IMPULSIVE DIFFERENTIAL EQUATIONS WITH APPLICATIONS TO SELF-CYCLING FERMENTATION

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To Shoshana Magnet,

and in memory of Kevin Abood

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Abstract

Self-cycling fermentation is a computer-aided process used for culturing microorganisms. Cells feeding off a growth-limiting nutrient in a tank grow and reproduce until a computer determines the time to end the cycle. At this point, a fraction of the volume of the tank is removed and replaced with an equal volume of fresh nutrient. The remaining cells then consume the fresh medium, grow, and reproduce. The process continues, releasing a fraction of the tank containing only a small amount of nutrient at the end of each cycle. Applications include sewage treatment, toxic waste cleanup, the production of antibiotics, and the examination of cell evolution. A basic model of growth will be formulated in terms of a system of impulsive differential equations. The predictions of the dynamics of the model will be discussed. The model will be refined to better describe the process for nutrient-minimizing applications such as sewage treatment. Criteria to ensure a positive, orbitally attractive periodic orbit with one impulse per period will be given. The predictions of the analysis will be supported by numerical simulations. The model will also be refined to include size-structured populations and a more accurate description of cell reproduction. The predictions of these refined models will be described. Competition of populations will also be considered and criteria for coexistence of more than one population on a single nonreproducing growth limiting nutrient will be given, and supported by numerical simulations.

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Outline

The aim of this thesis is to provide a comprehensive look at the process of self-cycling fermentation from the perspective of impulsive differential equations. The first two chapters are an extensive preamble, outlining the process as it appears in the literature and illustrating some potential problems with the oxygen-driven process, especially when the application is nutrient minimizing problems. We then reformulate the model in Chapter 3 to overcome some of the problems and prove the first set of main results, giving conditions that will ensure indefinite cycling in the form of an asymptotically stable periodic orbit with impulsive effect.

Chapter 4 further refines the model formulated in Chapter 3 to take the size of microorganisms into account and better describe reproduction. In Chapter 5, we look at competition in the self-cycling fermentation process. We prove further main results, combining impulsive Floquet theory and a persistence argument to prove that under certain conditions two species can coexist on a single nonreproducing nutrient.

Chapter summary

In Chapter 1, we introduce the self-cycling fermentation process. We discuss applications of the process to industry and its various uses and benefits. We also describe impulsive differential equations and list some of the aims for our analysis.

In Chapter 2, we analyse the oxygen-driven model for self-cycling fermentation. The amount of nutrient and biomass in each cycle is related by constants. We show that these constants converge to the input value of the nutrient. We illustrate a

potential problem with the model described in Wincure, Cooper and Rey [38]. It predicts that the amount of dissolved oxygen in the tank could theoretically become negative. Numerical simulations demonstrate further problems with this model: the process may never begin to cycle or the process may cycle a finite number of times, but not thereafter. We provide conditions on the input data and known constants that will guarantee that the system will run indefinitely. We then prove that if a periodic orbit exists, it will be stable.

In Chapter 3, we refine the model to better reflect the situations where the goal is to minimize nutrient. We include the death rate of the population that consumes the nutrient, and consider a more general uptake function. The nutrient-driven process relies on a predetermined level of nutrient, called the tolerance. This level will ensure that the amount of nutrient released into the environment will always be suitably small. We provide conditions for the existence of a positive periodic orbit with one impulse per period and state the initial conditions necessary to converge to this orbit. The convergence is shown to be monotonic, in terms of the concentration of the microorganisms at the end of each cycle. We also discuss the cycle times of solutions that converge to the periodic orbit. Numerical simulations demonstrate the various cases for the initial conditions and the monotonicity of the convergence. We discuss the impact this refined model has in practice and discuss appropriate choices for the tolerance.

In Chapter 4 we refine the model again to consider size-structure. Based on simple assumptions, we develop a model involving partial derivatives and then reduce this model to a system of ordinary differential equations with impulsive effect. We use impulsive theory to show that the model can be reduced to a two dimensional system for which the theory in Chapter 3 applies. Next we show that the average cell sizes and the standard deviation both approach a constant value, implying that the number of unnaturally large cells is negligible. We then consider a size-structured model for a population that reproduces by unequal fission. We reduce this model to a model for which the results of Chapter 3 again apply. This model is a more realistic description

of cell reproduction, where the ratio of mother to daughter size at fission is considered to be a random variable.

