

# Further studies of a reaction-diffusion system for an unstirred chemostat with internal storage

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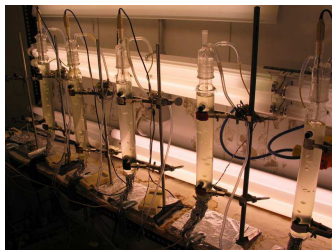
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# Chemostat

**Chemostat:** an apparatus for growing bacterial cultures at a constant rate by controlling the supply of nutrient medium



# Minimal chemostat model

**Simplest setup:** a vessel with volume  $V$  with an inflow  $F$  of the culture medium and nutrient (with a constant concentration  $S^0$ ), and an outflow  $F$  of the mixture of medium, nutrient and bacteria. Since the inflow and outflow are same, then the volume of the culture remains a constant. We assume that the culture is **well-stirred**.

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**Variables:**  $S(t)$  (concentration of nutrient),  $N(t)$  (concentration of bacteria)

**Model:**

$$\begin{cases} S_t = d(S^0 - S) - \frac{1}{\gamma} \frac{mS}{a + S} N, \\ N_t = \frac{mS}{a + S} N - dN. \end{cases}$$

$d = F/V$ : dilution rate of the chemostat,  $\gamma$ : the growth yield or the conversion rate  
 $\frac{mS}{a + S}$ : Monod growth function, similar to Michaelis-Menten enzyme kinetics function

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**Convergence:**  $(S + \gamma^{-1}N)_t = d[S^0 - (S + \gamma^{-1}N)]$  so  $\lim_{t \rightarrow \infty} [S(t) + \gamma^{-1}N(t)] = S^0$ .

**Limiting system:**  $N_t = \frac{m(\gamma S^0 - N)N}{\gamma a + \gamma S^0 - N}$ , and  $\lim_{t \rightarrow \infty} N(t) = \gamma S^0$ .

# Competition model and competition exclusion

Suppose there are two kinds of bacteria. Then

$$S_t = d(S^0 - S) - \frac{1}{\gamma_1} \frac{m_1 S}{a_1 + S} N_1 - \frac{1}{\gamma_2} \frac{m_2 S}{a_2 + S} N_2, \quad (N_i)_t = \frac{m_i S}{a_i + S} N_i - dN_i.$$

Rescaling:  $N_1 \mapsto N_1/\gamma_1$ , and  $N_2 \mapsto N_2/\gamma_2$

$$\begin{cases} S_t = d(S^0 - S) - \frac{m_1 S}{a_1 + S} N_1 - \frac{m_2 S}{a_2 + S} N_2, \\ (N_i)_t = \frac{m_i S}{a_i + S} N_i - dN_i, \end{cases}$$

**Conservation:**  $\lim_{t \rightarrow \infty} [S(t) + N_1(t) + N_2(t)] = S^0$

**Limiting system:**

$$\begin{cases} (N_1)_t = \frac{m_1(S^0 - N_1 - N_2)}{a_1 + S^0 - N_1 - N_2} N_1 - dN_1, \\ (N_2)_t = \frac{m_2(S^0 - N_1 - N_2)}{a_2 + S^0 - N_1 - N_2} N_2 - dN_2. \end{cases}$$

[Hsu-Hubble-Waltman, 1978, SIAM-AM], [Hsu, 1978, SIAM-AM] ( $n$ -species)

Let  $b_i = m_i/d$  and  $\lambda_i = a_i/(b_i - 1)$  for  $i = 1, 2$ .

(i) If  $b_1 \leq 1$  or  $\lambda_1 > S^0$ , then  $\lim_{t \rightarrow \infty} N_i(t) = 0$ .

(ii) If  $\lambda_1 < \lambda_2$  and  $\lambda_1 < S^0$ , then  $\lim_{t \rightarrow \infty} N_1(t) = \frac{d(S^0 - \lambda_1)(a_1 + \lambda_1)}{\lambda_1}$  and

$\lim_{t \rightarrow \infty} N_2(t) = 0$ .

