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Coexistence of an unstirred chemostat model with Beddington–DeAngelis functional response and inhibitor☆

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ABSTRACT

This paper deals with a N-dimensional competition model between plasmid-bearing and plasmid-free organisms in the unstirred chemostat, which incorporates the Beddington–DeAngelis functional response and inhibitor. By the application of degree theory in cones, bifurcation theory and perturbation technique, we obtain the uniqueness, multiplicity and stability of the coexistence solutions of the steady-state system when the effects of the inhibitor is large enough.

1. Introduction

The chemostat is a very important laboratory apparatus for the study of microbial population dynamics under nutrient limitation. For instance, it is used as a model for the commercial manufacture of products through the insertion of a plasmid, a piece of genetic material, into the cell of the desired product. The plasmid directs the manufacture of a product but it can be lost, with some probability, in reproduction, creating a better competitor, the plasmid-free organism goes into the chemostat. To counter this, selective media are used for the culture. One approach is to induce antibiotic resistance in the cell on the same plasmid that codes for the production and to introduce an inhibitor (an antibiotic) into the medium. If the plasmid is lost, the organism is sensitive to the antibiotic. In this respect, the inhibitor is helpful for the desired outcome.

Based on the above principle and the earlier work of Stephanopoulis and Lapidus [1] and Lenski and Hattingh [2], Hsu et al. [3–5] proposed the mathematical models for the competition between plasmid-free and plasmid-bearing populations in the case of well-stirred chemostat culture. Here the Michaelis–Menten response functions:

$$f(s) = \frac{s}{k+s}$$

are adopted. Moreover, they obtained some results on the global asymptotic behavior and gave some explanation on the effect of the inhibitor. In [6], a new Michaelis–Menten type chemostat model with time delay and pulsed input nutrient concentration in a polluted environment is considered. The results show that time delays and the polluted environment can lead the microorganism species to become extinct.

The chemostat models with the Michaelis–Menten functional response only incorporate competition between two species. However, in nature it is known that there is not only competition between two species but also mutual interference

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in species. Thus it is necessary to consider mutual interference in species. The pioneering work in this direction is that of Beddington and DeAngelis et al. in [7,8]. They proposed the following Beddington–DeAngelis (B.–D.) response functions

$$f(s,u)=\frac{s}{k_1+s+\beta_1 u},\qquad g(s,v)=\frac{s}{k_2+s+\beta_2 v},$$

where k_i, β_i are positive constants. It is similar to the Michaelis–Menten functional response but has an extra term $\beta_1 u$ or $\beta_2 v$ in the denominator that models mutual interference in species. It can be derived mechanistically via considerations of time utilization or spatial limits on predation. Harrison [9] showed that the B.–D. functional response (for intraspecific interference competition) was superior to functional response without such competition in a microbial predator–prey interaction.

The B.–D. functional response is different from the traditional monotone or non-monotone functional response in chemostat systems [10–15], and this issue in the well-stirred chemostat recently received considerable attention; see [6, 16–20]. The outcomes of [16,17] demonstrate that time delays affect the competitive results of the organisms. In [18–20], the authors mainly focused on the impulsive effect. The results show that periodic coexistence solutions to the associate well-stirred chemostat model emerge if the impulsive period satisfies some critical condition.

In our current paper, we allow a heterogeneous environment, and so we remove the well-stirred hypothesis and consider the unstirred chemostat system. That is, the goal of this paper is to give some description of the basic dynamical properties of a N-dimensional competition model between plasmid-bearing and plasmid-free organisms in the unstirred chemostat, which incorporates the B.–D. functional response and an inhibitor. Here the plasmid-bearing organism devotes a partition of its resource to produce an inhibitor, which diminishes the growth rate of the plasmid-free organism, but does not reduce that of the plasmid-bearing organism. Let $s(x,t)$ be the nutrient concentration at time t, $u(x,t)$, $v(x,t)$ be the concentrations of the plasmid-bearing, plasmid-free organism in the culture vessel, respectively and $p(x,t)$ be the concentration of the inhibitor. Then, by similar arguments as in [10,14,11,12], the model in the unstirred case takes the form:

