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Sensitivity analysis and feedback control of noise-induced extinction for competition chemostat model with mutualism ☆

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HIGHLIGHTS

- A stochastic chemostat model with two obligate mutualistic species is proposed.
- The dynamic phenomenon of noise-induced extinction is observed.
- Critical intensity of noise transiting from coexistence to extinction is estimated.
- Feedback control strategies preventing the noise-induced extinction are proposed.

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ABSTRACT

We consider a stochastic chemostat model involving two obligate mutualistic species feeding on a limiting substrate. It is shown that the spatial arrangement of the random states near the deterministic coexistence equilibrium is enlarged as noise intensity increases. More precisely, in this paper, based on the technique of stochastic sensitivity functions, a confidence ellipse of the random states is constructed and a critical value for the noise intensity is established. It is shown that a new dynamic phenomenon of noise-induced extinction can be observed when the noise intensity passes the critical value. We then propose some feedback control strategies which can reduce the size of the confidence ellipse so that to prevent the noise-induced extinction.

1. Introduction

It is well known that chemostat is an important apparatus used in laboratory for continuously culturing microorganisms, and mathematical model for chemostat is one of the few predictive models in microbial ecology [1,2]. Due to the facts:

(a) many new mathematical problems can be motivated by the experimental observations in chemostats [3], and

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(b) the experimental data obtained in the laboratory can be successfully verified by prediction of mathematical models [4,5],

the study of chemostat has been attracting great interests of researchers and many chemostat models have been developed and analyzed extensively, see [6–8] and the references therein.

It is known mathematically [2,9–11] and experimentally [4] that the chemostat exhibits competitive exclusion principle (CEP) [12]. That is, when multiple microorganisms compete for a single limiting substrate, there may be only one microorganism which drives all other microorganisms in the chemostat to extinction so that the microorganism itself may survive. For example, Hsu [9] considered a model of the chemostat involving n microorganisms competing for a single limiting substrate and showed that CEP holds for the case with Michaelis–Menten uptake functions. For a general class of uptake functions with inhibitory kinetics, Butler and Wolkowicz [2] proved the CEP by assuming that the death rates of all the microorganisms are negligible in comparison with the washout rate of the chemostat. In the case that both monotone and nonmonotone general uptake functions and distinct removal rates, Li [10] showed that the CEP holds when the variation of distinct removal rates relative to the dilution rate of the chemostat can be controlled by either the difference between the two lowest break-even concentrations or by a parameter based on the structure of uptake functions. Besides, Liu [11] obtained some sufficient conditions under which CEP holds for delayed chemostat models with a large variety of widely used uptake functions.

In order to explain the coexistence of competing populations in nature or to prevent competitive exclusion in the continuous culture of microorganisms, control theory (open-loop control and feedback control) is used in the chemostat. In Refs. [13,14], authors used open-loop control, e.g., periodic input or periodic washout, and observed that the coexistence of competing populations might be achieved as a stable positive periodic solution mathematically. Feedback control was applied to chemostat model [15,16], where authors used dilution rate as the feedback control variable which depends affinely on the concentrations of the competing microorganisms, and showed that coexistence might be achieved as a stable positive equilibrium or a stable positive periodic solution.

In some cases [17,18], phenomena of coexistence of competing populations may be due to mutualistic relationships between species. For example, Saccharomyces cerevisiae, a kind of yeast used in winemaking, brewing and baking, is genetically modified to obtain two strains which have different metabolic capabilities. In the continuous culture process, the two species compete on a single substrate for their growth while they are made obligatory mutualists: the first species produces a protein necessary for the growth of the second one and conversely. For this kind of systems, Hajji et al. [1] proposed a cooperation-competition chemostat model and investigated its dynamic behavior. They proved, under general and natural assumptions of monotony on the uptake functions, the existence of extinction domain and coexistence domain. That is to say, depending on initial concentrations, both species can coexist at a positive equilibrium, or both species go to extinction at the washout equilibrium.

For a practical system, due to multistability and high sensitivity of attractors, the environmental noise can give rise to unexpected phenomena which have no analogue in the deterministic cases [19,20]. In this aspect, many work has been done by Bashkirtseva and Ryashko [20–23], where, for example they studied stochastically forced predator–prey models with Allee effect and analyzed phenomena of noise-induced transitions from coexistence to extinction [20,21]; and studied a stochastic Truscott–Brindley dynamical model of the interacting populations of prey and predator, showing a new phenomenon of the stochastic cycle splitting which is accompanied by the noise-induced chaotization [22,23].

In this paper, we are interested in whether environmental noise can induce species extinction in a competition chemostat model proposed in [1]. To this end, we first estimate the critical value of the intensity of noise generating a transition from coexistence to extinction by constructing a corresponding confidence ellipse. Then, we propose some feedback control strategies so that to prevent the noise-induced extinction, achieving a state of coexistence of both microorganisms. We also refer the readers to Refs. [24–31] for the modeling and analysis of the chemostat influenced by environmental noise.

The rest of this paper is organized as follows. In Section 2, we formulate our stochastic model by briefly reviewing related results about competition chemostat models. The analysis and control of the noise-induced extinction will be presented in Sections 3 and 4, respectively. We finally conclude the paper by some discussions in Section 5. To be self-contained, some mathematical background of the stochastic sensitivity function technique will be briefly outline in the Appendix.

2. Competition chemostat model with mutualistic

2.1. Deterministic model

In this subsection, we briefly review the relevant works by Hajji et al. [1], where they proposed the following chemostat model involving two obligate mutualistic species of microorganisms feeding on a limiting substrate

$$\begin{cases} \dfrac{\mathrm{d}S}{\mathrm{d}t} = D(S^0 - S) - f_1(S, y)x - f_2(S, x)y, \\ \dfrac{\mathrm{d}x}{\mathrm{d}t} = x\big(f_1(S, y) - D\big), \\ \dfrac{\mathrm{d}y}{\mathrm{d}t} = y\big(f_2(S, x) - D\big). \end{cases} \tag{2.1}$$