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Confidence domain in the stochastic competition chemostat model with feedback control

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Abstract. This paper studies a stochastically forced chemostat model with feedback control in which two organisms compete for a single growth-limiting substrate. In the deterministic counterpart, previous researches show that the coexistence of two competing organisms may be achieved as a stable positive equilibrium or a stable positive periodic solution by different feedback schedules. In the stochastic case, based on the stochastic sensitivity function technique, we construct the confidence domains for different feedback schedules which allow us to find the configurational arrangements of the stochastic attractors and analyze the dispersion of the random states of the stochastic model.

§1 Introduction

Chemostat is an important laboratory apparatus and has long been used as a benchmark model in microbial ecology [18]. It is used for a wide variety of realistic systems, such as lakes, waste-water treatment and bioreactors for commercial production of substances by genetically altered organisms [7, 9, 12, 14, 22, 26]. When multiple organisms compete for a single growth-limiting nutrient source, there is only one organism which can survive while the others die out in the long run, which is known as "competitive exclusion principle" [10, 13, 21]. In order to obtain coexistence between competing organisms in a chemostat, there are quite a few of literatures devoted to modifying the chemostat model by using control theory, for example open-loop control used in [6, 17] and feedback control used in [7, 8, 12]. More precisely, De Leenheer and Smith [7] and Keeran *et al.* [12] took the dilution rate as a feedback variable and made dependent on the concentrations of the competing organisms, which based on the fact that the dilution rate is an operating parameter and concentrations of organisms are measurable. It is shown in Ref. [7] that if the dilution rate depends affinly on the concentrations of two

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competing organisms, coexistence may be achieved as a globally asymptotically stable positive equilibrium; Ref. [12] also shows that the existence of an asymptotically stable positive periodic solution is possible in a chemostat with two competing organisms and controlled by a new type feedback control law.

Notice that in all the aforementioned works, the chemostat models are described by the deterministic systems of ordinary differential equations. However, the real environment is full of stochasticity, and every chemostat is inevitably affected by environmental noise which is an important component in reality. To reflect this fact, researchers have developed some stochastic chemostat models to reveal how noise affects population growth and behavior of organisms [11, 19, 20, 23–25]. For example, the single-species stochastic chemostat model proposed by Imhof and Walcher [11] concluded that the stochastic solution can be expected to remain close to the interior deterministic stationary point if the deterministic counterpart admits persistence and the stochastic effects are not too strong. We also obtained that the dynamics of the stochastic model is completely determined by the stochastic break-even concentration [23] which is analogous to the corresponding deterministic version. In Ref. [24], we showed that the competitive exclusion principle holds for a stochastic competition chemostat model, i.e., the competition outcome in the chemostat is completely determined by the species' stochastic break-even concentrations: The species with the lowest stochastic break-even concentration survives and all other species will go to extinction in the chemostat.

Even though feedback control leads to much richer dynamics in competition chemostat models, to the best of our knowledge, there is no any literature considering the stochastic chemostat model with feedback control. Thus, in this paper, we intend to investigate the stochastic competition chemostat model with feedback control. A common conclusion for stochastically forced model is that the stochastic trajectories leave a deterministic attractor (equilibrium or cycle) to form a corresponding stochastically distributed attractor (stochastic equilibrium or stochastic cycle) near the deterministic one for weak noise [3, 16]. But the probabilistic description, also known as configurational arrangement, of the stochastic attractor is unknown. Motivated by this, we will devote ourselves to the construction of the confidence domains for the stochastic chemostat model with different feedback schedules. The main tool for the construction of the confidence domains is stochastic sensitivity function technique [15] which was successfully applied in the analyses noise-induced transitions in the Lorenz system [4], and Goodwin model of business cycle [5], stochastic bifurcations in a predator-prey plankton system [1], stochastic limit cycles for the forced Brusselator [2].

The rest of this paper is organised as follows. In Section 2, we propose the stochastic competition chemostat models with feedback control. For different feedback schedules, we construct the confidence domains, namely confidence ellipse in Section 3 and confidence band in Section 4, respectively. We then conclude the paper by a simple discussion in Section 5.

