \leq -D_2 x_2(t) < 0$ should also be fulfilled at any time $t \geq T$. Consequently, the trajectory has to enter the domain \mathcal{D}_1 in finite time, say at T_1 . If the trajectory leaves this domain at a future time, there should exist a finite time $T'_1 > T_1$ such that $S(T'_1) = S^0$ with $S'(T'_1) \geq 0$. But one has $S'(T'_1) = -x_1(T'_1)p_1(S^0) - x_2(T'_1)p_2(S^0) < 0$, leading to a contradiction.

We show now that there exists a finite time $T_2 \geq T_1$ such that $S(t) \leq \bar{S}$ for any $t > T_2$. Notice first that condition (4) guarantees that \bar{S} is below S_0 . If $S(t)$ stays above \bar{S} for any $t \geq T_1$, one should have $x_2'(t) \geq \eta_2 x_2(t)$ for any $t \geq T_1$, where $\eta_2 = \min_{\sigma \in [\bar{S}, S^0]} p_2(\sigma) - D_2$. But one has $[\bar{S}, S^0] \subset Q_2(\bar{D}_2)$, which implies $\eta_2 > 0$, and consequently $\lim_{t \rightarrow +\infty} x_2(t) = +\infty$, which is not possible. So, the trajectory enters the domain $\mathcal{D}_2 = \{S \leq \bar{S}\}$ in finite time. Furthermore, each time the trajectory leaves \mathcal{D}_2 , it has to enter it again at a future finite time. At a time t' when the trajectory leaves domain \mathcal{D}_2 , one should have $S(t') = \bar{S}$ with $S'(t') \geq 0$. Consider the variable $Z = \underline{S}^0 - S - x_1 - x_2$. From equations (2), one obtains

$$Z'(t) \leq -\bar{D}Z(t) \quad \text{for any } t \geq 0 ,$$

and

$$\begin{aligned} S'(t') &= (S^0 - \bar{S} - x_1(t') - x_2(t'))D + x_1(t')(D - p_1(\bar{S})) + x_2(t')(D - p_2(\bar{S})) \\ &\leq (S^0 - \underline{S}^0 + Z(t'))D + x_1(t')(\bar{D}_1 - p_1(\bar{S})) + x_2(t')(\bar{D}_2 - p_2(\bar{S})) \\ &= (S^0 - \underline{S}^0 + Z(t'))D + (\underline{S}^0 - \bar{S} - Z(t'))(\bar{D}_1 - p_1(\bar{S})) \\ &= Z(t')(D + p_1(\bar{S}) - \bar{D}_1) + (S^0 - \underline{S}^0)D - (\underline{S}^0 - \bar{S})(p_1(\bar{S}) - \bar{D}_1) , \end{aligned}$$

Conditions (4) and (7) ensures the sign of the quantity

$$\gamma = (\underline{S}^0 - \bar{S})(p_1(\bar{S}) - \bar{D}_1) - (S^0 - \underline{S}^0)D > 0 ,$$

and for t large enough, one has

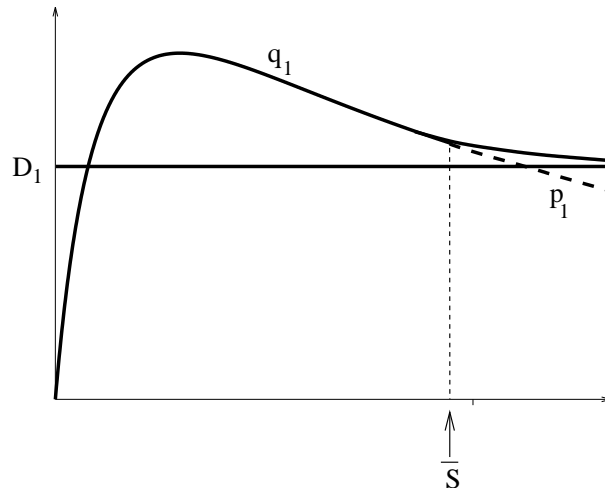
$$Z(t)(D + p_1(\bar{S}) - \bar{D}_1) < \gamma .$$

We deduce that t' cannot be arbitrarily large. The existence of a time T_2 such that the trajectory remains in \mathcal{D}_2 for any future time follows.

