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Necessary condition for the coexistence of species in a periodic chemostat

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ABSTRACT

Competition of arbitrary n-species in chemostat equations with periodic washout rate is considered. Convergence theorem [12] allows us to consider the asymptotic dynamics of the main system by the limiting system. Explicit values of Floquet exponents corresponding to the variational equations of the limiting system is calculated. A necessary condition for the coexistence of n-species is derived.

Key words: Chemostat equations, periodic washout rate, conservation principle, Floquet theory, Poincaré map, coexistence, Michaelis-Menten functional response

1 Introduction

Chemostat equations have been used to study population dynamics of microorganisms in experimental apparatuses or aquatic ecosystems such as lakes. The Competitive Exclusion Principle states that among several species competing for common resources, the number of coexistence species does not exceed the number of available resources [3]. The mathematical results for a standard chemostat equations of competition for a single limiting resource, only the species with lowest break even concentration survives (see Armstrong and McGehee [1], Smith and Waltman [10, Chapter 1, Chapter 2]). On the other hand, the competitive exclusion principle is not valid for the chemostat equations if the fluctuating environment is under consideration. Butler *et al.* showed that the coexistence of two species competing for one resource

is possible when the washout rate varies periodically [2]. In [2], coexistence is expected if the washout rate varies in such a way that each competitor has its own competitive advantage depending on the concentration of the resource.

It is a basic interest and problem on chemostat equations whether fluctuating environment can support the coexistence of more than three species under only one resource. Lenas and Pavlou [6] showed that the coexistence of three species is possible by numerical bifurcation analysis. Wolkowicz and Zhou [13] gave sufficient conditions for the uniform persistence of competing arbitrary n-species on a periodic chemostat. To obtain biological interpretation of the mechanism of coexistence, it should be derived necessary conditions which give a clear interpretation how competing species can coexist. In this paper, let us consider the chemostat equations of the form

$$\begin{cases} S' = (S^0 - S)D(t) - \sum_{j=1}^{n} f_j(S)x_j, \\ x_i' = x_i(f_i(S) - D(t)), \quad (i = 1, 2, \cdots n). \end{cases} \tag{1.1}$$

System (1.1) models that arbitrary n-species x_i $(i = 1, 2, \cdots n)$ compete for the same limiting nutrient S in the environment with an oscillatory washout $D(t)$. Here S^0 is a positive constant. $D : [0, \infty) \to [0, \infty)$ is a positive, periodic function with a period ω. The mean value of the periodic function $D(t)$ is denoted by $\langle D \rangle$. Then

$$\langle D \rangle = \frac{1}{\omega} \int_0^{\omega} D(s)\, ds.$$

We assume that $f_i : \mathbf{R}_+ \to \mathbf{R}_+$ is continuously differentiable, $f_i(0) = 0$ and $f'(S) > 0$. A typical example of f_i is Michaelis-Menten functional response of the form :

$$f_i(S) = \frac{m_i S}{a_i + S}, \quad (i = 1, 2, \cdots, n). \tag{1.2}$$

Here a_i and m_i $(i = 1, 2, \cdots, n)$ are positive constants.

Now let us measure all variables in units of S^0 and time in units of $\langle D \rangle^{-1}$:

$$\frac{S}{S^0} \mapsto S \ , \ \frac{x_i}{S^0} \mapsto x_i \text{ and } \langle D \rangle t \mapsto t.$$

Then (1.1) takes the form:

$$\begin{cases} S' = (1-S)D(t) - \sum_{j=1}^{n} f_j(S)x_j, \\ x_i' = x_i(f_i(S) - D(t)), \quad (i = 1, 2, \cdots n). \end{cases} \tag{1.3}$$

Here we relabeled $f_i(S)$ and $D(t)$ in the equations (1.3) each of which is actually $\langle D\rangle^{-1} f_i(S^0 S)$ and $\langle D\rangle^{-1} D(t/\langle D\rangle)$ in (1.1), respectively. Note that this scaling affects both the period and the mean value of D. The former becomes $\langle D\rangle\omega$, which we relabel ω and the latter becomes the unity: $\langle D\rangle = 1$.

In Section 2, some well known results of periodic system are summarized. Section 3 gives sufficient conditions for the extinction of all species and the survival of a single species. In Section 4, explicit values of Floquet exponent are calculated. Moreover the conditions of exclusion and invasion are given in terms of the sign of Floquet exponent. In Section 5, a necessary condition for the coexistence of competing n-species is derived. Finally we discuss our results in Section 6.

2 Preliminary results

In this section, basic contexts of periodic ordinary differential equations are summarized.