§2 Competition chemostat model with two organisms

The basic mathematical model that describes the competition of two organisms for a single nutrient in a chemostat in which the growth functional responses are of Michaelis-Menten type takes the following form [18]:

$$\begin{cases} \frac{\mathrm{d}S}{\mathrm{d}t} = D(S^0 - S) - \frac{m_1 x S}{\gamma_1(a_1+S)} - \frac{m_2 y S}{\gamma_2(a_2+S)}, \\ \frac{\mathrm{d}x}{\mathrm{d}t} = x\left(\frac{m_1 S}{a_1+S} - D\right), \\ \frac{\mathrm{d}y}{\mathrm{d}t} = y\left(\frac{m_2 S}{a_2+S} - D\right), \end{cases} \tag{2.1}$$

where S is the nutrient concentration, x and y are the concentrations of the two organisms in the chemostat, respectively. S^0 is the input nutrient concentration and D is the dilution rate of the chemostat. γ_1 and γ_2 denote the yield coefficients, m_1 and m_2 are the maximal growth rates of the two organisms, a_1 and a_2 are called the half-saturation constants. All parameters are assumed to be positive. After some variable transformations, an appropriately scaled version of Eqs. (2.1) is

$$\begin{cases} \frac{\mathrm{d}S}{\mathrm{d}t} = D(1 - S) - \frac{m_1 x S}{a_1+S} - \frac{m_2 y S}{a_2+S}, \\ \frac{\mathrm{d}x}{\mathrm{d}t} = x\left(\frac{m_1 S}{a_1+S} - D\right), \\ \frac{\mathrm{d}y}{\mathrm{d}t} = y\left(\frac{m_2 S}{a_2+S} - D\right). \end{cases} \tag{2.2}$$

The competitive exclusion principle obviously holds for model (2.2), see Ref. [13]. However, as indicated in the Introduction, the coexistence of the two organisms may be achieved by taking the dilution rate as a feedback variable which dependents on the concentrations of the two organisms, i.e., $D = D(x, y)$. For example, De Leenheer and Smith [7] took

$$D(x, y) = \varepsilon + k_1 x + k_2 y \tag{2.3}$$

as the feedback schedule, where ε, k_1 and k_2 are nonnegative constants. Then by defining

$$\lambda = \frac{a_2 m_1 - a_1 m_2}{m_2 - m_1}, \quad D^* = \frac{m_1 \lambda}{a_1 + \lambda} \quad \text{and} \quad \tilde{k} = \frac{D^* - \varepsilon}{1 - \lambda},$$

they obtained the following result:

Lemma 2.1. *(Ref. [7]) For any $\varepsilon \in [0, D^*)$, suppose that k_i, $i = 1, 2$, satisfy $k_2 < \tilde{k} < k_1$, and $k_2 > 0$ in the case $\varepsilon = 0$. Then model (2.2) with feedback schedule (2.3) has a positive equilibrium*

$$E^* = \left(\lambda, \frac{(1-\lambda)(\tilde{k} - k_2)}{k_1 - k_2}, \frac{(1-\lambda)(k_1 - \tilde{k})}{k_1 - k_2}\right),$$

and it is globally asymptotically stable.

In Ref. [12], Keeran *et al.* proposed the following feedback schedule

$$D(x, y) = \varepsilon - k_1 x - k_2 y, \tag{2.4}$$

where ε, k_1 and k_2 are constants such that $D(x, y)$ is a positive function. Let

$$\bar{k}_1 = \frac{m_1 a_1}{(a_1 + \lambda)^2}, \quad \bar{k}_2 = \frac{m_2 a_2}{(a_2 + \lambda)^2},$$

$$\mathrm{I} = \left(\max\{\bar{k}_1(1-\lambda) + D^*, \bar{k}_2\}, \bar{k}_2(1-\lambda) + D^*\right).$$

Then they proved:

Lemma 2.2. *(Ref. [12]) For model (2.2) with feedback schedule (2.4) and any* $\varepsilon \in \mathrm{I}$,

(a) *assume* $k_2 = \bar{k}_2$, *then when* k_1 *passes through* $\bar{k}_1$ *a supercritical Hopf bifurcation occurs at the positive equilibrium; furthermore,*

(b) *there exists a* $\delta > 0$ *such that for all* $k_1 \in (\bar{k}_1, \bar{k}_1 + \delta)$, *it has an asymptotically stable periodic solution.*

