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# STABILITY OF A CHEMOSTAT MODEL OF TWO MICROORGANISMS

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ABSTRACT

We studied stability analysis of a chemostat model of two microorganisms that incorporates both different response functions and we made a single code of the model using a computer algebra system (CAS) ***Mathematica*** for graphical illustration globally.

**Key words:** Chemostat, Steady States, Coexistence, Stability etc.

## I. INTRODUCTION

The chemostat [3] is a continuous culture device controlled by the concentration of limiting nutrient and dilution rate and it is used to model competition of several microorganisms. So, we consider a model in a chemostat with two organisms that both consume the single nutrient. The model of our interest [2] is as follows:

$$\left.\begin{aligned} c'(t) &= (c_0 - c(t))\delta - \frac{1}{\eta_1}K_1(c(t))p(t) - \frac{1}{\eta_2}K_2(c(t))q(t) \\ p'(t) &= p(t)\{K_1(c(t)) - \bar{\delta}_1\} \\ q'(t) &= q(t)\{K_2(c(t)) - \bar{\delta}_2\} \\ c(0) &= c_0 > 0,\ p(0) = p_0 > 0,\ q(0) = q_0 > 0 \end{aligned}\right\} \quad \dots (1)$$

where

$c(t)$ denotes the concentration of nutrient at time t

$p(t)$ denotes the concentration of first microorganism at time t

$q(t)$ denotes the concentration of second microorganism at time t

$c_0$ repesents the input concentration of the nutrient

$\delta$ represents the dilution rate of the chemostat

$\eta_1, \eta_2$ represent the yield constants of the two microorganisms repectively

$K_1, K_2$ represent the growth rate of the two microorganisms respectively

$\bar{\delta}_1 = \delta + \in_1; \bar{\delta}_2 = \delta + \in_2;$

$\in_1, \in_2$ represent the specific death rates of the two microorgisms respectively

Let $\delta_1 = \delta_2 = \delta$ result from assuming that the death rates of $p$ and $q$ are negligible so that the only loss of microorganisms is due to 'wash out' at the same rate that the nutrient is lost. To pass to non-dimensional variables, we measure concentrations of nutrient in units of $c_0$, time in unit of $1/\delta$, $p$ in units of $\eta_1 c_0$, and $q$ in unitsof $\eta_2 c_0$ (i.e. $\bar{c} := c/c_0$, $\bar{p} := p/\eta_1 c_0$ and $\bar{q} := q/\eta_2 c_0$) and obtains the following differential equations. After dropping the bars and writing $\kappa_i(c(t))$ instead of $K_i(c_0 c)$, we get the model of interest:

$$\left.\begin{aligned}
&c'(t)=1-c(t)-\kappa_1(c(t))p(t)-\kappa_2(c(t))q(t)\\
&p'(t)=p(t)\{\kappa_1(c(t))-\delta_1\}\\
&q'(t)=q(t)\{\kappa_2(c(t))-\delta_2\}\\
&c(0)=c_0>0,\ \ p(0)=p_0>0,\ \ q(0)=q_0>0
\end{aligned}\right\}\ldots(2)$$

where $\delta_i=\overline{\delta}_i/\delta,\ \kappa_i(c)=\delta^{-1}K(c_0c), i=1,2$. We assume the followings for our response function $\kappa_i(c(t))$ though out the rest of the paper:

(i) $\kappa_i: R_+\rightarrow R_+$,

(ii) $\kappa_i$ is continuously differentiable at one time (ie. $\kappa_i'$ exists),

(iii) $\kappa_i(0)=0$, and

(iv) $\kappa_i(c)$ is monotonically increasing (i.e. $\kappa_i'(c)>0\ \forall c\in R_+$).

## II. PRELIMINARIES

In this section, we present some useful preliminary results, the positivity and boundedness of solutions of our system (2), steady states and their stability[4].

### 2.1. Positivity and Boundedness of Solutions:

**Theorem 2.1.1:** The solutions $x(t)=(c(t),p(t),q(t))$ of (2) are positive $\forall\ t>0$ and $c(t)<1$ for large t.

**Proof:** Let the statement is false. First suppose that $c(t)>0$ for all $t>0$ is not true. Let $t^*=\min\{t: t>0\wedge c(t)=0\}$. Then $c(t)>0$, $\forall t\in[0,t^*)$. But from the first equation of (2), we have $c'(t^*)=\delta>0$. That is, $c'(t)>0$ on a neighbourhood of $t^*$. This implies there exists $\in>0$ such that $c(t)$ is increasing on $(t^*-\in,t^*+\in)$, which contradicts our assumption. Thus $c(t)>0$ for all $t>0$.