Consider the general periodic system:

$$x' = f(t, x), \tag{2.1}$$

where $f : \mathbf{R}\times\mathbf{R}^n$ is continuously differentiable with respect to its all arguments. Moreover for some $\omega > 0$,

$$f(t+\omega, x) = f(t, x)$$

holds for all (t, x). Let $p(t)$ be a periodic solution of system (2.1). Then the variational equations corresponding to $p(t)$ is defined by

$$z' = \frac{\partial f}{\partial x}(t, p(t))z. \tag{2.2}$$

Let $\Phi(t)$ be the fundamental matrix solution of (2.2). The Floquet multiplier of (2.2) are the eigenvalues of $\Phi(t)$; if μ is a Floquet multipliers and $\mu = e^{\omega\lambda}$ then λ is called a Floquet exponent. There is a useful theorem about the determinant of the fundamental matrix $\Phi(t)$. If $\Phi(0) = I$ where I is the $n \times n$ identity matrix, then

$$\det \Phi(\omega) = \exp\left[\int_0^\omega \mathrm{tr}A(s)ds\right].$$

Here $A(t)$ is the coefficient matrix of (2.2). Moreover "'det" and "tr" denote the determinant and the trace of the matrix, respectively. Thus the product of Floquet multipliers is the determinant of $\Phi(\omega)$.

Stability of periodic general systems associated with Floquet theory is studied by Hale [4].

Definition 2.1. *[4] $x(t)$ is uniformly asymptotically stable if*

(i) For every $\varepsilon > 0$ there exists $\delta > 0$ such that if $|x(t_0) - y(t_0)| < \delta$ for some $t_0 \geq 0$ and some solution $y(t)$, then $|x(t) - y(t)| < \varepsilon$ for all $t \geq t_0$.

(ii) There exists $b > 0$ such that if $|x(t_0) - y(t_0)| < b$ for some $t_0 \geq 0$, then $|x(t) - y(t)| \to 0$ as $t \to \infty$ uniformly in t_0.

Theorem 2.1. *[4] If $|\mu| < 1$ for all multipliers of (2.2), then $p(t)$ is a uniformly asymptotically stable periodic solution of (2.1). If $|\mu| > 1$ for some multiplier μ of (2.2), then $p(t)$ is unstable.*

Remark 2.1. *In terms of Floquet exponents, the condition for stability is $\Re\lambda < 0$ for all exponents and the condition for instability is that $\Re\lambda > 0$ for some exponent λ. Here $\Re\lambda$ denotes the real part of λ.*

Finally, let us introduce the Poincaré map. Let $x(t, x_0)$ be the solution of (2.1) satisfying $x(0) = x_0$. The Poincaré map is defined by

$$Px_0 = x(\omega, x_0).$$

Poincaré map P possesses some useful properties such that P is continuously differentiable with respect to x_0.

3 Extinction and survival of species

In this section, let us consider the extinction of competing n species and the survival of a single species. Set

$$\Sigma = S + \sum_{j=1}^{n} x_j - 1. \tag{3.1}$$

Adding the equations (1.3) gives the periodic linear system

$$\Sigma'(t) = -D(t)\Sigma(t). \tag{3.2}$$

Then (1.3) corresponds to

$$\begin{cases} \Sigma' = -D(t)\Sigma, \\ x_i' = x_i(f_i(S) - D(t)), \quad (i = 1, 2, \cdots n). \end{cases} \tag{3.3}$$

Since $\langle D \rangle = 1$, solving (3.2) gives

$$\Sigma(t) = \Sigma(0) \exp\left[- \int_0^t (D(s) - 1) ds \right] e^{-t}.$$

Hence we have

$$\lim_{t \to \infty} \Sigma(t) = 0.$$

It follows that solutions of (1.3) exist and are bounded for $t \geq 0$. Both $S(t)$ and $x_i(t)$ remain nonnegative from the form of (1.1), the convergence theorem obtained by Thieme [12] is applied to (1.3), which leads to consider the system (3.3) restricted to the invariant hyperplane $\Sigma = 0$, to which all solutions are attracted at some exponential rate.

Setting $\Sigma = 0$, or equivalently, $S = 1 - \sum_{j=1}^{n} x_j$ yields the limiting system:

$$\begin{gathered} x_i' = x_i \left(f_i \left(1 - \sum_{j=1}^{n} x_j \right) - D(t) \right), \\ i = 1, 2, \cdots n. \end{gathered} \tag{L}$$

Biologically relevant initial data for (L) belong to

$$\Omega = \left\{ (x_1, x_2, \cdots x_n)^T \in \mathbf{R}_+^n : \sum_{j=1}^{n} x_j \leq 1 \right\},$$

where

$$\mathbf{R}^n_+ = \left\{(x_1, x_2, \cdots x_n)^T \in \mathbf{R}^n : x_i \geq 0, (i = 1, 2, \cdots n)\right\}.$$

It is shown that Ω is positively invariant for (L).

