

ON THE EXISTENCE OF CHAOTIC BEHAVIOUR IN PURE AND SIMPLE MICROBIAL COMPETITION: THE ROLE OF CONTOIS KINETICS

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Abstract

Microbial competition for nutrients is a common phenomenon that occurs between species inhabiting the same environment. Bioreactors are often used for the study of microbial competition since the number and type of microbial species can be controlled, and the system can be isolated from other interactions that may occur between the competing species. A common type of competition is the so-called “pure and simple” competition, where the microbial populations interact in no other way except the competition for a single rate-limiting nutrient that affects their growth rates. The issue of whether pure and simple competition under time-invariant conditions can give rise to chaotic behaviour has been unresolved for decades. The third author recently showed, for the first time, that chaos can theoretically occur in these systems by analysing the dynamics of a model where both competing species grow following the biomass-dependent Contois model while the yield coefficients associated with the two species are substrate-dependent. In this paper we show that chaotic behaviour can occur in a much simpler model of pure and simple competition. We examine the case where only one species grows following the Contois model with variable yield coefficient while the other species is allowed to grow following the simple Monod model with constant yield. We show that while the static behaviour of the proposed model is quite simple, the dynamic behaviour is complex and involves period doubling culminating in chaos. The proposed model could serve as a basis to re-examine the importance of Contois kinetics in predicting complex behaviour in microbial competition.

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1. Introduction

Competition between microbial species is common in many natural ecosystems as well as in bioreactors used for waste treatment. The study of microbial

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competition is therefore important for understanding the dynamics of ecosystems and for optimization of biological treatment of wastes [6]. A bioreactor is a vessel in which a biological reaction or change takes place. The biological system may include enzymes, microorganisms, animal cells, plant cells or tissues. The bioreactor is a place where an optimum environment is provided to meet the needs of the biological system. Bioreactors are also considered as crude models of natural ecosystems since they are used to study, under controlled laboratory conditions, the different types of interactions that arise between microorganisms inhabiting the same environment. The fermentation process typically begins with the addition of a small amount of living cells, that is, inoculum to the liquid medium, containing the nutrients needed for the growth of the organism. During the growth process of the organism, the number of cells increases and forms the commonly known biomass [32]. An important type of bioreactor is the chemostat, whose name is a contracted form of “chemical static environment”. It is the continuous perfectly stirred tank bioreactor with constant volume and constant inlet streams. The chemostat has played an important role in microbiology and population biology. It represents the simplest idealization of a biological system where the parameters are measurable and the mathematics is tractable.

One type of microbial competition that has been intensively studied in the literature concerns the so-called pure and simple microbial competition. The competition is considered to be simple when the interacting species compete for a single resource that is affecting the growth rate of all of them. The competition is also said to be pure when microbial populations interact in no other way except the competition for a single rate-limiting nutrient. Theoretically, it has been established that under time-invariant conditions the competing populations cannot coexist except at discrete values of dilution rate [5, 9, 12, 15, 16, 19, 35]. However, even if the bioreactor is operated exactly at the required dilution rate, fluctuations will eventually cause the dominance of one species and the extinction of the other [31]. This result is a variation of the competitive exclusion principle [17]. Closely related to this principle is the *paradox of the plankton* put forward by Hutchinson [20], who observed the coexistence of many species of phytoplankton in a relatively homogeneous environment, competing for a limited number of resources. This paradox was explained by Hutchinson [20], who suggested that seasonal variations of environmental conditions provide the competitive advantage to each population for a period of time and allow them to coexist. Studies have effectively shown that when the feed conditions of the bioreactor are periodically varied (which mimics the seasonal variations in natural environments), the competing populations can coexist not only in a limit cycle [18, 29] but also in a chaotic state [24].

The issue of whether pure and simple competition under time-invariant conditions can give rise to complex behaviour has been investigated by a number of authors [2, 13, 28]. For the case of non-sterile feed conditions and constant yield coefficients, Ajbar and Alhumaizi [2, 3] uncovered the existence of periodic behaviour in the chemostat. Recently, Gaki et al. [13] studied the dynamics of competition in a gradostat (a configuration of two or more interconnected chemostats that mimics spatial heterogeneity) and showed the existence of complex dynamics including

quasi-periodic states and bifurcations of limit cycles via period-doubling sequences. However, the aforementioned studies could not establish the existence of chaotic behaviour in such competition. Recently, Ajbar [1] proposed and analysed a time-invariant model of pure and simple microbial competition which was capable of predicting chaotic behaviour. The model assumed that both species grow following the biomass-dependent Contois model [10], and that the yield coefficients associated with both species are linearly dependent on the substrate.

