A non-autonomous model for a chemostat with periodic nutrient supply

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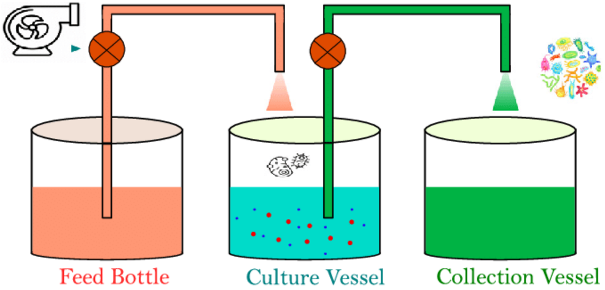
Outline

The model

Chemostat (continuous stirred-tank reactor): continuous bioreactor with constant volume V, whose operating parameters allow to reproduce the essential features of simple microbial ecosystems. Namely, a spatially homogeneous environment, where a supply of nutrient is introduced in order to be consumed by a microbial species.



$$\begin{cases} s'(t) = Ds^0 - Ds(t) - \mu(s(t))x(t) & t > 0, \\ x'(t) = \mu(s(t))x(t) - Dx(t) & t > 0. \end{cases} \tag{1}$$

$s(t) =$ density of the nutrient.
$x(t) =$ density of the microbial species.
$0 < s^0 :=$ nutrient supply.
$0 < D :=$ dilution rate.
$\mu\colon [0, +\infty) \to [0, +\infty) :=$ per-capita growth of the microbial species and its consumption of nutrient.

It is assumed that

(P) $\mu(\cdot)$ is C^1, $\mu'(s) > 0$ for any $s \geq 0$ and $\mu(0) = 0$,

e.g. the Michaelis-Menten function:

$$\mu(s) = \frac{\mu_{\max} s}{k_s + s} \quad \text{with } D < \mu_{\max} \text{ and } k_s > 0.$$

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2. The point $(s^0, 0)$ is an equilibrium, called trivial or *washout*, which corresponds to the extinction of the species.
3. The problem admits a strictly positive equilibrium if and only if $\mu(s^0) > D$.

A more careful analysis allows to show that all the positive trajectories are attracted by the trivial equilibrium when $\mu(s^0) \leq D$, and by the nontrivial one if $\mu(s^0) > D$.

Non-autonomous case $s^0 = s^0(t)$

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s^0 is ω-periodic $\Longrightarrow$ there exist positive ω-periodic solutions?

Remark: $x(0) = 0 \Longrightarrow x \equiv 0$ and

$$s'(t) = D(s^0(t) - s(t)),$$

which has a unique ω-periodic solution $v^*(t) > 0$.

$(v^*, 0) =$ *washout (trivial) solution.*

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$$(v^* - s)'(t) > -D(v^*(t) - s(t))$$

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whence

$$\overline{\mu(v^*)} > D. \tag{3}$$

Good news

Proposition

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Easy proof: (s^*, x^*) nontrivial ω-periodic solution $\Rightarrow s^* + x^* = v^*$. Thus, it suffices to find a nontrivial ω-periodic solution of

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Furthermore, all the positive trajectories:

- approach to (s^*, x^*) if (3) holds.
- approach to the washout otherwise.

Outline

The following model was firstly introduced in [3]

$$\begin{cases} s'(t) = Ds^0(t) - Ds(t) - \mu(s(t))x(t) \\ x'(t) = x(t)\left\{\mu(s(t-\tau)) - D\right\}, \end{cases} \tag{4}$$

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Theorem

The system (4) has a positive ω-periodic solution if and only if (3) holds.

Sketch of the proof

Solve (4) with an initial condition

$$s|_{[-\tau,0]} = \varphi \geq 0, \qquad x(0) = x_0 \geq 0$$

and define

$$P(\varphi, x_0)(t) := (s(t+\omega), x(\omega)) \qquad t \in [-\tau, 0].$$

Assume w.l.o.g. $\tau \leq \omega$, then P is compact.

