

Preface

The chemostat is a very important laboratory apparatus for the study of microbial population dynamics under nutrient limitation, whose importance stems from many roles it plays. Moreover, it is a model of a simple lake, the ideal place to study competition in its most primitive form-exploitative competition. And it is also used as a model of the waste water treatment process. For its commercial form the chemostat plays a central part in certain fermentation processes, particularly in the commercial production of products by genetically altered organisms (e.g., in the production of insulin). Therefore the theoretical literature is scattered; papers appear in mathematical, biological, and chemical engineering journals. In addition to being known as a chemostat, other common names are "continuous culture", and in the engineering literature, CSTR (continuously stirred tank reactor).

It is the extensive application of the chemostat in a variety of ecological problems that makes it having been a hot issue. The book written by Smith and Waltman in 1995 is an excellent reference for the theoretical description of ecological models based on the chemostat. In this book, the authors assume that the culture vessel is well mixed and that all other relevant variables (temperature, pH, etc.) are kept constants. Under these assumptions, the mathematical models for microorganisms to grow in the chemostat take the form of ordinary differential equations. They summarized all aspects of the study on the well stirred chemostat, including the competitive exclusion principle of the simple and general chemostat, the competitive coexistence in the form of limit cycle in the chemostat with food-chain, inhibitor, or periodic washout rate, and the competitive coexistence in the gradostat, etc. Also some new directions and open questions in the study of the chemostat are presented, such as the unstirred chemostat model, the chemostat model with delay, and so on.

Although the chemostat provides a simple model for many microbial habitats, the assumption of well-stirring is often questionable. Since coexistence of competing species is obvious in the nature, a candidate for an explanation is to remove the well-stirred hypothesis. Under this condition, the concentrations of the nutrients and competing populations depend on not only the temporal variable, but also the spatial location. The mathematical model to describe the growth of the competing populations in the chemostat is no longer given by an ordinary differential system, but given by a nonlinear reaction-diffusion system. A vast and challenging new problems open up when we turn to the chemostat model with diffusion. For instance, whether can the competing populations coexist in the unstirred chemostat with single nutrient;

what about the stability, uniqueness or multiplicity of coexistence solutions; how does the inhibitor or toxin affect the dynamical behavior of coexistence solutions; how many species can two or more essential resources support, etc.

As the sequel of the monograph *The Theory of the Chemostat: Dynamics of Microbial Competition*, the present book is devoted to provide an introduction to the dynamical theory of unstirred chemostat models. Naturally, the selection of the material is highly subjective and largely influenced by our personal interests. In fact, the contents of this book are predominantly from the recent works of our group. Also, the list of references is by no means exhaustive, and I apologize for the exclusion of many other related works.

In Chapter 1, we first review the derivation of the basic chemostat model and its competitive exclusion principle: only one competitor can survive on a single resource, which is a paradox to the coexistence phenomena in nature, for instance, the coexistence of phytoplankton. It is this paradox that makes us to take into account some new aspect that may produce coexistence. Hence, a variety of modified models in the chemostat are introduced to explain the coexistence phenomena, including the unstirred chemostat model, the periodic chemostat model, the chemostat model with delay and the chemostat model with inhibitor, etc. Before we put our heart into the competition models in the unstirred chemostat, we present a brief review on the study of the modified models in the well-stirred chemostat. The last task of this chapter is to provide some preliminary lemmas and theorems related to our study without proofs, such as some properties of the eigenvalue, the bifurcation theory and the topological fixed point theory.

Chapters 2-5 are devoted to the basic unstirred chemostat model, that is, a system of reaction-diffusion equations with two-species competing for one growth-limiting resource. In Chapter 2, the asymptotic behavior of solutions is given as a function of the parameter, and it is determined when neither, one, or both competing populations survive. Chapter 3 deals with the N -dimensional case, and the global structure of the coexistence solution is established by the theorem of global bifurcation and maximal principle. Moreover, stability criterion is also established. Chapter 4 deals with the uniqueness and stability of coexistence solutions of the basic N -dimensional competition model in the unstirred chemostat by Lyapunov-Schmidt procedure and perturbation technique. It turns out that the uniqueness of coexistence solutions relies on whether the critical parameter is zero or not, and stability of coexistence solutions depends on whether the same critical parameter is large or less than zero. Chapter 5 deals with the competition between two similar species in the unstirred chemostat. Due to the strict competition of the unstirred chemostat model, the global dynamics of the system is attained by analyzing the equilibria and their stability. The results show that the dynamics of the system essentially depends upon certain function of the growth rate. Moreover, one of the semi-trivial stationary solutions or the unique

coexistence steady state is a global attractor under certain conditions. Biologically, the results indicate that it is possible for the mutant to force the extinction of resident species or to coexist with it.