The Contois growth model is qualitatively different from substrate-dependent growth kinetics such as the well-known Monod model. In substrate-limited growth kinetics, for instance, the dependence of the specific growth rate on the substrate is usually in the form of saturation kinetics, meaning that there exists a maximum growth rate which cannot be exceeded even with the increase in the limiting substrate. In the Contois model, the specific growth rate depends on both substrate and biomass, with the latter playing an inhibiting role on the growth. The Contois growth model has been found to accurately describe the processing of certain industrial wastewaters such as the aerobic degradation of wastewater originating from the treatment of black olives [7], the anaerobic treatment of dairy manure [14], the anaerobic treatment of textile wastewater [21] and the aerobic biodegradation of solid municipal organic waste [23].

In this paper we propose a much simpler competition model than the one previously studied by Ajbar [1], and we show that the proposed model can predict chaotic behaviour for some range of its parameters. The proposed model assumes that only one species grows following Contois kinetics with variable yield coefficient while the other species is assumed to grow following the common Monod model with constant yield coefficient. The Monod equation relates microbial growth rate in an aqueous environment to the concentration of a limiting nutrient. The equation has been one of the most frequently used models in microbiology to describe the growth of microorganisms [22, 25, 30]. The Monod equation is also commonly used in environmental engineering such as the activated sludge model for wastewater treatment, as well as for the evaluation of the biodegradation kinetics of organic pollutants [8, 32]. The Monod equation was also used in the context of pure and simple competition [33]. In fact, the first models used to describe the competition were based on Monod models [5, 31]. We analyse both the static and dynamic behaviour of the model using standard bifurcation techniques. It is shown that while the model's static behaviour is quite simple, the dynamic behaviour is complex and includes period doubling leading to chaos. The organization of the rest of this paper starts with the description of the proposed model and the analysis of its static behaviour, followed by numerical simulations to show the complex behaviour predicted by the model.

2. Process model

We consider a continuous stirred tank bioreactor where two microbial populations X_1 and X_2 compete for a single substrate S . The unsteady-state balances for the

different species are given by the equations

$$\begin{aligned}\frac{dS}{dt} &= D(S_f - S) - \frac{r_1(S, X_1)}{Y_1(S)}X_1 - \frac{r_2(S)}{Y_2(S)}X_2, \\ \frac{dX_1}{dt} &= -DX_1 + r_1(S, X_1)X_1, \\ \frac{dX_2}{dt} &= -DX_2 + r_2(S)X_2,\end{aligned}$$

where D is the dilution rate, S_f is the substrate feed concentration, $r_1(S, X_1)$ and $r_2(S)$ are the specific growth rates of X_1 and X_2 respectively, and $Y_1(S)$ and $Y_2(S)$ are the yield coefficients associated with X_1 and X_2 . The model assumes the absence of biomass feed to the reactor (sterile feed conditions) which is more reminiscent of bioengineering practices.

The first species (X_1) grows following the biomass-dependent Contois model [10],

$$r_1(S, X) = \frac{\mu_1 S}{K_1 X_1 + S},$$

where μ_1 is the maximum specific growth rate and K_1 is the Contois saturation constant. It is seen that the growth is inhibited by the biomass concentration. The associated yield coefficient Y_1 is assumed to be linearly dependent on S :

$$Y_1(S) = a_1 + b_1 S,$$

where a_1 and b_1 are constants. The second species X_2 grows following Monod kinetics:

$$r_2(S) = \frac{\mu_2 S}{K_2 + S},$$

where μ_2 is the maximum specific growth rate and K_2 is the saturation constant. The associated yield coefficient Y_2 is assumed to be constant.