# Diffusion: unstirred model

[Hsu-Waltman, 1993, SIAM-AM]

$$\begin{cases} S_t = dS_{xx} - m_1 f_1(S) u - m_2 f_2(S) v, & x \in (0, 1), \\ u_t = du_{xx} + m_1 f_1(S) u, & x \in (0, 1), \\ v_t = dv_{xx} + m_2 f_2(S) v, & x \in (0, 1), \\ S_x(0, t) = -S^0, S_x(1, t) + \gamma S(1, t) = 0, \\ w_x(0, t) = 0, w_x(1, t) + \gamma w(1, t) = 0, & w = u, v, \end{cases} \quad (1)$$

where

$$f_i(S) = \frac{S}{a_i + S}, \quad (2)$$

Limiting system:

$$\begin{cases} u_t = du_{xx} + m_1 f_1(\phi - u - v) u, & x \in (0, 1), t > 0, \\ v_t = dv_{xx} + m_2 f_2(\phi - u - v) v, & x \in (0, 1), t > 0, \\ w_x(0, t) = 0, w_x(1, t) + \gamma w(1, t) = 0, & w = u, v, \end{cases} \quad (3)$$

where  $\phi(x) = S^0 \left( \frac{1 + \gamma}{\gamma} - x \right)$ .

# Coexistence

[Hsu-Waltman, 1993, SIAM-AM] [Hsu-Smith-Waltman, 1995, TAMS]

When  $m_1 > d\lambda_1(f_1(\phi))$  and  $m_2 > d\lambda_1(f_2(\phi))$ , there exist two semi-trivial steady state solutions  $(u_*, 0) = (w_*(\cdot; m_1, a_1), 0)$ , and  $(0, v_*) = (0, w_*(\cdot; m_2, a_2))$ . For the coexistence steady states:

- 1 If  $m_1 > d\lambda_1(f_1(\phi - w_*(m_2, a_2)))$  and  $m_2 > d\lambda_1(f_2(\phi - w_*(m_1, a_1)))$ , then both of  $(u_*, 0)$  and  $(0, v_*)$  are unstable, and there exists at least one positive coexistence steady state solution which is stable.
- 2 If  $m_1 < d\lambda_1(f_1(\phi - w_*(m_2, a_2)))$  and  $m_2 < d\lambda_1(f_2(\phi - w_*(m_1, a_1)))$ , then both of  $(u_*, 0)$  and  $(0, v_*)$  are locally asymptotically stable, and there exists at least one positive coexistence steady state solution.

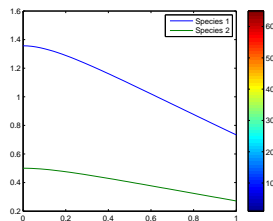
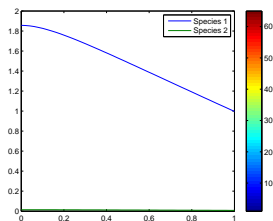
If  $a_1 = a_2$ , a coexistence steady state solution only exists for a unique  $m_1 = m_2 = d\lambda_1(f_1(\phi - w_*(m_1, a_2)))$ . A competition exclusion occurs when  $m_1 < m_2$  or  $m_1 > m_2$ .

**Question:** when  $a_1 \neq a_2$ , how do you characterize the set of coexistence parameter ranges

$\{(m_1, m_2) : m_1 > d\lambda_1(f_1(\phi - w_*(m_2, a_2))), m_2 > d\lambda_1(f_2(\phi - w_*(m_1, a_1)))$  and  
 $\{(m_1, m_2) : m_1 < d\lambda_1(f_1(\phi - w_*(m_2, a_2))), m_2 < d\lambda_1(f_2(\phi - w_*(m_1, a_1)))\}$ .



# Numerical simulations



Here  $m_1 = m_2 = 1.5$ ,  $\gamma = 1$ ,  $d = 0.05$ ,  $a_2 = 1$ .

Left (competition exclusion):  $a_1 = 0.8$ ; Right (coexistence):  $a_1 = 0.98$ .