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Easy computation:

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Thus, writing $P = (P_1, P_2)$ and taking $C := \{0 \leq \varphi \leq \varphi^*\}$, it is seen that

$$P_1 : C \times [0, +\infty) \to C,$$

namely

$$\mathrm{Fix}_{x_0} := \{\varphi : P_1(\varphi, x_0) = \varphi\} \neq \emptyset \qquad x_0 \geq 0.$$

A theorem by F. Browder

Theorem

For arbitrary $b \geq a \geq 0$ there exists a ***continuum***

$$\mathcal{C} \subset \bigcup_{x_0 \in [a,b]} \mathrm{Fix}_{x_0} \times \{x_0\}$$

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$$\iff \varphi \in \mathrm{Fix}_{x_0} \text{ and } F(\varphi, x_0) = 0,$$

where $F(\varphi, x_0) := \overline{\mu(s)} - D.$

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that is

$$\overline{\mu(s)} \leq \frac{k}{L} < D \qquad L \gg 0.$$

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Conclusion: F changes sign on $\mathcal{C} = \mathcal{C}_{0,L}$.

You'd better washout...

Theorem

Assume $\overline{\mu(v^*)} < D$. *Then the washout solution* $(v^*(t), 0)$ *of (4) is globally asymptotically stable for any initial condition* $\varphi(t) \geq 0$, $x_0 \geq 0$, *that is*

$$\lim_{t\to+\infty} (s(t) - v^*(t)) = 0 \quad \text{and} \quad \lim_{t\to+\infty} x(t) = 0,$$

for any solution $(s(t), x(t))$ *with initial condition* (φ, x_0).

Sketch

Let $(s(t), x(t))$ be a nontrivial solution of (4). A simple argument shows: $\forall\, \varepsilon > 0\, \exists\, T := T_\varepsilon > 0$ such that

$$s(t) \le v^*(t) + \varepsilon \quad \text{for any} \quad t > T_\varepsilon. \tag{5}$$

If, moreover, $\overline{\mu(v^*)} < D \Longrightarrow \exists\, \varepsilon_0 > 0$ s. t.

$$\frac{1}{\omega} \int_0^\omega \mu(v^*(t) + \varepsilon_0)\, dt < D$$

$\Longrightarrow$

$$\int_t^{t+\omega} [\mu(s(\xi - \tau)) - D] d\xi \le c_0 < 0 \qquad t \gg 0$$

whence $$\ln x(t) \le \ln x_0 + \lfloor t/\omega \rfloor c_0 + (||\mu \circ s||_\infty - D)\, \omega \to -\infty.$$

Non-extinction scenario

Theorem

Assume $\overline{\mu(v^*)} > D$*. Then the positive* ω*-periodic solution* $(s^*(t), x^*(t))$ *of (4) is unique when the delay* $\tau > 0$ *is sufficiently small.*

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Very recent result: the nontrivial solution is attractive.

Proofs are based on the non-delayed case:

Lemma (Wolkowicz-Zhao)

The positive ω-periodic solution $(s_0^*(t), x_0^*(t))$ for $\tau = 0$ is unique and globally asymptotically stable.

Small delays

Let $\mathcal{A} := \{(s,x) : 0 < s < v^*, x > 0\}$ and $\Phi : \mathcal{A} \times \mathbb{R} \to C_\omega \times C_\omega$,

$$\Phi(s,x,\tau)(t) := (s'(t), x'(t)) - N(s,x)(t).$$

with $N(s,x)(t) =$ Nemitskii operator. Then

$$D_{(s,x)}\Phi(s,x,0)(\varphi,\psi) = \Big(\varphi' + a\varphi + b\psi, \psi' + c\varphi + d\psi\Big),$$

where

$$\begin{array}{ll} a(t) = D + \mu'(s(t))x(t), & b(t) = \mu(s(t)) \\ c(t) = -x(t)\mu'(s(t)), & d(t) = -[\mu(s(t)) - D]. \end{array}$$

It is verified that

$$D_{(s,x)}\Phi(s_0^*, x_0^*, 0) : C^1_\omega \times C^1_\omega \to C_\omega \times C_\omega \text{ isomorphism.}$$

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Implicit Function Theorem $\Longrightarrow \exists$ (locally unique) continuous branch of positive ω-periodic solutions $(s(\tau), x(\tau))$ for τ small.