In Chapter 5, we turn to two-species competition in the nutrient-driven model. We consider the Monod form of the function, the one most often used in the literature. We ignore the death rate, to simplify the calculations. We prove that coexistence is not possible if the uptake function of one species dominates the other. We then use the impulsive Floquet theory to give conditions ensuring that the nontrivial Floquet multipliers of each species are greater than one. By letting certain parameters in one uptake function vary over all possible positive values, we find a central region of coexistence in parameter space. Numerical simulations demonstrate that we do in fact have coexistence of two competitors, as a stable positive periodic orbit. We then use a suitable map and apply the analogue of the Butler-McGehee theorem for maps to prove that we have persistence in the regions where the nontrivial Floquet multipliers are greater than one. Numerical simulations demonstrates that coexistence of three populations is also possible.

Appendix A contains background material on systems with impulsive effect. We discuss impulsive semidynamical systems, define impulsive trajectories and periodicity and give simple examples. We discuss existence, uniqueness and continuability of impulsive solutions, redefine stability notions for impulsive differential equations and discuss autonomous systems.

Appendix B contains the Floquet theory for impulsive differential equations. We define the Floquet multipliers and discuss impulsive Floquet theory. We provide the calculation of the nontrivial multiplier of a periodic orbit in a two dimensional system. An analogue of the Poincaré criterion provides a useful result for determining the stability of periodic orbits in two dimensions.

Chapter 1

An Introduction to Self-Cycling Fermentation

1.1 Introduction

> *The microbial quality of drinking water is the most important aspect of drinking water quality because of its association with waterborne diseases. [...] The introduction of a well managed water treatment system with effective chemically-assisted filtration and disinfection, an adequately maintained chlorine residual in the distribution system and the implementation of bacteriological surveillance programs to ensure the delivery of safe drinking water are measures that have demonstrated their effectiveness in eliminating water-related illnesses.*
>
> - Ontario Drinking Water Standards [25], page 12.

The issues of sewage treatment and toxic waste cleanup are important in today's industrialized society. Many approaches have been taken to deal with these and other, similar, problems. Continuous and batch fermentation are two processes that involve bacteria consuming the waste to produce a cleaner environment. In this thesis

we will be concentrating on a relatively new approach to such problems, known as self-cycling fermentation (SCF).

Although the SCF process has been used with considerable success since its development in 1990 (see Sheppard and Cooper, [30]), very little analysis of the model has been carried out. It is important to analyse the underlying structure in order to understand both the benefits of the process and also the drawbacks. It is the goal of this thesis to provide a comprehensive analysis of the model as it has been used and also suggest some potential improvements that can be made.

The process of self-cycling fermentation can be described as follows. A culture in a tank feeds off a limiting nutrient. It is assumed that the tank is well-stirred, so cells and nutrient are distributed uniformly throughout the tank. Oxygen diffuses into the tank from the air above the surface of the tank. The cells use this dissolved oxygen to process the nutrient in order to grow and reproduce. Cell biomass is measured, accounting for cell size and population. When the nutrient is almost entirely consumed, the cells decrease their use of oxygen. There is a correspondingly sharp increase in the dissolved oxygen level in the tank.

A probe inserted in the tank measures the dissolved oxygen level and relays the information back to a computer. The computer monitors the situation until it detects a minimum in dissolved oxygen concentration. A set fraction of the volume of the tank, usually half, is then removed (containing cells, nutrient and oxygen) and replaced by an equal volume of fresh medium (containing nutrient and oxygen, but not cells). The time of this action is referred to variously as the time of impulsive effect, the harvesting time, the moment of impulse or the end of cycle time. The time between impulsive effects is referred to as the cycle time.

Once the fresh medium has been added to the tank, the culture is again left undisturbed until the computer next detects a dissolved oxygen minimum. The same fraction of the contents is again removed and then replaced with an equal volume of fresh medium. This process continues, hopefully indefinitely. See Brown and Cooper [7] or Sheppard and Cooper [30] for more information.

In practice, of course, the time taken to empty and refill the tank is not zero, but compared to the cycle time, it is quite short. It can thus be useful to assume that this process occurs instantly, although it should be noted that this means there is at least a slight discrepancy between theory and practice from the beginning.

The main advantage of the SCF process over other culturing methods is the fact that the cycle time is incorporated in the process as a dependent variable (depending on the cellular metabolism). If the requirements of the cells change over successive generations then the system automatically responds. With no specific period of nutrient dosing imposed on the cells, there is also no prior knowledge of the specific growth rate of the cells required. Another advantage is the production of two identical portions of synchronized cells at the end of each cycle.

A potential disadvantage is that we have no way to guarantee the indefinite cycling of the system. We cannot guarantee that the system will necessarily reach a dissolved oxygen minimum in the first place, nor can we guarantee that it will continue to reach subsequent dissolved oxygen minima indefinitely.