# Droop model

For the variable yield case, [Droop, 1973, J. Phycology] formulated the following model with an internal storage of the nutrient:

$$\begin{cases} S' = (S^{(0)} - S)D - f_1(S, Q_1)u - f_2(S, Q_2)v, \\ u' = (\mu_1(Q_1) - D)u, \\ Q_1' = f_1(S, Q_1) - \mu_1(Q_1)Q_1, \\ v' = (\mu_2(Q_2) - D)v, \\ Q_2' = f_2(S, Q_2) - \mu_2(Q_2)Q_2, \\ S(0) \geq 0, u(0) \geq 0, v(0) \geq 0, Q_1(0) \geq Q_{\min,1}, Q_2(0) \geq Q_{\min,2}. \end{cases} \quad (4)$$

Here  $Q_i(t)$  ( $i = 1, 2$ ) is the average amount of stored nutrient per cell of the  $i$ -th population.  $\mu_i(Q_i)$  is the growth rate of the  $i$ -th population as a function of cell quota  $Q_i$ ,  $f_i(S, Q_i)$  is the per capital nutrient uptake rate per cell of the  $i$ -th population as a function of nutrient concentration  $S$  and cell quota  $Q_i$ , and  $Q_{\min,i}$  is the threshold cell quota below which no growth of the  $i$ -th population occurs. Typically the functions  $\mu_i(Q_i)$  and  $f_i(S, Q_i)$  satisfy the following assumptions: ( $i = 1, 2$ )

(H1)  $\mu_i(Q_i)$  is continuously differentiable for  $Q_i \geq Q_{\min,i}$ ,  $\mu_i(Q_{\min,i}) = 0$ ,  $\mu_i(Q_i) > 0$  and  $\mu_i'(Q_i) > 0$  for  $Q \geq Q_{\min,i}$ .

(H2)  $f_i(S, Q_i)$  is continuously differentiable for  $S > 0$  and  $Q \geq Q_{\min,i}$ ,  $f_i(0, Q_i) = 0$ ,  $f_i(S, Q_i) \geq 0$ ,  $\frac{\partial f_i}{\partial S}(S, Q_i) > 0$  and  $\frac{\partial f_i}{\partial Q_i}(S, Q_i) \leq 0$  for  $S > 0$  and  $Q_i \geq Q_{\min,i}$ .

# Functions

Some specific functions  $\mu_i(Q_i)$  and  $f_i(S, Q_i)$  are

$$\begin{aligned}\mu_i(Q_i) &= \mu_{i\infty} \left(1 - \frac{Q_{\min,i}}{Q_i}\right), \\ \mu_i(Q_i) &= \mu_{i\infty} \frac{Q_i - Q_{\min,i}}{K_i + Q_i - Q_{\min,i}},\end{aligned}\tag{5}$$

where  $\mu_{i\infty}$  is the maximal growth rate of the  $i$ -th population, and

$$\begin{aligned}f_i(S, Q_i) &= \rho_i(Q_i) \frac{S}{k_i + S}, \text{ where } \rho_i(Q_i) \text{ is defined by} \\ \rho_i(Q_i) &= \rho_{\max,i}^{\text{high}} - (\rho_{\max,i}^{\text{high}} - \rho_{\max,i}^{\text{low}}) \frac{Q_i - Q_{\min,i}}{Q_{\max,i} - Q_{\min,i}}, \text{ or} \\ \rho_i(Q_i) &= \rho_{\max,i} \frac{Q_{\max,i} - Q_i}{Q_{\max,i} - Q_{\min,i}}, \text{ or} \\ \rho_i(Q_i) &= \rho_i^c, \text{ (constant),}\end{aligned}\tag{6}$$

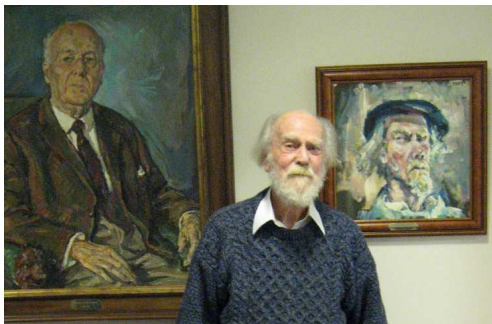
where  $Q_{\min,i} \leq Q_i \leq Q_{\max,i}$  (a maximal possible quota).