The model is rendered dimensionless using the following variables:

$$\begin{aligned}\bar{S} &= \frac{S}{S_f}, \quad \bar{X}_1 = \frac{X_1}{Y_1(S_f)S_f}, \quad \bar{X}_2 = \frac{X_2}{Y_2 S_f}, \quad \bar{r}_1 = \frac{r_1}{\mu_1}, \quad \bar{r}_2 = \frac{r_2}{\mu_1}, \\ \bar{t} &= t\mu_1, \quad \bar{D} = \frac{D}{\mu_1}, \quad \bar{Y}_1(\bar{S}) = \frac{Y_1(S)}{Y_1(S_f)}.\end{aligned}$$

The dimensionless specific growth rates and yield coefficient are

$$\bar{r}_1 = \frac{\bar{S}}{\bar{K}_1 \bar{X}_1 + \bar{S}}, \quad \bar{r}_2 = \frac{\lambda_1 \bar{S}}{\bar{K}_2 + \bar{S}}, \quad \bar{Y}_1(\bar{S}) = \frac{1 + \lambda_2 \bar{S}}{1 + \lambda_2},$$

with

$$\bar{K}_1 = K_1 Y_1(S_f), \quad \bar{K}_2 = \frac{K_2}{S_f}, \quad \lambda_1 = \frac{\mu_2}{\mu_1}, \quad \lambda_2 = \frac{b_1 S_f}{a_1}. \quad (2.1)$$

The dimensionless model is therefore

$$\frac{d\bar{S}}{d\bar{t}} = \bar{D}(1 - \bar{S}) - \frac{\bar{S}(1 + \lambda_2)}{(\bar{K}_1\bar{X}_1 + \bar{S})(1 + \lambda_2\bar{S})}\bar{X}_1 - \frac{\lambda_1\bar{S}}{\bar{K}_2 + \bar{S}}\bar{X}_2, \tag{2.2}$$

$$\frac{d\bar{X}_1}{d\bar{t}} = -\bar{D}\bar{X}_1 + \frac{\bar{S}}{\bar{K}_1\bar{X}_1 + \bar{S}}\bar{X}_1, \tag{2.3}$$

$$\frac{d\bar{X}_2}{d\bar{t}} = -\bar{D}\bar{X}_2 + \frac{\lambda_1\bar{S}}{\bar{K}_2 + \bar{S}}\bar{X}_2. \tag{2.4}$$

At steady state, the model has the following solutions.

- Total washout defined by $\bar{X}_1 = \bar{X}_2 = 0$ and $\bar{S} = 1$.
- Washout of X_1 alone, that is, $\bar{X}_1 = 0$ and $\bar{X}_2 \neq 0$. Setting the right-hand side of equation (2.4) to zero yields a direct relation between \bar{D} and \bar{S} :

$$\bar{D} = \frac{\lambda_1\bar{S}}{\bar{K}_2 + \bar{S}}.$$

The value of \bar{X}_2 is obtained by setting the right-hand side of equation (2.2) to zero to yield $\bar{X}_2 = 1 - \bar{S}$.

- Washout of X_2 alone, that is, $\bar{X}_1 \neq 0$ and $\bar{X}_2 = 0$. Equation (2.3) yields

$$\bar{X}_1 = \frac{\bar{S}(1 - \bar{D})}{\bar{D}\bar{K}_1}.$$

Substituting in equation (2.2) yields the following quadratic equation for \bar{S} as a function of the model parameters:

$$-\bar{D}\bar{K}_1\lambda_2\bar{S}^2 + (-1 + \bar{D} - \bar{D}\bar{K}_1 - \lambda_2 + \bar{D}\lambda_2 + \bar{D}\bar{K}_1\lambda_2)\bar{S} + \bar{D}\bar{K}_1 = 0.$$

It is seen that the product of the first and last coefficients of the quadratic equation is always negative, confirming the existence of one positive and meaningful root. The value of \bar{X}_1 can be obtained from equation (2.2), yielding

$$\bar{X}_1 = \frac{(1 - \bar{S})(1 + \lambda_2\bar{S})}{(1 + \lambda_2)}.$$

- Coexistence of the two species: $\bar{X}_1 \neq 0$ and $\bar{X}_2 \neq 0$. Equation (2.4) yields

$$\bar{D} = \frac{\lambda_1\bar{S}}{\bar{K}_2 + \bar{S}}, \quad \text{that is,} \quad \bar{S} = \frac{\bar{D}\bar{K}_2}{\lambda_1 - \bar{D}}.$$

The value of \bar{X}_1 can be obtained from equation (2.3), yielding

$$\bar{X}_1 = \frac{\bar{S}(\bar{1} - \bar{D})}{\bar{D}\bar{K}_1},$$

while \bar{X}_2 can be obtained by adding equations (2.2)–(2.4).