1.2 Applications to industry

Although Self-Cycling Fermentation is a relatively new technique, it has already been applied in various situations. One practical example is that of sewage treatment, as described in Sarkis and Cooper [28]. In this case, the nutrient is effluent and the organism is one that feeds on effluent and thus purifies the water. The goal here is to have as little nutrient remaining as possible at the end of the cycle and in practice the SCF process leaves very little.

The uses of self-cycling fermentation have been quite versatile. In Wentworth and Cooper [36], the aim is to cultivate a synchronous population of a strain of *Candida lipolytica* cells. The harvested volume is then used to produce citric acid in a second stage reactor. It is also possible to use the synchronization of cell populations to observe developments at a particular stage in the growth cycle of an organism, as in

Zenaitis and Cooper [40].

In Hughes and Cooper [18], the SCF process is used for the removal of pollutants. There are aromatic organic compounds that are toxic at low concentrations and resistant to degradation in the environment. Maximal elimination of these compounds is vitally important, since at even very small concentrations they can actually be more toxic than at the original levels. In Brown and Cooper [8], the SCF process is used to eliminate industrial pollutants, such as insoluble carbon.

Because the cycle time is a dependent variable, the SCF also allows observation of the stability rate of various organisms consuming nutrients. In Sheppard and Cooper [30], it was observed that *Pseudomonas putida* consumed sodium benzoate in a significantly shorter time period than *Pseudomonas fluorescens.* In Wentworth and Cooper [36], *Candida lipolytica* consumed ammonium sulphate in the SCF process and the production rates were compared to the rates from other processes in the literature. Their observations demonstrated a full order of magnitude improvement in the rate of biomass production using the SCF process.

Self-Cycling Fermentation can also be used to produce antibiotics. In Zenaitis and Cooper [40], the SCF process was used for both a first and second stage reaction. *Streptomyces aurofaciens* was grown and harvested in a self-cycling fermenter using sucrose as a nutrient. As a result of stress placed upon the microorganism, it produced tetrocyclines and its derivatives.

The production of antibiotics is quite desirable and the SCF process is a considerable improvement over other methods in terms of stabilization. However, as a result of harvesting, half the amount of antibiotic remains in the tank at the beginning of each cycle. Since antibiotics can act as an inhibitor to the growth of the microorganisms which produce them, this is a problem. To overcome this problem, a two-stage method can be used to obtain the antibiotic products exclusively (or at least mostly) in the second tank. In this case, while the SCF process is not used in the second stage, it still plays a significant part in the rate of stabilization of the growth of the microorganisms.

In Pinchuck, Brown, Hughes and Cooper [26], the SCF process lends itself to testing biological models through a genetic algorithm. The SCF process provided sufficient richness with which to generate data required for the modelling purposes.

It can thus be seen that the applications of self-cycling fermentation are quite varied. Whether the goal is optimizing the cell count or minimizing the nutrient, the same process appears to work quite well.

1.3 Impulsive differential equations

Impulsive Differential Equations are usually given in the form

$$\begin{aligned} \frac{dy}{dt} &= f(t,y) \qquad & \phi(t,y) &\neq c \\ \Delta y &= I(t,y) \qquad & \phi(t,y) &= c \end{aligned}$$

where $\Delta y \equiv y^+ - y$ describes the (usually discontinuous) change in state when the criterion $\phi(t,y) = c$ is fulfilled. Here y^+ is the value immediately after the impulsive effect; in general it is not equal to y. We assume continuity from the left.

The motion is continuous for $\phi(t,y) \neq c$ and there are a finite or infinite number of instantaneous changes in state occurring when $\phi(t,y) = c$. It is also possible to consider partial differential equations with impulsive effect.

The theory of impulsive differential equations is relatively new. The main results are found in Lakshmikantham, Bainov and Simeonov [20] and Bainov and Simeonov [2], [3]. The theory has found applications in many areas where evolutionary processes undergo rapid changes at certain times of their development. In the mathematical simulation of such processes, the duration of this rapid change is ignored and instead it is assumed that the process changes its state instantaneously. The theory has been applied to problems in mechanics, radio engineering, biotechnology and control theory.

Since the self-cycling fermentation process undergoes a rapid change when the dissolved oxygen reaches a minimum, it can be modelled by a series of impulsive

differential equations, which describe both the intracycle evolutionary process and the impulsive effect taking the end of one cycle to the beginning of the next.

Most of the theory of impulsive differential equations has been carried out for non-autonomous equations, where the times of the impulsive effect are fixed. This makes the analysis relatively straightforward, although it should be noted that the detail is still quite complicated. The equations modelling self-cycling fermentation are autonomous, with variable (and non-explicit) moments of impulse. There is some material in Lakshmikantham, Bainov and Simeonov [20] and Bainov and Simeonov [2], [3] that deals with these types of equations, but the majority deals with simpler systems.