The following result gives a sufficient condition for the washout of a competitor from the chemostat which is independent of the presence or absence of adversaries.

Proposition 3.1. *If* $f_i(1) \leq 1$, *then* $\lim_{t\to\infty} x_i(t) = 0$ $(i = 1, 2, \cdots n)$.

As the proof of Proposition 3.1 proceeds in the same manner given in the book of the chemostat [10, pp. 165, Chapter 7], we omit the proof.

Proposition 3.1 implies that the extinction of species does not result in the effect of competition; it occurs even in the absence of the other competitor. As our interest is in the effects of competition, hereafter we assume that

$$f_i(1) > 1, \quad (i = 1, 2, \cdots, n). \tag{3.4}$$

The following result states that under (3.4) competitor can survive in the chemostat in the absence of competition and with its concentration oscillating in response to the periodically varying washout rate.

Proposition 3.2. *The notation* $(0, \cdots, 0, x_i, 0, \cdots, 0)$ *represents that all components except for the* i*-th are zero. There exist unique, positive periodic functions* $\xi_i(t)$ *such that* $(0, \cdots, 0, \xi_i(t), 0, \cdots, 0)$ *are solutions of* (L).
If $(0, \cdots, 0, x_i(t), 0, \cdots, 0)$ *is a solution of* (L) *satisfying* $x_i(0) > 0$, *then*

$$\lim_{t\to\infty} |x_i(t) - \xi_i(t)| = 0, \quad (i = 1, 2, \cdots, n).$$

The proof of Proposition 3.2 also proceeds in the same manner as in the book of the chemostat (see [10, pp. 166, Chapter 7]).

4 Calculation of Floquet exponents

It will be convenient to use familiar notation E_i for the single competitor periodic solutions whose existence is asserted by Proposition 3.2,

$$E_i(t) = (0, \cdots, 0, \xi_i(t), 0, \cdots, 0).$$

Theorem 4.1. *Floquet exponents of $E_i(t)$ are given by*

$$\lambda_{ij} = \begin{cases} - < \xi_i f_i'(1-\xi_i) >, & (i=j), \\ < f_j(1-\xi_i) > -1, & (i \neq j). \end{cases} \tag{4.1}$$

$E_i(t)$ is asymptotically stable if $\lambda_{ij} < 0$ $(j = 1, 2, \cdots, n)$. On the other hand, $E_i(t)$ is unstable if at least one Floquet exponent λ_{ij} is positive.

Proof. It suffices to consider only the case $i = 1$ for the symmetricity. The variational equations corresponding to $E_1(t)$ is

$$z' = A(t)z,$$

where

$$A(t) = (a_{ij}(t)) = \begin{pmatrix} f_1(1-\xi_1) - D - \xi_1 f_1'(1-\xi_1) & \cdots & -f_1'(1-\xi_1)\xi_1 & \cdots & -f_1'(1-\xi_1)\xi_1 \\ \vdots & & \vdots & & \vdots \\ 0 & \cdots & f_i(1-\xi_1) - D & \cdots & 0 \\ \vdots & & \vdots & & \vdots \\ 0 & \cdots & 0 & \cdots & f_n(1-\xi_1) - D \end{pmatrix}.$$

Note that $a_{1j} = -f_1'(1-\xi_1)\xi_1$ $(j = 2, 3, \cdots, n)$, $a_{ii} = f_i(1-\xi_1) - D$ $(i = 2, 3, \cdots, n)$ and $a_{ij} = 0$ $(i \neq j,\ i = 2, \cdots, n,\ j = 1, 2, \cdots, n)$.

A computation gives the fundamental matrix $\Phi(t)$:

$$\Phi(t) = (\phi_{ij}(t)) = \begin{pmatrix} \exp\left[\int_0^t a_{11}(s)ds\right] & \cdots & u_i(t) & \cdots & u_n(t) \\ \vdots & & \vdots & & \vdots \\ 0 & \cdots & \exp\left[\int_0^t a_{ii}(s)ds\right] & \cdots & 0 \\ \vdots & & \vdots & & \vdots \\ 0 & \cdots & 0 & \cdots & \exp\left[\int_0^t a_{nn}(s)ds\right] \end{pmatrix},$$

where $\phi_{1j} = u_j$ $(j = 2, 3, \cdots, n)$, $\phi_{ii} = \exp\left[\int_0^t a_{ii}(s)ds\right]$ $(i = 1, 2, 3, \cdots, n)$ and $\phi_{ij} = 0$ $(i \neq j,\ i = 2, \cdots, n,\ j = 1, 2, \cdots, n)$.