Due to the existence of environmental noise, the parameters involved in model (2.2) always fluctuate around some average values but do not attain fixed values with the time evolution. Notice that the maximal growth rate of the organism is one of the crucial parameters in the chemostat model, and it is more affected by the environmental noise. Then, in this paper, we introduce randomness into the deterministic model (2.2) by perturbing the maximal growth rate m_i by $m_i + \sigma_i \dot{B}_i(t)$ and obtain the following system of stochastic differential equations:

$$\begin{cases} \mathrm{d}S = \Big(D(1-S) - \frac{m_1 xS}{a_1+S} - \frac{m_2 yS}{a_2+S}\Big)\mathrm{d}t - \frac{\sigma_1 xS}{a_1+S}\mathrm{d}B_1 - \frac{\sigma_2 yS}{a_2+S}\mathrm{d}B_2, \\ \mathrm{d}x = x\big(\frac{m_1 S}{a_1+S} - D\big)\mathrm{d}t + \frac{\sigma_1 xS}{a_1+S}\mathrm{d}B_1, \\ \mathrm{d}y = y\big(\frac{m_2 S}{a_2+S} - D\big)\mathrm{d}t + \frac{\sigma_2 yS}{a_2+S}\mathrm{d}B_2, \end{cases} \tag{2.5}$$

where $B_1(t)$ and $B_2(t)$ are standard one-dimensional independent Brownian motions defined on a complete probability space $(\Omega, \mathscr{F}, \{\mathscr{F}_t\}_{t\geq 0}, \mathrm{Prob})$, σ_1 and σ_2 denote the noise intensities.

From Refs. [7, 12], we can conclude that

$$\Delta := \{(S, x, y) \in \mathbb{R}_+^3 | S + x + y = 1\}$$

is an invariant set for model (2.5). Thus we can study the dynamics of the original model (2.5) restricted to set Δ, which results in the reduced model of two equations:

$$\begin{cases} \mathrm{d}x = x\Big(\frac{m_1(1-x-y)}{a_1+1-x-y} - D\Big)\mathrm{d}t + \frac{\sigma_1 x(1-x-y)}{a_1+1-x-y}\mathrm{d}B_1, \\ \mathrm{d}y = y\Big(\frac{m_2(1-x-y)}{a_2+1-x-y} - D\Big)\mathrm{d}t + \frac{\sigma_2 y(1-x-y)}{a_2+1-x-y}\mathrm{d}B_2, \end{cases} \tag{2.6}$$

where $(x, y) \in \{(x, y) \in \mathbb{R}_+^2 | x + y \leq 1\}$.

In the following two sections, using the stochastic sensitivity function technique from the Appendix, we will construct the confidence domains for stochastic model (2.6) with $\sigma_1 = \sigma_2 = \sigma$ and different feedback schedules.

§3 Confidence ellipse in model (2.6) with feedback (2.3)

When the corresponding deterministic model has a stable equilibrium $E^*(x^*, y^*)$, random trajectories of the stochastic model generally leave the equilibrium but remain in a neighbourhood of it for small noise. In order to investigate the probabilistic description of the random states, in this section, we will construct the confidence ellipse of model (2.6) with feedback (2.3) by using the theory of stochastic sensitivity function technique.

To this end, define

$$F = \begin{pmatrix} f_{11} & f_{12} \\ f_{21} & f_{22} \end{pmatrix}, \quad G = \begin{pmatrix} g_{11} & 0 \\ 0 & g_{22} \end{pmatrix},$$

where

$$f_{11}=-x^*\left(\frac{a_1m_1}{(a_1+1-x^*-y^*)^2}+k_1\right),\quad f_{12}=-x^*\left(\frac{a_1m_1}{(a_1+1-x^*-y^*)^2}+k_2\right),$$
$$f_{21}=-y^*\left(\frac{a_2m_2}{(a_2+1-x^*-y^*)^2}+k_1\right),\quad f_{22}=-y^*\left(\frac{a_2m_2}{(a_2+1-x^*-y^*)^2}+k_2\right),$$

and

$$g_{11}=\left(\frac{x^*(1-x^*-y^*)}{a_1+1-x^*-y^*}\right)^2,\quad g_{22}=\left(\frac{y^*(1-x^*-y^*)}{a_2+1-x^*-y^*}\right)^2.$$

It then follows from (A.2) in Ref. [5] that the stochastic sensitivity matrix

$$W=\begin{pmatrix} w_{11} & w_{12}\\ w_{21} & w_{22}\end{pmatrix}$$

satisfies the following equations

$$\begin{cases}2f_{11}w_{11}+f_{12}w_{12}+f_{12}w_{21}=-g_{11},\\ f_{21}w_{11}+(f_{11}+f_{22})w_{12}+f_{12}w_{22}=0,\\ f_{21}w_{11}+(f_{11}+f_{22})w_{21}+f_{12}w_{22}=0,\\ f_{21}w_{12}+f_{21}w_{21}+2f_{22}w_{22}=-g_{22}.\end{cases}$$