As can be seen from this analysis, the different branches forming the static behaviour of the model consist of simple linear or quadratic expressions. This is not the case for dynamic bifurcation. The conditions of the existence of Hopf points are quite involved and do not lend themselves easily to algebraic manipulations. We opt therefore for numerical simulations to study the existence of Hopf points in the model. The numerical analysis of the model is carried out using the AUTO [11] software and by constructing Poincaré bifurcation diagrams. The nominal values of the model parameters are $\bar{K}_1 = 1.5$, $\bar{K}_2 = 1.0$, $\lambda_1 = 9.0$ and $\lambda_2 = 200$.

3. Numerical simulations

Figure 1 shows an example of bifurcation diagrams using the dilution rate \bar{D} as the main bifurcation parameter. The diagram in Figure 1(a) is characterized by the existence of the four static branches discussed earlier, namely the horizontal total washout line ($\bar{X}_1 = \bar{X}_2 = 0, \bar{S} = 1$), the existence of X_2 alone ($\bar{X}_1 = 0$), the existence of X_1 alone ($\bar{X}_2 = 0$) and the nontrivial coexistence branch ($\bar{X}_1 \neq 0, \bar{X}_2 \neq 0$). Note that in the (\bar{D}, \bar{S}) diagram, the coexistence branch coincides with the branch $\bar{X}_1 = 0$ since both of these branches are represented by the same equation

$$\bar{S} = \frac{\bar{D}\bar{K}_2}{\lambda_1 - \bar{D}}.$$

The crossing of the coexistence branch with the other branches can be seen more clearly in the parameter space (\bar{D}, \bar{X}_2) of Figure 1(b).

Figure 2 shows that the behaviour of the model is also characterized by the existence of two Hopf points HB1 and HB2 on the branch associated with the existence of X_1 alone. The coordinates of these points are, respectively, $(\bar{D}, \bar{S}, \bar{X}_1, \bar{X}_2) = (0.3213, 0.0116, 0.0163, 0)$ and $(0.4563, 0.2195, 0.1743, 0)$. A third Hopf point HB3 is seen to appear on the coexistence branch at the coordinates $(\bar{D}, \bar{S}, \bar{X}_1, \bar{X}_2) = (0.4557, 0.0533, 0.0425, 0.2149)$. Another Hopf point also exists at the coordinates $(0.3722, 0.0431, 0.0485, -0.0560)$. However, this Hopf point is not meaningful since it corresponds to a negative value of \bar{X}_2 . In the following we concentrate the analysis on the Hopf point HB3. The existence of two Hopf points HB1 and HB2 on the branch $\bar{X}_2 = 0$ is expected, since microbial species growing following the Contois model with variable yield coefficient are known to exhibit periodic behaviour [4, 26, 27]. Figure 2 also shows that stable periodic branches emanate from HB3 and then lose their stability through a period-doubling bifurcation as is shown later.

At this point, it is useful to show the effect of some model parameters on the existence of periodic behaviour in the nontrivial coexistence branch. Figure 3(a) shows the effect of the parameter λ_1 . This parameter (see (2.1)) represents the ratio of the maximum specific growth rates of the two species. It is seen that Hopf points are expected only within a range of this parameter. Figure 3(b) shows, on the other hand, the effect of λ_2 . Recall that λ_2 (see (2.1)) incorporates both the substrate feed concentration and the parameters of the yield coefficient associated with the growth

