Mathematical Models of Microbial Competition in Phytoplankton Communities

Sze-Bi Hsu

National Tsing-Hua University, Hsinchu, Taiwan

Dec. 11, 2008

Simple Chemostat Equations with monotone Functional Responses

Consider *n* microbial species competing for a single-limited nutrient in a chemostat.

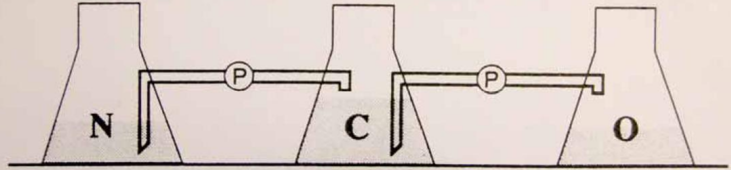
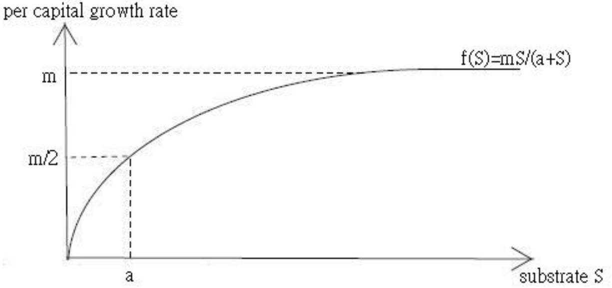
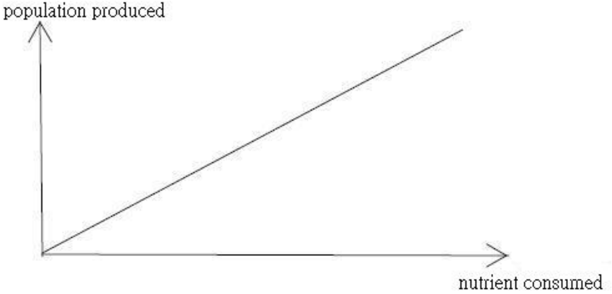


Figure 2.1. A schematic of the simple chemostat. (From [W2], Copyright 1990, Rocky Mountain Mathematics Consortium. Reproduced by permission.)

The chemostat is perhaps the best laboratory idealization of nature for population studies. The close parallels in nature are the planktonic communities of unicellular algae in lakes and oceans. The multiple species communities receieve nutrient inputs from streams draining eroding watersheds or continental margins, and in lakes from nutrient regeneration during spring and fall overturn. Nonspecific death occurs as cell continually sink out of the well-lit upper layers of water to unlit bottom of water column. The nutrient may be phosphours, nitrogen, silica, vitamin B_{12}. These nutrients are metabolic complementary. Growth is limited by the nutrient in shortest supply.

From Mond's experiment (1942), we have





Let

- $S(t) =$ The concentration of nutrient at time t.
- $x_i(t) =$ The population density of i-th microorganism, $i = 1, 2, \ldots, n$.
- $S^{(0)} =$ Input concentration of nutrient.
- $D =$ dilution rate $=$ flow rate/volume.
- $\gamma_i =$ yield constant of i-th species $= \frac{nutrient\ \ consumed}{population\ \ produced}$.
- $m_i =$ maximal growth rate of i-th species.
- $a_i =$ Michalis-Menten constant or half-saturation constant of i-th species.

Simple chemostat equation with Holling type II functional responses

$$\begin{aligned}
\frac{dS}{dt} =& (S^{(0)} - S)D - \sum_{i=1}^{n} \frac{1}{\gamma_i} \frac{m_i S}{a_i + S} x_i \\
\frac{dx_i}{dt} =& (\frac{m_i S}{a_i + S} - D) x_i \\
& S(0) \geq 0,\ x_i(0) > 0,\ i = 1, 2, \cdots n.
\end{aligned}$$

Theorem (Hsu, Hubbell, Waltman SIAM J. Appl. Math 1977)

Let $m_i > D$ and $\frac{m_i \lambda_i}{a_i + \lambda_i} = D, \ \lambda_i = \frac{a_i}{(\frac{m_i}{D}) - 1}$.

λ_i is the break-even concentration for i-th species.