From (A.3) in Ref. [5], we know that the confidence ellipse equation is

$$\left\langle (x-x^*,y-y^*)^T, W^{-1}(x-x^*,y-y^*)^T\right\rangle = 2\sigma^2\log\frac{1}{1-P}, \tag{3.1}$$

where P is a fiducial probability. Next, we give a numerical example. Let

$$m_1=1.4, m_2=2.5, a_1=0.2, a_2=0.75, k_1=0.52, k_2=0.32, \varepsilon=0.8.$$

It follows from Lemma 2.1 that the corresponding deterministic model has a stable positive equilibrium $E^*(0.2,0.3)$. In this case, the stochastic sensitivity matrix and its inverse matrix are

$$W=\begin{pmatrix} 0.5758 & -0.6478\\ -0.6478 & 0.7833\end{pmatrix},\quad W^{-1}=\begin{pmatrix} 24.8992 & 20.5896\\ 20.5896 & 18.3026\end{pmatrix},$$

respectively. Then from equation (3.1) the confidence ellipse equation is

$$24.8992(x-0.2)^2+41.1792(x-0.2)(y-0.3)+18.3026(y-0.3)^2=2\sigma^2\log\frac{1}{1-P}.$$

We next illustrate how noise affects the confidence domain. Initially taking noise intensity $\sigma=0.035$ and fiducial probability $P=0.95$, one can obtain the random states of stochastic model (2.6) with feedback (2.3) and the corresponding confidence ellipse as shown in Figure 1. Obviously, the random states of the stochastic model are distributed around the corresponding deterministic equilibrium, and they belong to the interior of the ellipse domain with large probability (its value is approximately 0.95).

If we vary either noise intensity or fiducial probability, it follows from equation (3.1) that the configurational arrangement of the confidence ellipse begin to expand as the noise intensity or fiducial probability increases. This is also verified by Figure 2.

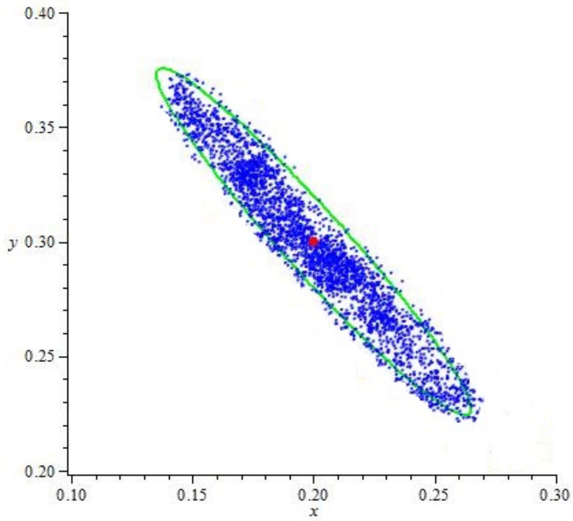


Figure 1: Random states (blue) of stochastic model (2.6) with feedback (2.3) around E^* (red) and confidence ellipse (green) for $\sigma = 0.035$ and $P = 0.95$.

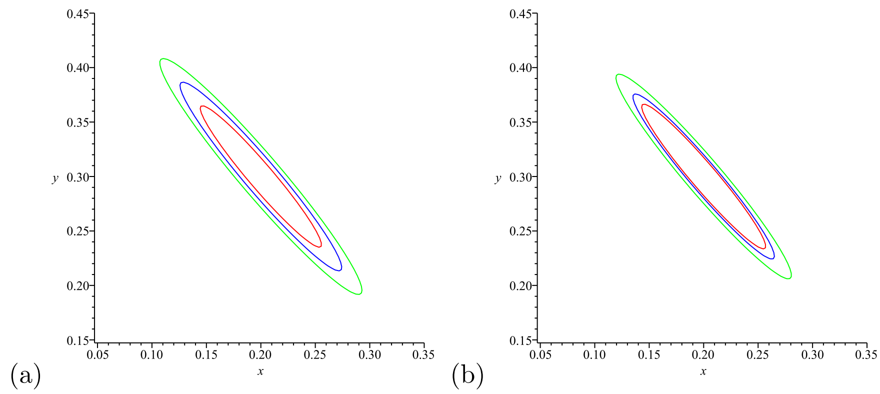


Figure 2: Effects of noise intensity and fiducial probability on the confidence ellipses for stochastic model (2.6) with feedback (2.3). (a): $P = 0.95$ and $\sigma = 0.03$ (red), $\sigma = 0.04$ (blue), $\sigma = 0.05$ (green); (b): $\sigma = 0.035$ and $P = 0.90$ (red), $P = 0.95$ (blue), $P = 0.99$ (green).