Now to prove $p(t)>0\ \forall\ t>0$, we let $t_1=\min\{t: t>0\ \wedge p(t)q(t)=0\}$. We assume first that $p(t_1)=0$. Then $q(t)>0$ for all $t\in[0,t_1]$. Let $M=\min_{0\le t\le t_1}\{\kappa_1(c(t))-\delta_1\}$. Then for $t\in[0,t_1]$, second equation of (2) becomes $p'(t)\ge Mp(t)$ which implies that $p(t_1)\ge p(0)\ e^{Mt_1}>0$, a contradiction. Therefore, $p(t)>0$ for all $t>0$.

A similar argument shows that $q(t)>0$ for all $t>0$.

Thus, the system (2) with positive initial conditions at $t=0$ produces a positive solution for $t>0$.

Finally, from the first equation of (2), we have $c'(t)<1-c(t)$ for $t>0$. This implies that $c(t)<1+(c(0)-1)e^{-t}$ for $t>0$. Hence if t becomes large then $c(t)<1$. □

**Theorem 2.1.2**: For $\in>0$, the solutions $c(t),p(t),q(t)$ of (2) satisfy

$$\frac{1}{\delta_{max}}-\in\ \le\ c(t)+p(t)+q(t)\ \le\ \frac{1}{\delta_{min}}+\in$$

for large t, where $\delta_{max}=\max\{1,\delta_1,\delta_2\}$ and $d_{min}=\min\{1,\delta_1,\delta_2\}$

**Proof:** Adding the three equations in (2) yields

$$(c+p+q)'=1-(c+\delta_1p+\delta_2q)$$

This leads to

$$1-\delta_{max}(c+p+q)\le(c+p+q)'\le1-\delta_{min}(c+p+q)$$

Now

$$1-\delta_{max}(c+p+q)\le(c+p+q)'$$

$$\Rightarrow\frac{1}{\delta_{max}}-\frac{(c+p+q)'}{\delta_{max}}\le(c+p+q),$$

Again,

$$\frac{(c+p+q)'}{\delta_{min}}\le\frac{1}{\delta_{min}}-(c+p+q)$$

$$\Rightarrow(c+p+q)\le\frac{1}{\delta_{min}}-\frac{(c+p+q)'}{\delta_{min}}$$

Obviously $\frac{(c+p+q)'}{\delta_{min}}\ge\frac{(c+p+q)'}{\delta_{max}}$,

Let

$$\frac{(c+p+q)'}{\delta_{max}}\le\varepsilon\le\frac{(c+p+q)'}{\delta_{min}}$$

Therefore,

$$\frac{1}{\delta_{max}} - \varepsilon \le \frac{1}{\delta_{max}} - \frac{(c+p+q)'}{\delta_{max}}$$

And also $\frac{1}{\delta_{min}} - \frac{(c+p+q)'}{\delta_{min}} \le \frac{1}{\delta_{min}} + \varepsilon$

Hence, $\frac{1}{\delta_{max}} - \varepsilon \le (c+p+q) \le \frac{1}{\delta_{min}} + \varepsilon$.

## III. STEADY STATES

The steady states of system (2) are:

$$E_1 := (1,0,0),\ E_2 := \left(c_1, \frac{1-c_1}{\delta_1}, 0\right),\ E_3 := \left(c_2, 0, \frac{1-c_2}{\delta_2}\right)$$

where the $c_i$ are implicitly defined as $\kappa_i(c_i) = \delta_i$, for $i = 1,2$. And the coexistence or interior steady state is denoted by $E_{int} := (c^*, p^*, q^*)$, where $c^*$ is defined as the unique solution of $\kappa_i(c(t) - d_i) = 0$ and $p^*, q^*$ are the solutions of the inequality $p(t) + q(t) < 1$ with $c^* < 1$.

### 3.1: Existence of Steady States

(I) $E_1$ is always exists as its components are nonnegative.

(II) Since $\kappa_i(c)$ is increasing with $\kappa_i(0) = 0$, $c_i$ exists with $0 < c_i < 1$ and $\kappa_i(c_i) = \delta_i \Leftrightarrow \kappa_i(1) > \delta_i$, $i = 1,2$. In these cases, $E_2$ and $E_3$ exist.