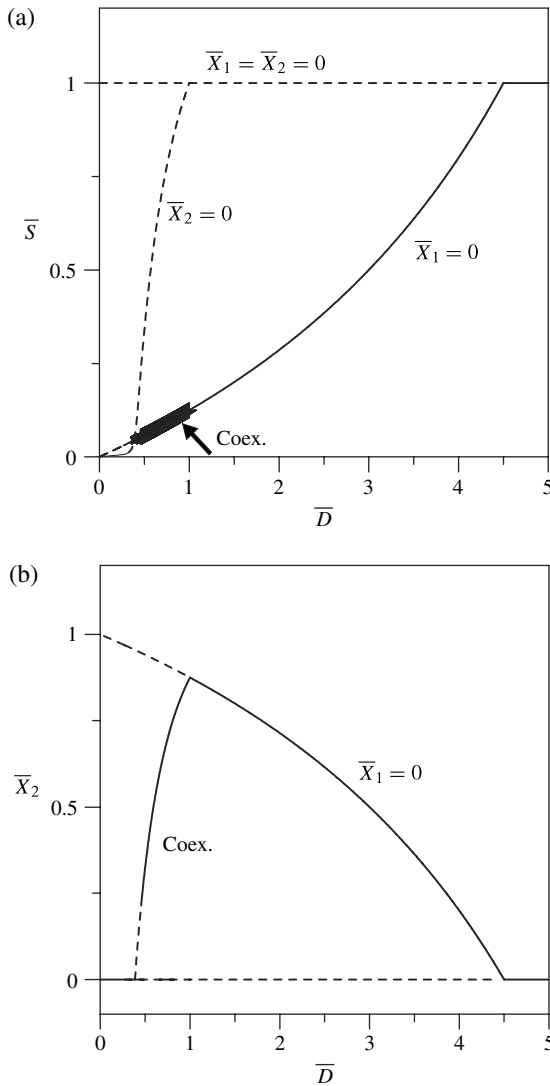


FIGURE 1. Bifurcation diagram in (a) parameter space (\bar{D}, \bar{S}) , (b) parameter space (\bar{D}, \bar{X}_2) . Solid line, stable branch; dashed line, unstable branch; bold line, nontrivial coexistence branch (labelled “Coex.”).

of X_1 . It is seen that the range of Hopf points increases with the increase in λ_2 . Figure 3(b) also shows that when the yield coefficient is constant ($\lambda_2 = 0$), the model cannot predict periodic behaviour.

Next we investigate whether the periodic behaviour encountered can give rise to complex behaviour. Our investigation revealed that this is actually the case and it occurs for some range of model parameters. The bifurcation mechanism is shown in the Poincaré diagram in Figure 4(a). The accurate characterization of the emerging

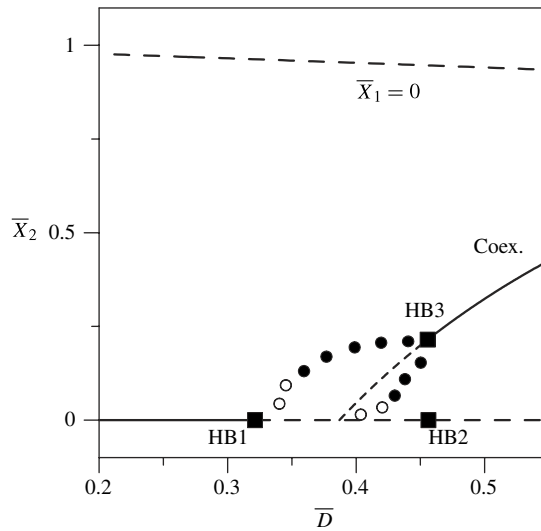


FIGURE 2. Bifurcation diagram showing periodic branches emanating from the Hopf point HB3 on the coexistence branch. HB, Hopf point; solid line, stable branch; dashed line, unstable branch; filled circle, stable periodic branch; open circle, unstable periodic branch; “Coex.,” branch of nontrivial coexistence.

attractors of Figure 4(a) can be best achieved by computing the maximum Lyapunov exponent. The Lyapunov spectrum computed using the algorithm of Wolf et al. [34] is shown in Figure 4(b) where a negative value indicates a periodic regime while a chaotic attractor would be characterized by a positive value of the spectrum. It can be seen on the scale of Figure 4(a) (enlarged and in greater detail in Figure 5) that as the dilution rate decreases, the period-1 limit cycle undergoes a complex bifurcation sequence characterized by the existence of branches of high periodicity (which explains the thick lines). The periodic nature of these attractors is confirmed by the Lyapunov spectrum. Then just before the value of $\bar{D} = 0.3234$, a period-doubling bifurcation occurs (shown in Figure 5) leading to a chaotic strip that bifurcates to a period-1 attractor, as the dilution rate further decreases. The chaotic behaviour of the region is also confirmed by the positive values of the maximum Lyapunov exponent. Figure 6 shows an example of chaotic behaviour for the value of $\bar{D} = 0.32337$. The maximum Lyapunov exponent is 0.0272, confirming further the chaotic nature of the attractor.