§4 Confidence band in model (2.6) with feedback (2.4)

The conclusion of Lemma 2.2 allows us to assume that the corresponding deterministic model has an asymptotically stable limit cycle. In the stochastic case, the limit cycle disappears, but the trajectories will remain in a small neighbourhood for small noise. To find the configurational arrangement of this neighborhood, in what follows, we will construct the confidence band for model (2.6) with feedback (2.4). To this end, let

$$f_1(x,y)=x\left(\frac{m_1(1-x-y)}{a_1+1-x-y}-\varepsilon+k_1x+k_2y\right)$$

and

$$f_2(x,y)=y\left(\frac{m_2(1-x-y)}{a_2+1-x-y}-\varepsilon+k_1x+k_2y\right),$$

and denote the limit cycle by $\Gamma(x(t),y(t))$, $t\in[0,T]$. Then we can write matrices $F(t)$ and $G(t)$ as follows:

$$F(t)=\begin{pmatrix} f_{11}(t) & f_{12}(t)\\ f_{21}(t) & f_{22}(t)\end{pmatrix},\quad G(t)=\begin{pmatrix} g_{11}(t) & 0\\ 0 & g_{22}(t)\end{pmatrix},$$

where

$$f_{11}(t)=\left.\frac{\partial f_1(x,y)}{\partial x}\right|_\Gamma,\quad f_{12}(t)=\left.\frac{\partial f_1(x,y)}{\partial y}\right|_\Gamma,$$
$$f_{21}(t)=\left.\frac{\partial f_2(x,y)}{\partial x}\right|_\Gamma,\quad f_{22}(t)=\left.\frac{\partial f_2(x,y)}{\partial y}\right|_\Gamma,$$

and

$$g_{11}(t)=\left.\left(\frac{x(1-x-y)}{a_1+1-x-y}\right)^2\right|_\Gamma,\quad g_{22}(t)=\left.\left(\frac{y(1-x-y)}{a_2+1-x-y}\right)^2\right|_\Gamma.$$

It follows from (A.4) in Ref. [5] that stochastic sensitivity function $\mu(t)$ satisfies the following boundary problem

$$\begin{cases}\frac{\mathrm{d}\mu(t)}{\mathrm{d}t}=a(t)\mu(t)+b(t),\\ \mu(0)=\mu(T),\end{cases}$$

where

$$a(t)=2f_{11}(t)p_1^2(t)+2(f_{12}(t)+f_{21}(t))p_1(t)p_2(t)+2f_{22}(t)p_2^2(t)$$

and

$$b(t)=g_{11}(t)p_1^2(t)+g_{22}(t)p_2^2(t).$$

Here,

$$p_1(t)=\left.\frac{f_2(x,y)}{\sqrt{f_1^2(x,y)+f_2^2(x,y)}}\right|_\Gamma,\quad p_2(t)=-\left.\frac{f_1(x,y)}{\sqrt{f_1^2(x,y)+f_2^2(x,y)}}\right|_\Gamma$$

are elements of a vector function $p(t)=(p_1(t),p_2(t))^T$ orthogonal to vector $(f_1(x,y),f_2(x,y))^T\big|_\Gamma$. And from (A.5) in Ref. [5], we know the boundaries $\Gamma_{1,2}(t)$ of the confidence band have the following explicit parametrical form:

$$\Gamma_1(t)=\Gamma(t)+\sigma k\sqrt{2\mu(t)}p(t),\quad \Gamma_2(t)=\Gamma(t)-\sigma k\sqrt{2\mu(t)}p(t),\tag{4.1}$$

where $k=\mathrm{erf}^{-1}(P)$ and P is the fiducial probability. Next we numerically illustrate this region. To this end, we take

$$m_1=1.4, m_2=2.5, a_1=0.2, a_2=0.75, k_1=0.6214, k_2=1.2 \text{ and } \varepsilon=1.45$$

as suggested in [12]. Then by using Lemma 2.2, we know that the corresponding deterministic model has a stable limit cycle Γ. Then, we report the numerical simulations for the noise intensity $\sigma = 0.003$ and fiducial probability $P = 0.95$ in Figure 3. The red line is the deterministic limit cycle, the blue points are the random states on different time and the two green lines are the boundaries of the confidence band. Obviously, the random states are distributed around the corresponding deterministic limit cycle, and they belong to the interior of the confidence band with probability 0.95.