(III) Since $\kappa_i$ is increasing with $\kappa_i(0) = 0$, $c^*$ exists, satisfying $\kappa_i(c^*) = \delta_i$ iff $\lim_{c\to\infty} \kappa_i(c) > \delta_i$. So for the existence of $E_{int}$, $p^*$ and $q^*$ must be positive.

### 3.2. Stability Analysis

**Theorem 3. 2.1**[6]: Let $X^s$ be a steady state of the first order system of differential equations $x' = F(x)$ on $R^n$, where F is a $C^1$ function from $R^n$ to $R^n$.

(i) If each eigenvalue of the Jacobian matrix $DF(x^s)$ of F at $X^s$ is negative or has negative real part, then $X^s$ is an asymptotically stable steady state of $x' = F(x)$.

(ii) If $DF(x^s)$ has at least one positive real eigenvalue or one complex eigenvalue with positive real part, then then $X^s$ is an unstable steady state of $x' = F(x)$.

**Remark:** If $DF(x^s)$ has some pure imaginary eigenvalues or zero eigenvalues but no positive eigenvalues or eigenvalues with positive real part, then we can't use the Jacobian at $X^s$ to determine the stability of $X^s$. In this situation the steady states $X^s$ may or may not be stable.

**Theorem 3.2.2** :If $c_i > 1$, then only $E_1$ exists and is locally asymptotically stable. If $E_2$ and $E_3$ exist, they are locally asymptotically stable if and only if $\kappa_i(c_j) < \delta_i$, for $i = 2, j = 1$ and $i = 1, j = 2$ respectively. If $E_{int}$ exists then it may stable i.e. the solution may coexist.

**Proof:** The Jacobian matrix of (2) takes the form:

$$J = \begin{bmatrix} -1 - p\kappa_1'(c) - q\kappa_2'(c) & -\kappa_1(c) & -\kappa_2(c) \\ p\kappa_1'(c) & \kappa_1(c) - \delta_1 & 0 \\ q\kappa_2'(c) & 0 & \kappa_2(c) - \delta_2 \end{bmatrix} \ldots(3)$$

When $E_1 = (1,0,0)$ exist, the Jacobian matrix is

$$J_{E_1} = \begin{bmatrix} -1 & -\kappa_1(1) & -\kappa_2(1) \\ 0 & \kappa_1(1) - \delta_1 & 0 \\ 0 & 0 & \kappa_2(1) - \delta_2 \end{bmatrix} \ldots\ldots (4)$$

Since $J_{E_1}$ is an upper triangular matrix, so the eigenvalues lie on the diagonal. Hence $E_1$ exists and locally asymptotically stable if all the eigenvalues are negative. i.e., $\kappa_i(1) - \delta_i < 0$ or equivalently, $c_i > 1$.

At $E_2 = \left(c_1, \frac{1-c_1}{\delta_1}, 0\right)$ the Jacobian matrix takes the form

$$J_{E_2} = \begin{bmatrix} -1-\frac{1-c_1}{\delta_1}\kappa_1'(c_1) & -\kappa_1(c_1) & -\kappa_2(c_1) \\ \frac{1-c_1}{\delta_1}\kappa_1'(c_1) & \kappa_1(c_1)-\delta_1 & 0 \\ 0 & 0 & \kappa_2(c_1)-\delta_2 \end{bmatrix} = \begin{bmatrix} -1-\frac{1-c_1}{\delta_1}\kappa_1'(c_1) & -\kappa_1(c_1) & -\kappa_2(c_1) \\ \frac{1-c_1}{\delta_1}\kappa_1'(c_1) & 0 & 0 \\ 0 & 0 & \kappa_2(c_1)-\delta_2 \end{bmatrix} \quad \ldots (5)$$

The determinant of the upper left-hand $2\times 2$ matrix is positive and its trace is negative, so its eigenvalues have negative real parts. The third eigenvalue of $J_{E_2}$ is $\kappa_2(c_1)-\delta_2$, the entry in the lower right-hand corner. Therefore $E_2$ is asymptotically stable if and only if $\kappa_2(c_1)-\delta_2 < 0$.