Further details can be found in Appendices A and B.

1.4 Aims

Our aim in this thesis is to investigate self-cycling fermentation from a mathematical viewpoint. The relatively new theory of impulsive differential equations will be applied to the system. The fact that solutions of impulsive differential equations are non-continuous trajectories means that we have to redefine our notions of stability. We can apply the Floquet theory for impulsive differential equations to low-dimensional systems to determine the orbital stability of (impulsive) periodic orbits.

We shall examine some of the problems inherent in the oxygen-driven model and postulate some improvements. Some of these improvements have been suggested in Sheppard and Cooper [30]. It can be demonstrated that in the oxygen-driven model, the impulsive effect may not be reached, or may only be reached a finite number of times.

Our aim is to refine the model so that the system cycles indefinitely. We intend to provide conditions that will determine in advance whether a stable periodic orbit can be reached for a given species. Furthermore, we wish to guarantee that the amount of waste product released into the environment by the self-cycling fermentation process

is never greater than the maximal allowable concentration set by the Ontario Ministry of the Environment.

We also examine the nutrient-driven system as a size-structured model, since it is possible that some cells may grow quite large. We will also use a model for self-cycling fermentation, where the nature of reproduction is taken into account.

Finally, we shall look at competition in the nutrient-driven self-cycling fermentation process. We will investigate the question of whether more than one species can coexist in the SCF process and whether we can predict this in advance.

Chapter 2

The Oxygen-Driven Self-Cycling Fermentation Process

2.1 Introduction

In this chapter we examine the model of self-cycling fermentation used in Wincure, Cooper and Rey [38], which uses a dissolved oxygen minimum to end each cycle. We shall demonstrate that there are potential problems with this model. This model is not suitable for describing a biological process and there are further problems with the use of oxygen to trigger the impulsive effect. The process may cycle indefinitely (the desirable outcome), cycle a finite number of times or not at all. Furthermore, the oxygen-driven process may not be the best method for nutrient minimizing problems such as sewage treatment, since we cannot guarantee that the output will be within acceptable environmental limits.

One solution to the problem is to find conditions on the input data so we can predict whether the system will cycle indefinitely. In the case that a periodic orbit does exist, we will show that it is always stable.

2.2 The oxygen-driven model

The equations for the self-cycling fermentation process, as described in Wincure, Cooper and Rey [38], but given here as impulsive differential equations, are

$$\begin{aligned}
\frac{ds}{dt} &= -\frac{\mu x s}{Y(K_s + s)} && [O_2] \neq [O_2]_{\min} \\
\frac{dx}{dt} &= \frac{\mu x s}{K_s + s} && [O_2] \neq [O_2]_{\min} \\
\frac{d[O_2]}{dt} &= -g(s, x, [O_2]) + k\left([O_2]^* - [O_2]\right) && [O_2] \neq [O_2]_{\min} \\
\Delta s &= -rs + rs^i && [O_2] = [O_2]_{\min} \\
\Delta x &= -rx && [O_2] = [O_2]_{\min} \\
\Delta[O_2] &= -r[O_2] + r[O_2]^i && [O_2] = [O_2]_{\min},
\end{aligned} \tag{2.2.1}$$

where

- s is the limiting substrate concentration (g/L)
- x is the biomass concentration (g/L)
- $[O_2]$ is the dissolved oxygen concentration (g/L)
- t is the time (min)
- μ is the maximum specific growth rate ($\min^{-1}$)
- K_s is the half saturation constant (g/L)
- $[O_2]_{\min}$ is the dissolved oxygen concentration at dissolved oxygen minimum (g/L)
- Y is the cell yield (g biomass/g limiting substrate)
- $g(s, x, [O_2])$ is the oxygen transfer function. We assume

i. $g : \mathbb{R}^3 \to \mathbb{R}$ is continuously differentiable,

ii. $g(0, x, [O_2]) = g(s, 0, [O_2]) = g(s, x, 0) = 0$,

iii. g is increasing in s, x and $[O_2]$,

iv. $g(s, \alpha x, [O_2]) = \alpha g(s, x, [O_2])$ for any $\alpha \in \mathbb{R}$,

v. g is bounded.

The specific function chosen in Wincure, Rey and Cooper is

$$g(s, x, [O_2]) = \frac{Y_0 \mu x s}{K_s + s},$$

where Y_0 is the oxygen consumed per limiting substrate consumed (g[O_2]/g limiting substrate). This function does not depend on [O_2], and hence does not satisfy criteria (ii). See section 2.5 for more discussion.