Note that one has $p_1(\bar{S}) > \bar{D}_1 \geq D_1$, and consider the fictitious response function (see Figure 2)

$$q_1(S) = \begin{cases} p_1(S) & \text{if } S \leq \bar{S} , \\ D_1 + (p_1(\bar{S}) - D_1) \exp \left(\frac{dp_1(\bar{S})}{dS}(\bar{S}) \frac{S - \bar{S}}{p_1(\bar{S}) - D_1} \right) & \text{if } S > \bar{S} . \end{cases}$$

Then, one can easily check that $q_1(S) > D_1$ for any $S \geq \bar{S}$ and functions $q_1(\cdot), p_2(\cdot)$ fulfill conditions of Theorem 2.1. From state $(S(T_2), x_1(T_2), x_2(T_2))$, the trajectory of (2) is clearly identical to the one solution of system (2), where $p_1(\cdot)$ is replaced by $q_1(\cdot)$. Consequently, the trajectory converges asymptotically toward E^* . \square

FIGURE 2. Functions $p_1(\cdot)$ and $q_1(\cdot)$.

4. The Haldane/Monod case with output membrane. In this section, we assume that the response function $p_1(\cdot)$ is of Haldane's type

$$p_1(S) = \frac{M_1 S}{K_1 + S + I_1 S^2},$$

where M_1 , K_1 and I_1 are positive parameters. Notice that when $M_1 > D$, Assumption A2 is fulfilled for any $D_1 \leq D$. For any $d \leq D$, one has

$$\begin{aligned} \lambda_1(d) &= \frac{M_1 - d - \sqrt{(M_1 - d)^2 - 4K_1 I_1 d^2}}{2I_1 d}, \\ \mu_1(d) &= \frac{M_1 - d + \sqrt{(M_1 - d)^2 - 4K_1 I_1 d^2}}{2I_1 d}. \end{aligned} \quad (8)$$

We consider in this case study a chemostat equipped with output membranes, assuming $D_1 < D$ and $D_2 < D$. Then, the following result gives conditions for the existence of a biological control of (1) by a species with response of Monod type

$$p_2(S) = \frac{M_2 S}{K_2 + S},$$

where M_2 and K_2 are parameters.

Proposition 2. *Assume $M_1 > D > D_1, D_2$ and $\mu_1(D) \leq S^0$. When the condition*

$$\nu_1(D, D_1, D_2, S^0) := \lambda_1(D_1) + \left(\frac{D}{\min(D_1, D_2)} - 1 \right) S^0 < \frac{D_2}{D} \mu_1(D) \quad (9)$$

is fulfilled, there exist positives values of M_2 and K_2 such that E^ is a globally asymptotically stable equilibrium of (2).*

Proof. Function $p_2(\cdot)$ has to fulfill Assumptions A2, A3 and condition (3) for the statement of Proposition 1 to hold (Assumption A4 is necessarily fulfilled because

$\underline{S}^0 = S^0$). A2 is fulfilled when $M_2 > D$. One has, for any $d \leq D$,

$$\lambda_2(d) = \frac{K_2 d}{M_2 - d} \text{ and } \mu_2(d) = +\infty . \tag{10}$$

Then, $p_2(\cdot)$ fulfills A3 and (3) exactly when it satisfies

$$\lambda_2(D) < \mu_1(D) \text{ and } \lambda_2(D_2) > \nu_1(D, D_1, D_2, S^0) .$$

Using expression (10), this amounts to require parameters M_2, K_2 to fulfill

$$DK_2 < \mu_1(D)(M_2 - D) \text{ and } D_2K_2 > \nu_1(D, D_1, D_2, S^0)(M_2 - D) .$$

There exist such values of K_2 when M_2 is such that

$$D_2\mu_1(D)(M_2 - D) > D\nu_1(D, D_1, D_2, S^0)(M_2 - D) ,$$

which is possible exactly when condition (9) is fulfilled. Then, any values M_2, K_2 such that

$$M_2 > \frac{DD_2(\mu_1(D) - \nu_1(D, D_1, D_2, S^0))}{D_2\mu_1(D) - D\nu_1(D, D_1, D_2, S^0)} ,$$

$$K_2 \in \left[\frac{\nu_1(D, D_1, D_2, S^0)(M_2 - D)}{D_2}, \frac{\mu_1(D)(M_2 - D)}{D} \right] ,$$

guarantee the conditions of Proposition 1 to be satisfied. □

As noticed in [7, 5], this condition is fulfilled when D_1 and D_2 are not too small compared to D .

As a numerical example, the following parameters have been used.