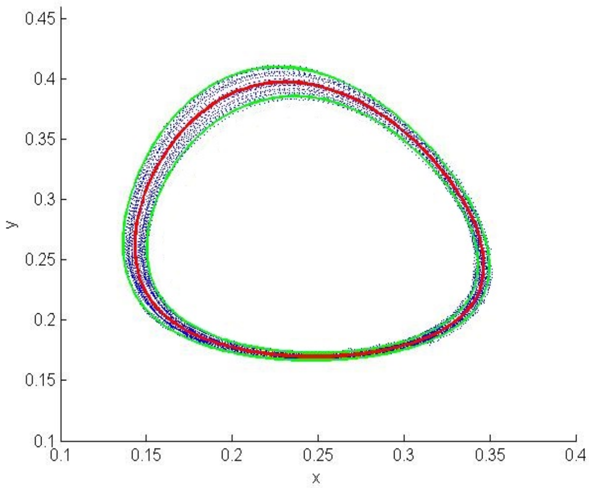


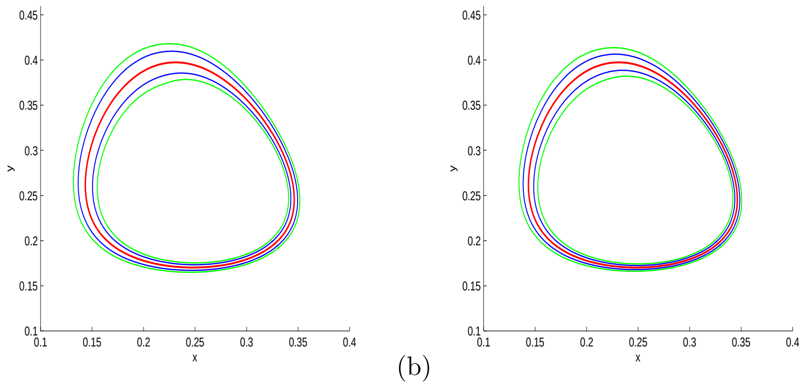
Figure 3: Random states (blue) of stochastic model (2.6) with feedback (2.4) around Γ (red) and confidence band (green) for $\sigma = 0.003$ and $P = 0.95$.

In Figure 4, we illustrate the effects of the noise intensity or fiducial probability on the size of the confidence bands. It is easy to see that the configurational arrangement of the confidence band begin to expand as the noise intensity or fiducial probability increases. This result can be deduced from equation (4.1).

§5 Discussion

The two species competition chemostat models with feedback control have been studied by De Leenheer and Smith [7], Keeran *et al.* [12]. They obtained some very interesting results that the competitive exclusion principle does not hold, and the two competing organisms may be coexisting in the form of a stable positive equilibrium or stable positive periodic solution. In the presence of environmental noise in the growth rates of the two organisms, in this paper, we proposed a stochastic competition chemostat model with feedback control.

By applying the stochastic sensitivity function technique and method of confidence domains, we constructed the confidence ellipse and confidence band for the stochastic model with different feedback schedules. This confidence domains allow us to find the configurational arrangements



(a) (b)

Figure 4: Confidence bands for stochastic model (2.6) with feedback (2.4). (a): $P = 0.95$ and $\sigma = 0.003$ (blue), $\sigma = 0.005$ (green); (b): $\sigma = 0.003$ and $P = 0.85$ (blue), $P = 0.99$ (green).

of the stochastic attractors, and analyze the dispersion of the random states of the stochastic model. The explicit parametrical forms of the confidence ellipse and the boundaries of the confidence band are given in equations (3.1) and (4.1), respectively. From this, we know that the configurational arrangement of the stochastic attractors begin to expand as the noise intensity increases, see Figure 2 (a) and Figure 4 (a).

The results obtained in this paper may enrich the research of asymptotic behavior in chemostat model and help us better understand the population growth and behavior of organisms in the chemostat with environmental noise. Except for the maximal growth rates, other parameters in the chemostat model are inevitably affected by environmental noise. Then there is an interesting problem that whether the stochastic sensitivity function technique can be extended for the competition chemostat model with feedback control in which the dilution rate is affected by environmental noise.

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