The focus of Chapter 6 is to study the unstirred chemostat model with different diffusion rates. Under quite general conditions the existence of a compact global attractor with finite Hausdorff dimension for the dynamical system is established, which is roughly analogous to the conservation principle for the case where the boundary conditions and diffusion coefficients are identical. It indicates that the unmixed bio-reactor has a finite carrying capacity for nutrient and biomass. However, in contrast to the earlier studies, this conclusion does not allow the explicit reduction of the system to a simpler set of equations. In the remainder of this chapter, we focus on the steady state solutions which belong to the attractor. Conditions for the existence and uniqueness of single-population equilibria are established, and in the case of two competing microbial populations, we establish sufficient conditions for the existence of a coexistence equilibrium solution. This is an equilibrium in which both populations are simultaneously present in the reactor. Unfortunately, because it is no longer possible to reduce the system to a monotone dynamical system, we are unable to obtain much information about the global asymptotic behavior of solutions.

The goal of Chapter 7 is devoted to the unstirred chemostat model with crowding effects. The introduction of crowding effects makes the conservation law invalid, and the equations cannot be combined to eliminate one of the variables. Consequently, the usual reduction of the system to a competitive system of one order lower is lost. Thus the system with predation and competition is non-monotone, and the single population model can not be reduced to a scalar system. First, the uniqueness and asymptotic behavior of the semi-trivial solutions are established. Second, the existence and structure of coexistence solutions are given by the degree theory and bifurcation theory. It turns out that the positive bifurcation branch connects one semi-trivial solution branch with another. Finally, the stability and asymptotic behaviors of coexistence solutions are discussed in some cases. It is shown that crowding effects are sufficiently effective in the occurrence of coexisting, and overcrowding of a species has an inhibiting effect on itself.

In Chapters 8 and 9, we study the unstirred chemostat models with two growth-limiting resources. When more than one resource is limiting, it is necessary to consider how these resources promote growth. Leon, Tumpson and Rapport classified nutrients as perfectly complementary, perfectly substitutable, or imperfectly substitutable. In Chapter 8, we study the extreme case of the unstirred chemostat model with two substitutable resources. The existence of a positive steady-state solution and the longtime behavior of the corresponding limiting system are determined for a certain range of the parameter. In the special case of $m = n$, the uniqueness and global attractivity of the positive steady-state solution of the original system are established.

Chapter 9 is devoted to the study of the other extreme case of the unstirred chemostat model involving two complementary resources. The existence, uniqueness and global attractivity of positive steady-state solution to the single population model are established firstly. For the two-species model, the exact range of the parameters so that the system possesses positive solutions is determined by the monotone iterative method. Furthermore, by combining the topological fixed point index theory and the monotone method, we investigate multiplicity of positive steady states of the system.

The main purpose of Chapter 10 is to investigate the effect of inhibitor on the plasmid-bearing and plasmid-free model in the unstirred chemostat. The motivation comes from the numerical simulations (see Fig.10-2.), which seem to indicate that when the parameters sit in a certain range, the exact shape of the bifurcation diagram of coexistence solutions to the system looks like Fig.10-1. A crucial point for the confirmation of the numerical results is to make use of the limiting problems of the system which are obtained by letting the parameter $\mu \rightarrow \infty$ formally. Based on the further analysis of the bifurcation diagram of the limit problems, the multiple coexistence solutions of this model and their stability are established by perturbation theory. Thus the exact shape of bifurcation curve of coexistence solutions to this model is determined when the parameters lie in a certain range, which gives analytic confirmation of some of the numerical results.

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