If

$$(H_n) \qquad \begin{aligned} &0 < \lambda_1 < \lambda_2 \leq \ldots \leq \lambda_n \\ &\lambda_1 < S^{(0)} \end{aligned}$$

then we have competitive exclusion principle

$$\lim_{t \to \infty} S(t) = \lambda_1$$

$$\lim_{t \to \infty} x_1(t) = x_1^* > 0$$

$$\lim_{t \to \infty} x_i(t) = 0, \ i = 2, \cdots n.$$

Biological Interpretations

Write

$\lambda_i = \frac{a_i}{(\frac{m_i}{D})-1} = \frac{a_i D}{m_i - D} = (\frac{a_i}{r_i})D$

$r_i = m_i - D =$intrinsic rate of i-th species

Species with smallest λ_i wins the competition. Thus, the species whose Michalis-Menten constant is smallest in comparison with its intrinsic rate of increase will win. If the rates of increase for a series of competing micro-organisms are all roughly equivalent, then the species whose Michaelis-Menten constant is smallest (r's equal) for the limiting nutrient will win.

Extension I

Simple Chemostat Equation with general functional response

$$\begin{cases} \frac{dS}{dt} = (S^{(0)} - S)D - \sum_{i=1}^{n} f_i(S)\frac{x_i}{\gamma_i} \\ \frac{dx_i}{dt} = (f_i(S) - D)x_i \\ S(0) \geq 0,\ x_i(0) > 0, i = 1, 2, \ldots, n. \end{cases}$$

- $f_i(S) =$ general monotone functional response.
- $f_i : \mathbb{R}^+ \longrightarrow \mathbb{R}^+$.
- $f_i(0) = 0$.
- $f_i(S)$ is differentiable and $f'(S) > 0$, $\forall S \geq 0$.
- Example
  $f(S) = KS$ Type I
  $f(S) = \frac{mS}{a+S}$ Type II
  $f(S) = \frac{mS^n}{a+S^n},\ n \geq 2$ Type III

Theorem (McGhee, American Naturalist, 1980)

Let λ_i be the unique solution of $f_i(S) = D$ if one exists; otherwise $\lambda_i = +\infty$.

$$\begin{array}{ll}(\mathrm{H}_n) & 0 < \lambda_1 < \lambda_2 \leq \ldots \leq \lambda_n \\ & \qquad \lambda_1 < S^{(0)}\end{array}$$

Competitive Exclusion Principle

Under assumption (H_n), we have

$$\lim_{t\to\infty} S(t) = \lambda_1$$

$$\lim_{t\to\infty} x_1(t) = x_1^* > 0$$

$$\lim_{t\to\infty} x_i(t) = 0,\ 2 \leq i \leq n.$$

Extension II

- Seasonally Fluctuating nutrient (Hsu, J. Math. Biology, 1980)

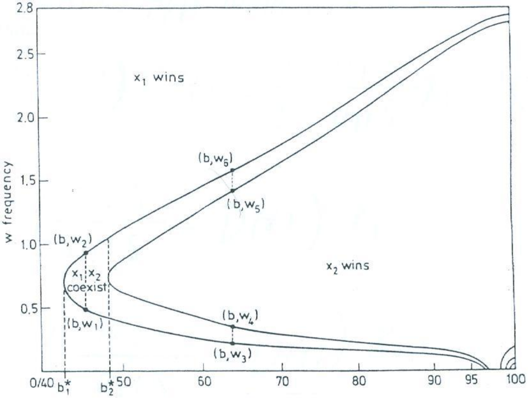
$$
\begin{aligned}
S'(t) =& (S^{(0)} + bsin\omega t - S)D - \frac{1}{\gamma_1}\frac{m_1 S}{a_1 + S}x_1 - \frac{1}{\gamma_2}\frac{m_2 S}{a_2 + S}x_2 \\
x_1'(t) =& (\frac{m_1 S}{a_1 + S} - D_1)x_1 \\
x_2'(t) =& (\frac{m_2 S}{a_2 + S} - D_2)x_2 \\
& S(0) > 0,\ x_1(0) > 0,\ x_2(0) > 0
\end{aligned}
$$

Coexistence is possible

Extinction Result

If $\lambda_1 < \lambda_2,\ \frac{m_1}{D_1} \geq \frac{m_2}{D_2}$, then $\lim_{t\to\infty} x_2(t) = 0$.