$$\begin{aligned}
&s_t = d\Delta s-\frac{1}{r}auf(s,u)-\frac{1}{r}bvg(s,v)e^{-\mu p}, && x\in\Omega,\ t>0,\\
&u_t = d\Delta u+a(1-q-k)uf(s,u), && x\in\Omega,\ t>0,\\
&v_t = d\Delta v+bvg(s,v)e^{-\mu p}+aquf(s,u), && x\in\Omega,\ t>0,\\
&p_t = d\Delta p+akuf(s,u), && x\in\Omega,\ t>0
\end{aligned}\tag{1.1}$$

with boundary conditions and initial conditions

$$\begin{aligned}
&\frac{\partial s}{\partial n}+\gamma(x)s=s^0(x), \quad \frac{\partial p}{\partial n}+\gamma(x)p=0,\\
&\frac{\partial u}{\partial n}+\gamma(x)u=0, \quad \frac{\partial v}{\partial n}+\gamma(x)v=0,
\end{aligned}\qquad x\in\partial\Omega,\ t>0,\tag{1.2}$$

$$\begin{aligned}
&s(x,0)=s_0(x)\geq 0, && p(x,0)=p_0(x)\geq 0,\not\equiv 0,\\
&u(x,0)=u_0(x)\geq 0,\not\equiv 0, && v(x,0)=v_0(x)\geq 0,\not\equiv 0,
\end{aligned}\qquad \text{on } \overline{\Omega}.\tag{1.3}$$

Here Ω is a bounded region in R^N ($N\geq 1$) with smooth boundary $\partial\Omega$, n is the outward unit normal to $\partial\Omega$. $s^0(x)>0$ ($\forall x\in\partial\Omega$) is the input concentration of the nutrient, which satisfies the consistent condition with $s_0(x)$ for $x\in\partial\Omega$. d is the diffusion rate of the chemostat, r is the growth yield constant. a, b are the maximal growth rates of the plasmid-bearing and plasmid-free organism (without an inhibitor), respectively. The term $e^{-\mu p}$ used by Lenski and Hattingh in [2] represents the degree of inhibition of p on the growth rate of v, where $\mu>0$ is a constant and represents the effect of the inhibitor on v. The constant q is the fraction of plasmid lost, and k is the fraction of consumption devoted to the production of the inhibitor. Hence, $0<q,k<1$ and $1-q-k>0$. $\gamma(x)$ is nonnegative, continuous on $\partial\Omega$. In this model, the corresponding yield constants are assumed to be equal, just as in [4].

The study of mathematical models for the unstirred chemostat has been a problem of considerable interest; see [10,11, 21,12,22,14,15] and the references therein. Especially, in [21,22], the exact range of the parameters of two species so that the system possesses positive solutions are given by applying the monotone methods and the topological fixed point theory. Furthermore, it is also shown that the system has at least two positive solutions in a certain subregion. But the stability of positive solutions are not given. Asymptotic behavior of an unstirred chemostat model with an internal inhibitor was discussed in [12]. It turns out that if μ is sufficiently large, this model has no coexistence solution and one of the semi-trivial equilibria is a global attractor when the maximal growth rate a of the species u lies in a certain range; but when a belongs to another range, two semi-trivial equilibria are bistable. In [15], the effects of the inhibitor on the plasmid-bearing and plasmid-free model in the unstirred chemostat are considered. The results show that the parameter μ plays a very important role in deciding the number of the coexistence solutions. More precisely, if μ is sufficiently large, it is possible for this model to possess unique or multiple coexistence solutions.

However, all these papers studied the unstirred chemostat models with the Michaelis–Menten functional response. Our study focuses on the N-dimensional unstirred chemostat model (1.1)–(1.3), which incorporates the B.–D. functional response and an inhibitor. For the sake of convenience, we simplify the Eqs. (1.1)–(1.3) by non-dimensionalizing the