4. Conclusion

Pure and simple competition occurring in a chemostat with sterile feed and time-invariant input conditions is one of the simplest and most studied microbial interactions in the literature. When the microbial species grow following substrate-dependent growth models, experimental and theoretical studies rule out the existence of any complex behaviour resulting from these interactions. This paper studied a simple model of the competition when one species grows following the Contois model with

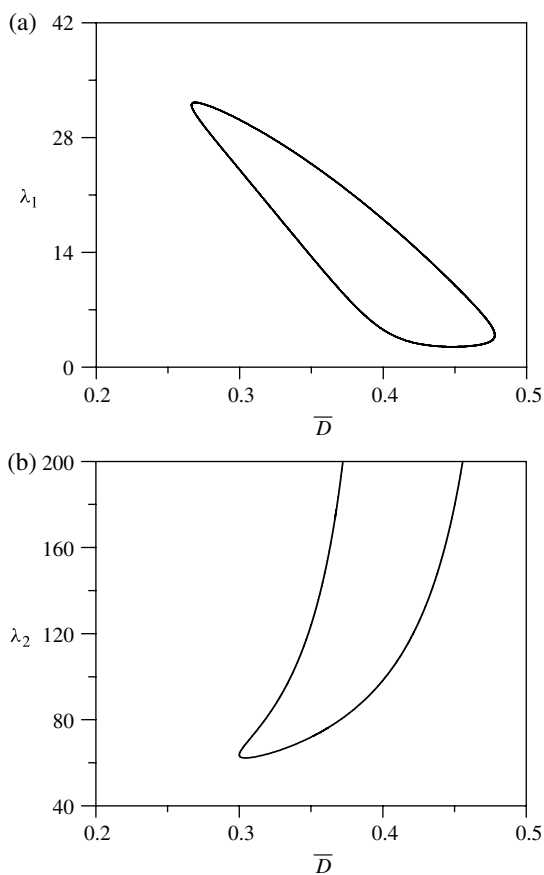


FIGURE 3. Parameter diagrams showing the loci of the Hopf points of the coexistence branch in (a) (\bar{D}, λ_1) , (b) (\bar{D}, λ_2) .

variable yield coefficient while the other species is assumed to grow following the Monod model with constant yield. The analysis of the model showed the complexity of its dynamics compared to the simplicity of its static behaviour. In this regard, the model was shown to exhibit chaotic behaviour for some range of parameters. Unlike the previous model proposed by the third author [1], the current model is much simpler since it assumes that only one species grows following the Contois model. We conclude therefore that a variable yield coefficient coupled with the inhibition effects of the biomass for one species alone is enough to produce a wide range of complex behaviour including period doubling leading to chaos. It is hoped that the results of this paper can stimulate more interest in the study of the biomass-dependent Contois growth model. Some final observations should be made about the usefulness of this analysis. It would be useful to validate the proposed model and to confirm the existence of the complex behaviour. It would also be interesting to analyse the