Coexistence Result



$$a_1 = 1,\ a_2 = 2,\ m_1 = 2.1111,\ m_2 = 1.6578, S^{(0)} = 100,$$

$$\gamma_1 = 2m_1,\ \gamma_2 = \frac{2m_2}{3},\ D = 1,\ D_1 = 2,\ D_2 = 1.5,$$

$$a_1 < a_2,\ \lambda_1 = 18 < \lambda_2 = 19.011, \frac{m_1}{D_1} = 1.055 < \frac{m_2}{D_2} = 1.1052.$$

- Periodic Washout Rate $D(t)$, $D(t+\omega) = D(t)$ (Butler, Hsu, Waltman, SIAM J. Appl. Math., 1985)

$$
\begin{aligned}
S'(t) =&(S^{(0)} - S)D(t) - \frac{1}{\gamma_1}\frac{m_1 S}{a_1 + S}x_1 - \frac{1}{\gamma_2}\frac{m_2 S}{a_2 + S}x_2 \\
x_1'(t) =&(\frac{m_1 S}{a_1 + S} - D(t))x_1 \\
x_2'(t) =&(\frac{m_2 S}{a_2 + S} - D(t))x_2 \\
&S(0) > 0,\ x_1(0) > 0,\ x_2(0) > 0
\end{aligned}
$$

Coexistence is possible due to periodic washout rate.

- Competition of Phytoplankton under Fluctuating light (Litchman & Klausmeier , American Naturalist, 2001)

$$
\begin{aligned}
\frac{dx_1}{dt} &=(\frac{m_1 I}{a_1 + I} - d_1)x_1 \\
\frac{dx_2}{dt} &=(\frac{m_2 I}{a_2 + I} - d_1)x_1 \\
I &=I_0 e^{-(c_1x_1+c_2x_2)} \\
I_0 &=\text{Intensity of the incoming light.} \\
&=I_0(t) \text{ is a periodic function.} \\
c_i &= \text{ the light attenuation coefficient of } i\text{-th species.}
\end{aligned}
$$

Coexistence is possible.

Variable Yield Model

Relax the assumption of constant yield.
The growth rate of i-th species depends on internal storage $Q_i(t)$ and the nutrient uptake $f_i(S, Q_i)$ which is increasing in S and decreasing in Q_i.

Model Equations:

$$
(1) \begin{cases} \frac{dS}{dt} = (S^{(0)} - S)D - \sum_{i=1}^{n} x_i f_i(S, Q_i) \\ \frac{dx_i}{dt} = [\mu_i(Q_i) - D]x_i \\ \frac{dQ_i}{dt} = f_i(S, Q_i) - \mu_i(Q_i)Q_i \end{cases}
$$

$$
S(0) \geq 0, x_i(0) > 0, Q_i(0) \geq Q_{min,i}, \;\; i = 1, 2, \ldots, n.
$$

Assumptions

(H$_1$) $\mu_i(Q_i)$ is continuous differentiable for $Q_i \geq P_i > 0$,
$\mu_i(Q_i) \geq 0, \mu_i'(Q_i) > 0$ for $Q_i \geq P_i, \mu_i(P_i) = 0$.

(H$_2$) $f_i(S, Q_i)$ is continuous differentiable for $S > 0$, $Q_i \geq P_i$,
$f_i(0, Q_i) = 0$, $\frac{\partial f_i}{\partial S} > 0$, $\frac{\partial f_i}{\partial Q_i} \leq 0$.

Example:(Droop)

$$\mu_i(Q_i) = \mu_{i\infty}(1 - \frac{Q_{min,i}}{Q_i})$$
$$f_i(S, Q_i) = \rho_i(Q_i)\frac{S}{a_i+S}$$
$$\rho_i(Q_i) = \rho_{max}^{high} - (\rho_{max}^{high} - \rho_{max}^{low})\frac{Q_i - Q_{min,i}}{Q_{max,i} - Q_{min,i}}$$

Equilibria

Existence of Equilibria: $E = (S, x_1, Q_1, \ldots, x_n, Q_n)$

$$\begin{aligned}
E_0 &= (S^{(0)}, 0, Q_1^0, 0, Q_2^0, \ldots, 0, Q_n^0) \text{ washout state} \\
E_1 &= (\lambda_1, x_1^*, Q_1^*, 0, \hat{Q}_2^1, \ldots, 0, \hat{Q}_n^1) \\
E_2 &= (\lambda_2, 0, \hat{Q}_1^2, x_2^*, Q_2^*, \ldots, 0, \hat{Q}_n^2) \\
&\vdots \\
E_n &= (\lambda_n, 0, \hat{Q}_1^n, 0, \hat{Q}_2^n, \ldots, x_n^*, Q_n^*)
\end{aligned}$$