S^0	D	M_1	K_1	I_1	D_1	M_2	K_2	D_2
200	80.0	200	20.0	0.01	70.0	260	280	60.0

Graphs of functions $p_1(\cdot)$ and $p_2(\cdot)$ are depicted on Figure 3.

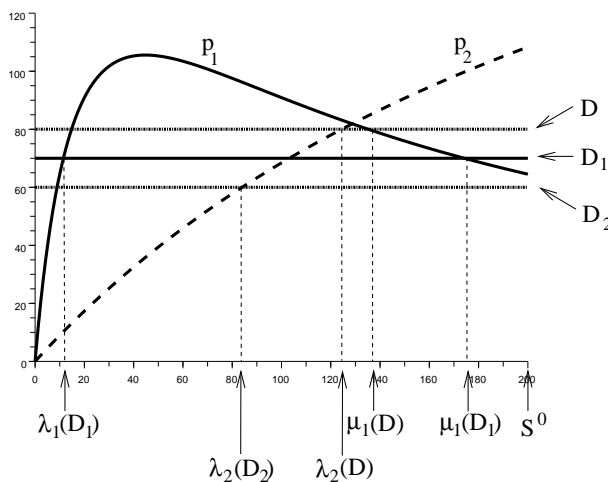


FIGURE 3. Response functions $p_1(\cdot)$ and $p_2(\cdot)$.

From expressions (8), (9) and (10), the following values are computed.

$\lambda_1(D_1)$	$\nu_1(D, D_1, D_2, S^0)$	$\lambda_2(D_2)$	$\lambda_2(D)$	$\mu_1(D)$	$\mu_1(D_1)$
11.48	78.15	84.00	124.44	135.2	174.2

One can check that assumptions of Proposition 2 are fulfilled. For the numerical simulations, we have computed trajectories from two initial conditions: one without the additional species

$$(S(0), x_1(0), x_2(0)) = (150, 20.0, 0) ,$$

which belongs to basin of E_1^* , and the same one but with a nonnull $x_1(0)$:

$$(S(0), x_1(0), x_2(0)) = (150, 20.0, 0.01) .$$

Trajectories are represented on Figures 4 and 5.

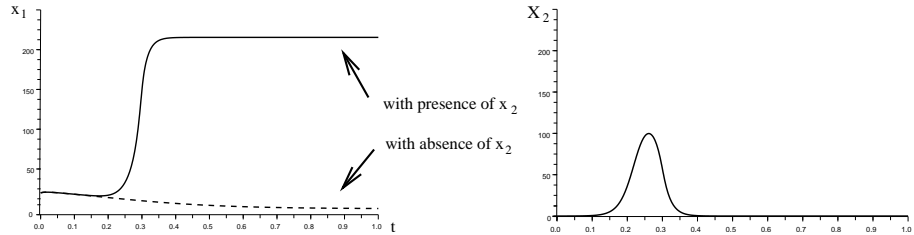


FIGURE 4. Concentrations x_1 and x_2 w.r.t. time.

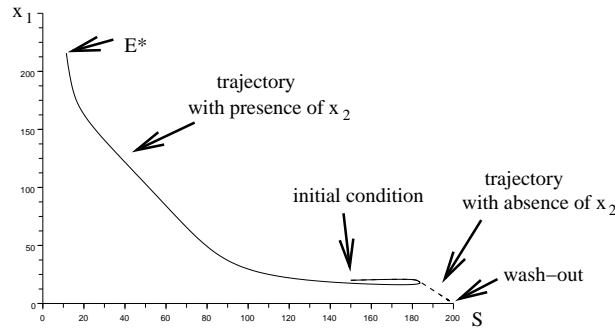


FIGURE 5. Trajectories in (S, x_1) phase portrait.

5. Conclusion. In this work, we show that a chemostat with nonmonotonic response can be globally stabilized, simply introducing a new species while the removal rate of the two considered species are different. Mathematically, the idea is to embed the dynamics in a higher dynamics such that the equilibrium in the presence of the original species is globally attractive on the positive domain. Technically, the difficulty comes from the different removal rates (which typically appear in the presence of an output membrane or when the mortality of the micro organisms are considered). The response of the additional species has to fulfill precise conditions. Roughly speaking, its growth rate (relatively to its removal rate) has to overcome

one of the original species for large nutrient concentrations, and on the opposite, be overcome for small ones. Practically, the new species can be introduced with any arbitrary small quantity. Although necessary for the global stabilization, the additional species will not survive asymptotically.

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