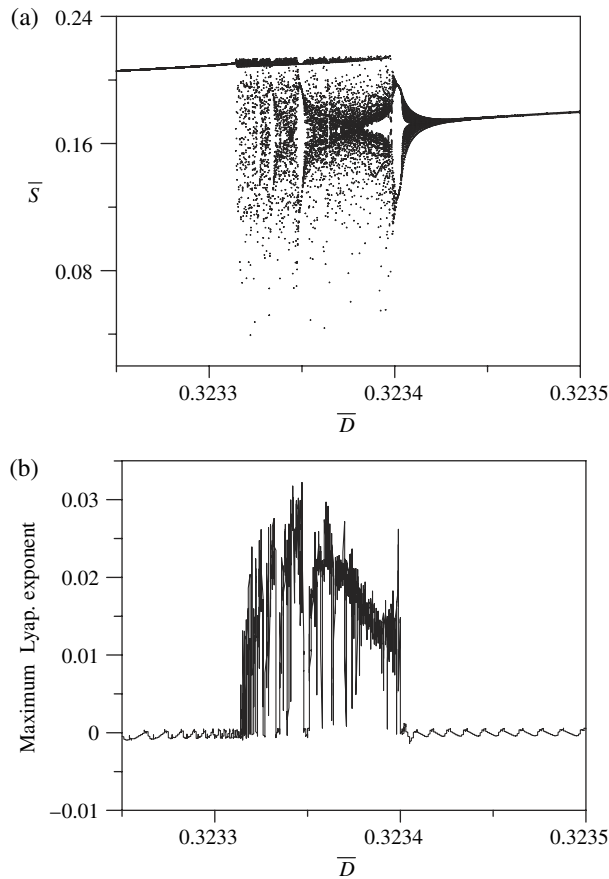


FIGURE 4. (a) Poincaré bifurcation diagram showing complex behaviour. (b) Corresponding maximum Lyapunov exponent spectrum.

performance of the biodegradation when the reactor is operated within the chaotic regime. Previous work [3] yielded conflicting results on the advantage of operating the reactor within a chaotic regime as opposed to a stable nontrivial steady state.

The results of this paper have shown that for a waste treatment bioreactor where the objective is for the biomass to consume the resource/substrate, the presence of chaotic behaviour is detrimental to the biodegradation process. Figure 2 showed that above a discrete value of the dilution rate (around HB1), the system goes from a predictably low level of substrate to a higher amplitude oscillation. Thus instead of having a predictable steady consumption of the substrate so that one can be relatively sure of when waste levels are low enough, the chaotic behaviour introduced a region of low substrate consumption. The paper has therefore shown that chaos can not only be easily predicted by a simple model, but also be detrimental to the performance of the wastewater treatment process.

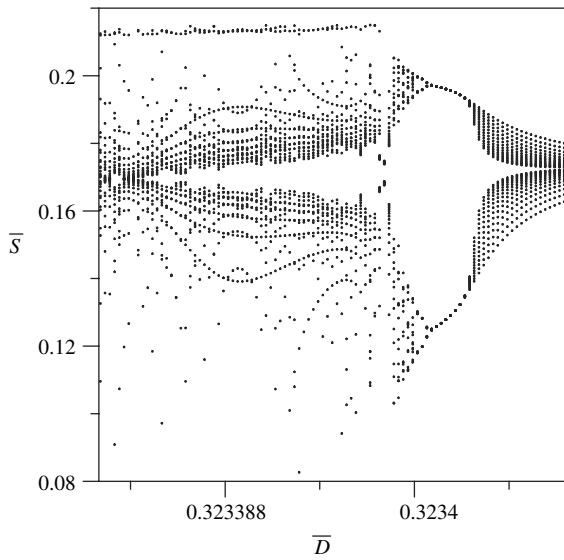


FIGURE 5. Enlargement of Figure 4(a) showing detailed behaviour.

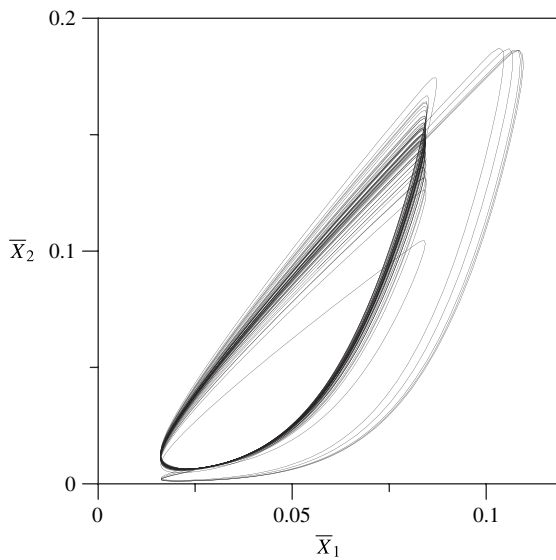


FIGURE 6. Phase plane showing chaotic behaviour for $\bar{D} = 0.32337$ in Figure 4.

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