- $\mu_i(Q_i^*) = D$
- $f_i(\lambda_i, Q_i^*) = \mu_i(Q_i^*)Q_i^* = DQ_i^*$
- $x_i^* = \frac{(S^{(0)} - \lambda_i)D}{f_i(\lambda_i, Q_i^*)} = \frac{S^{(0)} - \lambda_i}{Q_i^*}$
- $f_j(\lambda_j, \hat{Q}_j^i) = \mu_j(\hat{Q}_j^i)\hat{Q}_j^i, \ j \neq i$

$$\lambda_I = \frac{K_i D}{\mu_{max,i} - D}$$

$$\mu_{max,i} = \frac{\rho^{lo}_{max,i}}{Q_{max,i}}$$

$$K_I = a_i \frac{Q_{min,i}}{Q_{max,i}} \frac{\rho^{lo}_{max,i}}{\rho^{h}_{max,i}}$$

$$(H_n) \qquad \begin{aligned} &0 < \lambda_1 < \lambda_2 \leq \ldots \leq \lambda_n \\ &\lambda_1 < S^{(0)} \end{aligned}$$

Theorem (S.B. Hsu & T.H. Hsu, SIAM J. Appl. Math 2008)

Let (H_n) hold. Then

$$\lim_{t\to\infty} S(t) = \lambda_1, \ \lim_{t\to\infty} x_1(t) = x_1^* > 0,$$
$$\lim_{t\to\infty} x_i(t) = 0, \ 2 \leq i \leq n,$$
$$\lim_{t\to\infty} Q_1(t) = Q_1^* > 0, \ \lim_{t\to\infty} Q_i(t) = \hat{Q}_i^1, \ 2 \leq i \leq n.$$

Mathematical Model of Two Species Competing for Two Complementary Nutrients

* Hsu, Cheng, Hubbell, SIAM J.Appl. Math 1981,
* Korch, J. Theoretical Biology 1974

- $S^{(0)}, R^{(0)} =$ Input concentration for resource S and R respectively.
- $D =$ Input flow rate of medium containing S and R and also the output flow rate of medium containing unused S, R and cells x_1, x_2.
- $m_{si}, m_{ri} =$ maximum per captical birth rate of species i on resource S or R alone.
- $y_{si}, y_{ri} =$ yield of species i per unit of resource S or R consumed.
- $a_{si}, a_{ri} =$ half-saturation constant for species i on resource S or R.

Governing equations

$$\begin{aligned}
\frac{dS}{dt} =& (S^{(0)} - S)D - \frac{1}{y_{s1}} g_1(S,R)x_1 - \frac{1}{y_{s2}} g_2(S,R)x_2 \\
\frac{dR}{dt} =& (R^{(0)} - R)D - \frac{1}{y_{r1}} g_1(S,R)x_1 - \frac{1}{y_{r2}} g_2(S,R)x_2 \\
\frac{dx_1}{dt} =& (g_1(S,R) - D)x_1 \\
\frac{dx_2}{dt} =& (g_2(S,R) - D)x_2 \\
S(0) \geq& 0, \ \ R(0) \geq 0, x_1(0) > 0, \ \ x_2(0) > 0,
\end{aligned}$$

$$g_1(S,R) = \min\{\frac{m_{s1}S}{a_{s1}+S}, \frac{m_{r1}R}{a_{r1}+R}\}$$

$$g_2(S,R) = \min\{\frac{m_{s2}S}{a_{s2}+S}, \frac{m_{r2}R}{a_{r2}+R}\}$$

(Lieberg's Law of minimum)

Four possible outcomes like Lotka-Volterra two species competition models

- Species 1 wins, species 2 loses.
- Species 2 wins, species 1 loses.
- Species 1 and species 2 coexist in equilibrium form.
- Bistability: Outcomes depends on initial populations.

Extension I

- n species, $n \geq 2$, compete for two complementary resources: Competitive exclusion holds, i.e. at most two species survives (Smith and Li, SIAM J. Appl. Math 2001).
- When the number of resources k is greater than two, coexistence of n species, $n > k$ is possible in the form of periodic oscillations, even chaos (Huisman, Nature 2000).