At $E_3 = \left(c_2, 0, \frac{1-c_2}{\delta_2}\right)$ the Jacobian matrix takes the form

$$J_{E_3} = \begin{bmatrix} -1-\frac{1-c_2}{\delta_2}\kappa_2'(c_2) & -\kappa_1(c_2) & -\kappa_2(c_2) \\ 0 & \kappa_1(c_2)-\delta_1 & 0 \\ \frac{1-c_2}{\delta_2}\kappa_2'(c_2) & 0 & \kappa_2(c_2)-\delta_2 \end{bmatrix}$$

$$= \begin{bmatrix} -1-\frac{1-c_2}{\delta_2}\kappa_2'(c_2) & -\kappa_1(c_2) & -\kappa_2(c_2) \\ 0 & \kappa_1(c_2)-\delta_1 & 0 \\ \frac{1-c_2}{\delta_2}\kappa_2'(c_2) & 0 & 0 \end{bmatrix} \quad \ldots (6)$$

The determinant of the $2\times 2$ matrix $\begin{bmatrix} -1-\frac{1-c_2}{\delta_2}\kappa_2'(c_2) & -\kappa_1(c_2) \\ \frac{1-c_2}{\delta_2}\kappa_2'(c_2) & 0 \end{bmatrix}$ is positive and its trace is negative, so its eigenvalues have negative real parts. The third eigenvalue is $\kappa_1(c_2)-\delta_1$, the entry in the middle of $J_{E_3}$. Therefore $E_3$ is asymptotically stable if and only if $\kappa_1(c_2)-\delta_1 < 0$.

At $E_{int} = (c^*, p^*, q^*)$ the Jacobian matrix is

$$J_{E_{int}} = \begin{bmatrix} -1-p^*\kappa_1'(c^*)-q^*\kappa_2'(c^*) & -\kappa_1(c^*) & -\kappa_2(c^*) \\ p^*\kappa_1'(c^*) & \kappa_1(c^*)-\delta_1 & 0 \\ q^*\kappa_2'(c^*) & 0 & \kappa_2(c^*)-\delta_2 \end{bmatrix} = \begin{bmatrix} -1-p^*\kappa_1'(c^*)-q^*\kappa_2'(c^*) & -\kappa_1(c^*) & -\kappa_2(c^*) \\ p^*\kappa_1'(c^*) & 0 & 0 \\ q^*\kappa_2'(c^*) & 0 & 0 \end{bmatrix} \quad \ldots (7)$$

The characteristic equation of $J_{E_{int}}$ takes the form

$$\lambda^3 + \alpha\lambda^2 + \beta\lambda = 0 \quad \ldots\ldots\ldots\ldots\ldots\ldots (8)$$

where

$$\alpha = 1 + \kappa_1'(c^*)p^* + \kappa_2'(c^*)q^*$$

$$\beta = \kappa_1(c^*)\kappa_1'(c^*)p^* + \kappa_2(c^*)\kappa_2'(c^*)q^*$$

Clearly, in this case one eigenvalue is zero. Now since the constant terms $\alpha$ and $\beta$ are positive, so the other two eigenvalues are negative or they have negative real parts. Hence if $E_{int}$ exists then it may stable [6] i.e. the solution may coexist.

### 3.3. Global Analysis:

we have some results in [1] which imply that $E_1$ is globally asymptotically stable if only $E_1$ exists; if only $E_1, E_2$ and $E_3$ exist, under a reasonable additional assumptions $E_2$ and $E_3$ is globally asymptotically stable and if $E_{int}$ exists, the two organisms coexist in the sense that the system is uniformly persistent. In this case, the stability of $E_{int}$ may occur.

**Theorem 3.3.1.** If $c_i > 1$, then all solutions of (2) satisfy

$$\lim_{t\to\infty}\left(c(t), p(t), q(t)\right) = (1,0,0) \quad \ldots\ldots\ldots\ldots\ldots (9)$$

(That is, the above theorem states that $E_1$ is a global attractor if it is the only steady state.)

**Proof:** Since $c(t)<1$ for large t and $\kappa_i(1)-\delta_i<0$ (i.e., $c_i>1$), there are two constants $A>0, B>0$ such that $p'(t)<-Ap(t)$ and $q'(t)<-Bq(t)$. For t sufficiently large, it follows from the second and third equations of (2) that $\lim_{t\to\infty} p(t)=0$ and $\lim_{t\to\infty} q(t)=0$ respectively while the first equation of (2) yields $\lim_{t\to\infty} c(t)=1$, which proves the theorem.