Suppose $\tau_n \to 0$ and $(s_n^1, x_n^1) \neq (s_n^2, x_n^2)$ positive C_ω-solutions $\Longrightarrow$ we may assume $(s_n^j, x_n^j) \to (s^j, x^j)$ uniformly, with (s^j, x^j) solutions for $\tau = 0$.

$\overline{\mu(s_n^j)} = D$ for all $n \Longrightarrow s^j \neq v^*$ and by (WZ):

$$(s^1, x^1) = (s_0^*, x_0^*) = (s^2, x^2).$$

Thus, for $n \gg 0$ both sequences enter into the neighbourhood provided by the Implicit Function Theorem, a contradiction.

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Then, nontrivial (positive) solutions exist if and only if $\lambda > 1$.

Theorem

Assume that μ *is* C^2. *Then,*

- $(1, v^*, 0)$ *is a (unique) bifurcation point.*
- *There exists exactly one unbounded connected component* $\mathcal{C}_+$ *of nontrivial (positive) triples, whose closure contains* $(1, v^*, 0)$, *and satisfies the following properties:*
  - *Every* $(\lambda, s, x) \in \mathcal{C}_+$ *verifies* $\lambda > 1$, $0 < s < v^*$ *and* $x > 0$,
  - *In a neighborhood of* $(1, v^*, 0)$, *every nontrivial triple belongs to* $\mathcal{C}_+$.

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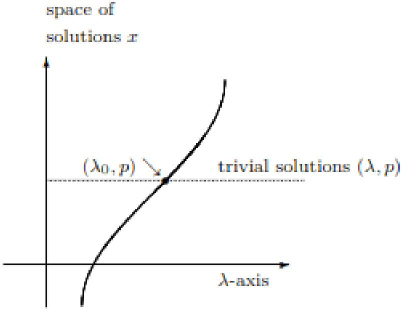
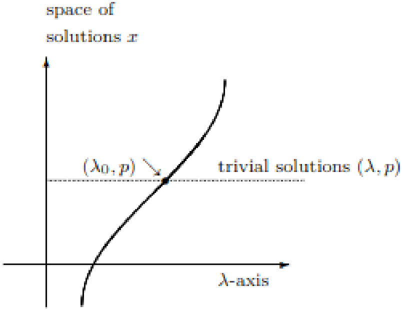
The proof in [1] is based on a Crandall-Rabinowitz theorem.



$$\lambda_0 = 1, p = (v^*, 0)$$



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Furthermore,

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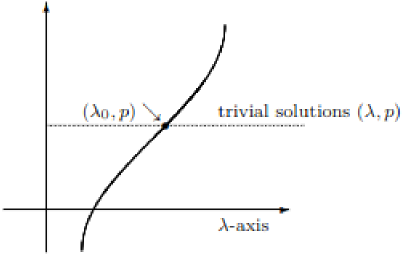
and $s \to 0$ uniformly as $\lambda \to +\infty$.



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Furthermore,

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and $s \to 0$ uniformly as $\lambda \to +\infty$. More precisely, $s \sim O(1/\lambda)$.

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The role of v^* is played by Σ^*, the unique (positive) ω-periodic solution of

$$\Sigma_{t+1} = (1-E)\Sigma_t + ES_t^0. \tag{7}$$

An alternative model:

$$\begin{cases} s'(t) = D(t)s^0(t) - D(t)s(t) - \mu(s(t))x(t) \\ x'(t) = \mu(s(t-\tau))x(t-\tau)e^{-\int_{t-\tau}^{t} D(\xi)\,d\xi} - D(t)x(t), \end{cases} \tag{8}$$

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Theorem

Let $c > 0$ be the unique ω-periodic solution of the linear problem

$$c'(t) = -D(t)c(t) + c(t-\tau)\mu(v^*(t-\tau))e^{-\int_{t-\tau}^{t} D(\xi)\,d\xi}, \qquad c(0) = 1$$

and

$$\psi(t) := \frac{c(t)}{c(t+\tau)}e^{-\int_{t}^{t+\tau} D(\xi)\,d\xi}.$$

Then the system (8) is persistent if and only if $\overline{\mu(v^*)\psi} > \overline{D}$.

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Using Horn fixed point theorem, the existence of an attractive ω-periodic solution is deduced.

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Thanks for your attention!