$u_j(t)$ is given by

$$u_j(t) = \int_0^t \exp\left[\int_r^t a_{11}(s)ds\right] a_{1j}(r) \exp\left[\int_0^r a_{jj}(s)ds\right] dr.$$

Evaluating $\Phi(t)$ at $t = \omega$, we obtain that the multipliers $\exp\left[\int_0^\omega a_{ii}(s)ds\right]$ $(i = 1, 2, \cdots, n)$. It follows that λ_{1j} are Floquet exponents. The remaining assertions follow from the discussion in Theorem 2.1. □

Note that Theorem 4.1 generalizes the result obtained by Butler *et al.* [2].

5 Average competition

In this section, a necessary condition for the coexistence of competing n-species is derived by using a function in terms of the ratio between x_i and x_j $(i \neq j)$.

Let $P_{ij} : [0, \infty) \times (0, \infty) \to [0, \infty)$ be a continuously differentiable function $(i, j = 1, 2, \cdots, n,\ i \neq j)$. Average competition functions P_{ij} are defined by

$$P_{ij}(x_i, x_j) = x_i/x_j \tag{5.1}$$

for $x_j \neq 0$. The derivative of P_{ij} along the solution of (L) is denoted by $\dot{P}_{ij}(x_i(t), x_j(t))$. Direct calculation gives

$$\frac{\dot{P}_{ij}(x_i(t), x_j(t))}{P_{ij}(x_i(t), x_j(t))} = f_i\left(1 - \sum_{k=1}^{n} x_k(t)\right) - f_j\left(1 - \sum_{k=1}^{n} x_k(t)\right). \tag{5.2}$$

Theorem 5.1. *Let* $(\bar{x}_1(t), \bar{x}_2(t), \cdots, \bar{x}_n(t))$ *be a positive* ω*-periodic solution of* (L). *Then*

$$\left\langle \frac{\dot{P}_{ij}(\bar{x}_i, \bar{x}_j)}{P_{ij}(\bar{x}_i, \bar{x}_j)} \right\rangle = 0, \quad i, j = 1, 2, \cdots, n, \quad i \neq j. \tag{BC}$$

Proof. Since $\bar{x}_i(t)$ is a positive ω-periodic solution of (L),

$$\bar{x}_i(0) = \bar{x}_i(\omega) = \bar{x}_i(0) \exp\left[\int_0^\omega \left(f_i\left(1 - \sum_{k=1}^{n} x_k\right) - D(s)\right) ds\right].$$

Since $\langle D \rangle = 1$, $\langle f_i\,(1 - \sum_{k=1}^{n} x_k)\rangle = 1$ for all i. Since $\langle \dot{P}_{ij}/P_{ij}\rangle = -\langle \dot{P}_{ji}/P_{ji}\rangle$, (BC) holds. This completes the proof. □

Note that the right hand side of (5.2) describes the difference of nutrient uptake between x_i and x_j. That is, $\dot{P}_{ij}/P_{ij}$ measures the superiority (or inferiority) of competition between x_i and x_j. Hence (BC) implies that the average competition between x_i and x_j is balanced. Theorem 5.1 states that all of the average competition must be balanced among competing n-species if they coexist.

6 Conclusions

In this paper, we considered chemostat equations with periodic washout rate where n-species compete for one limiting nutrient. In Section 4, it was shown that the limiting system (L) is unstable if all $E_i(t)$ are unstable. In other words, it was shown that system (L) is unstable if at least one Floquet exponent λ_{ij} is positive for each i. Theorem 4.1 gives a generalization of the result obtained by Butler *et al.* [2] for the two-species competition case. In Section 5, we found that all of the average competition among species is balanced when they coexist. In [9], the authors demonstrated that the coexistence of three species competing for one limiting nutrient is not likely to occur by mathematical and numerical study. The coexistence of more than three-species is also observed on autonomous chemostat equations in the form of periodic oscillation when they compete for *several* resources (see Huisman and Weissing [5], Li and Smith [7], [8]). In [7], it is suggested that with a wide range of parameter values, sustained oscillations of species abundances for the model of three species competing for three nutrients are possible. It is also expected that all of the average competition among competing species are balanced on each model considered in [5], [7] and [8]. Then it should be figured out why *several* resources availability can support the coexistence of more than three species on a wide range of parameter values. Further studies are left for our future consideration.

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