**Theorem 3.3.2. [1]:** If $c_1<1$ and $\frac{1-c_1}{\delta_1}>c_2$, then system (2) is uniformly persistent; i.e., there exists a constant $\varepsilon>0$, independent of initial conditions, such that

$$\liminf_{t\to\infty} c(t)\ge\varepsilon,\ \liminf_{t\to\infty} p(t)\ge\varepsilon,\ \liminf_{t\to\infty} q(t)\ge\varepsilon$$

### 3.3.3 Mathematica Code and Graphical Illustration:

To generate the Mathematica [5] code we take the response functions proposed by Monod as $\kappa_1(c)=\frac{mc}{a+c}, \kappa_2(c)=\frac{nc}{b+c}$ and the same dilution rate $\delta_1=\delta_2$ for this purpose.

```
<< Graphics`Legend`
```

```
Clear["`*"]
chemo[{α_, β_, σ_, τ_, r_, rr_},
  {u_, v_, w_}, {xmax_, ymax_}] :=
 Module[{m = α, a = β, d1 = r, d2 = rr,
   n = σ, b = τ, c0 = u, p0 = v, q0 = w},
  k1[c_] := (m * c)/(a + c); k2[c_] := (n * c)/(b + c);

   results =
  NDSolve[
   {c'[t] == 1 - c[t] - k1[c[t]] * p[t] -
      k2[c[t]] * q[t], c[0] == c0,
    p'[t] == p[t] * (k1[c[t]] - d1),
    p[0] == p0,
    q'[t] == q[t] * (k2[c[t]] - d2),
    q[0] == q0}, {c, p, q}, {t, 0, xmax},
   MaxSteps -> 5000];
   Plot[
  Evaluate[{c[t], p[t], q[t]} /.
    results], {t, 0, xmax},
  Frame -> False, Axes -> Automatic,
  PlotRange -> {{0, xmax}, {0, ymax}},
  ImageSize -> Automatic,
  AspectRatio -> 1/GoldenRatio,

PlotStyle -> {{Thickness[.005]},
    {Dashing[{.008}],
     Thickness[.006]},
    {Dashing[{.02, .025}],
     Thickness[.007]}},
  Background -> None,
  AxesLabel -> {"t", "c,p,q"},
  PlotLegend ->
   {"c(t)", "p(t)", "q(t)"},
  LegendPosition -> {1.1, -.3},
  LegendLabel -> "Solution Functions",
  LegendOrientation -> Horizontal,
  LegendShadow -> {.03, -.03},
  LegendLabelSpace -> .8]];
```

CASE ONE:

```
chemo[{3.6, 0.8, 3, 0.6, 1.1, 1.1},
  {0.5, 0.2, 0.6}, {100, 1}];
```

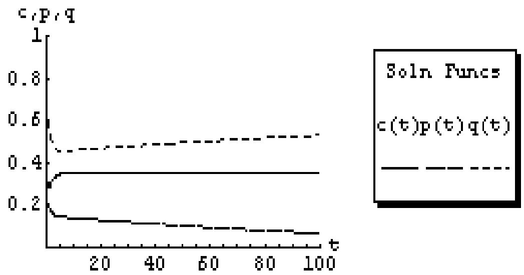


FIG. 1 The solution approaches the first organism free steady state.

CASE TWO:

```
chemo[{3.6, 0.8, 3, 0.6, 1.2, 1.2}, {0.5, 0.2, 0.6},
  {100, 1}];
```

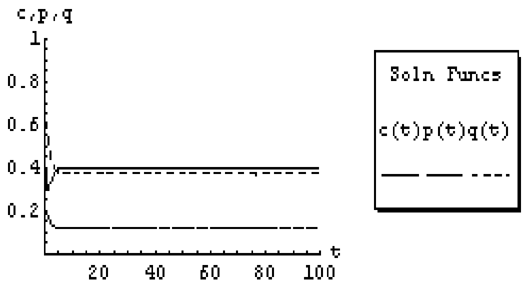


FIG. 2 : The solution approaches the Second organism free steady state.

CASE THREE:

```
chemo[{3.6, 0.8, 3, 0.6, 1.3, 1.3},
  {0.5, 0.2, 0.6}, {500, 1}];
```

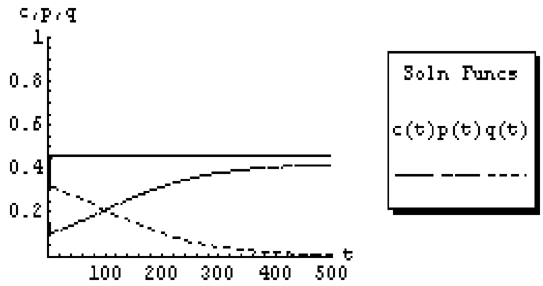


FIG. 3 : The solution approaches a positive steady state.

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