# Michael Droop (1918-2011)

Michael Droop is a well-known British marine biologist who is famous for his Cell-Quota model of phytoplankton growth.

[1968] M. Droop, Vitamin B12 and marine ecology. IV. The kinetics of uptake, growth and inhibition in *Monochrysis lutheri*. *J. Mar. Biol. Assoc. UK* 48 (1968) 689–733. (cited 542 times on Google scholar)

[1973] M. Droop, Some thoughts on nutrient limitation in algae, *J. Phycol.*, 9 (1973), 264–272. (cited 523 times on Google scholar)



# Result for the ODE Droop model

[Smith-Waltman, 1994, SIAM-AM]

1. Trivial steady state solution  $E_0 = (\tilde{S}, 0, \tilde{Q}_1, 0, \tilde{Q}_2)$ .
2. Semi-trivial steady state solution  $E_1 = (S^1, u^1, Q_1^1, 0, Q_2^1)$ .
3. Semi-trivial steady state solution  $E_2 = (S^2, 0, Q_1^2, v^2, Q_2^2)$ .

$E_1$  exists if there exists  $Q_1^1 > Q_{min,1}$  such that  $\mu_1(Q_1^1) = D$  and  $DQ_1^1 < f_1(S^{(0)}, Q_1^1)$ .

$E_2$  exists if there exists  $Q_1^2 > Q_{min,2}$  such that  $\mu_2(Q_2^2) = D$  and  $DQ_2^2 < f_2(S^{(0)}, Q_2^2)$ .

**Theorem.** Assume that the steady state solutions are all non-degenerate.

1. If  $E_1$  and  $E_2$  do not exist, then  $E_0$  is globally asymptotically stable.
2. If  $E_1$  exists but  $E_2$  does not exist, then  $E_1$  is globally asymptotically stable.
3. If  $E_2$  exists but  $E_1$  does not exist, then  $E_2$  is globally asymptotically stable.
4. If  $E_1$  and  $E_2$  both exist, and  $S^1 > S^2$ , then  $E_2$  is globally asymptotically stable.
5. If  $E_1$  and  $E_2$  both exist, and  $S^1 < S^2$ , then  $E_1$  is globally asymptotically stable.
6. If  $E_1$  and  $E_2$  both exist, and  $S^1 = S^2$ , then there exists a family of steady states connecting  $E_1$  and  $E_2$ .

No coexistence steady state solutions except the degenerate case.

# Conclusions

- 1 The dynamics of the reaction-diffusion competitive system for an unstirred chemostat with internal storage is completed. A sharp threshold diffusion coefficient  $d_{0,1}$  exists, and when  $d$  is above  $d_{0,1}$  both species become extinct. A second sharp threshold diffusion coefficient  $d_{0,2}$  so that species 1 always survives for  $d_{0,2} < d < d_{0,1}$ . For  $0 < d < d_{0,2}$ , a coexistence steady state is possible.
- 2 For one-species model, it is proved that the limiting steady state is larger for smaller  $d$ . The limiting quota  $Q(x)$  appears to be smaller for smaller  $d$ , and  $Q(x)$  also appears to be decreasing in  $x$ . This indicates that when the bacteria and nutrient mobility is low, bacteria tends to store less nutrient. And the nutrient storage rate is higher when it is closer to the nutrient source point ( $x = 0$  here). (Prove the monotonicity of  $Q_d(x)$  in  $d$  and  $x$ .)
- 3 Similar to the unstirred Monod chemostat model, it is hard to determine the parameter ranges where a coexistence steady state is achieved. The coexistence steady state is observed in numerical simulations for various parameters values. It appears that a coexistence steady state is more robust for smaller  $d$ . Note that a coexistence steady state in general does not exist for well-stirred chemostat models. (Obtain explicit parameter range for the coexistence for both Monod and Droop unstirred chemostat models)

Thank You!