- k is the liquid-side dissolved oxygen mass transfer coefficient (min^{-1})
- $[O_2]^*$ is the dissolved oxygen concentration at saturation (g/L)
- r is the emptying/refilling fraction; r can be any number strictly between zero and one
- s^i is the nutrient input concentration at the beginning of each cycle (g/L)
- $[O_2]^i$ is the dissolved oxygen input concentration at the beginning of each cycle (g/L)

The conditions for a dissolved-oxygen minimum are

$$\begin{aligned} \frac{d[O_2]}{dt} &= 0 \qquad & [O_2] &= [O_2]_{\text{min}} \\ \frac{d^2[O_2]}{dt^2} &> 0 \qquad & [O_2] &= [O_2]_{\text{min}}. \end{aligned} \tag{2.2.2}$$

The dissolved oxygen minimum is assumed to be a true minimum due to the sharp increase in oxygen content near the exhaustion of the limiting nutrient.

Let $x = \tilde{x}\hat{x}$ and $s = \tilde{s}\hat{s}$. In (2.2.1), we obtain

$$\begin{aligned}
\frac{d(\tilde{s}\hat{s})}{dt} &= -\frac{1}{Y}\frac{\mu\tilde{x}\hat{x}\tilde{s}\hat{s}}{K_s + \tilde{s}\hat{s}} & [O_2] &\neq [O_2]_{\min} \\
\hat{s}\frac{d\tilde{s}}{dt} &= -\frac{1}{Y}\frac{\mu\tilde{x}\hat{x}\tilde{s}\hat{s}}{K_s + \tilde{s}\hat{s}} & [O_2] &\neq [O_2]_{\min} \\
\frac{d\tilde{s}}{dt} &= -\frac{\hat{x}}{\hat{s}Y}\frac{\mu\tilde{x}\tilde{s}}{K_s/\hat{s} + \tilde{s}} & [O_2] &\neq [O_2]_{\min} \\
\Delta(\tilde{s}\hat{s}) &= -r\tilde{s}\hat{s} + r\tilde{s}^i\hat{s}^i & [O_2] &= [O_2]_{\min} \\
\hat{s}\Delta\tilde{s} &= -r\hat{s}\tilde{s} + r\tilde{s}^i\hat{s}^i & [O_2] &= [O_2]_{\min} \\
\Delta\tilde{s} &= -r\tilde{s} + r\tilde{s}^i & [O_2] &= [O_2]_{\min}
\end{aligned}$$

and

$$\begin{aligned}
\hat{x}\frac{d\tilde{x}}{dt} &= \hat{x}\frac{\mu\tilde{x}\tilde{s}\hat{s}}{K_s + \tilde{s}\hat{s}} & [O_2] &\neq [O_2]_{\min} \\
\frac{d\tilde{x}}{dt} &= \frac{\mu\tilde{x}\tilde{s}}{K_s/\hat{s} + \tilde{s}} & [O_2] &\neq [O_2]_{\min} \\
\Delta(\tilde{x}\hat{x}) &= -r\tilde{x}\hat{x} & [O_2] &= [O_2]_{\min} \\
\hat{x}\Delta\tilde{x} &= -r\hat{x}\tilde{x} & [O_2] &= [O_2]_{\min} \\
\Delta\tilde{x} &= -r\tilde{x} & [O_2] &= [O_2]_{\min}.
\end{aligned}$$

Let us choose $\hat{s} = K_s$, $\hat{x} = K_sY$ and rescale g as appropriate. Note that we have rescaled s^i, Then, removing the tildes for notational convenience, we obtain the dimensionless form of the equations

$$
\begin{aligned}
\frac{ds}{dt} &= -\frac{\mu x s}{1+s} && [O_2] \neq [O_2]_{\min} \\
\frac{dx}{dt} &= \frac{\mu x s}{1+s} && [O_2] \neq [O_2]_{\min} \\
\frac{d[O_2]}{dt} &= -g(s,x,[O_2]) + k\left([O_2]^* - [O_2]\right) && [O_2] \neq [O_2]_{\min} \\
\Delta s &= -rs + rs^i && [O_2] = [O_2]_{\min} \\
\Delta x &= -rx && [O_2] = [O_2]_{\min} \\
\Delta[O_2] &= -r[O_2] + r[O_2]^i && [O_2] = [O_2]_{\min}.
\end{aligned} \tag{2.2.3}
$$

2.3 The non-impulsive system

Before looking at the impulsive system, we shall analyse the dimensionless system of ODEs

$$\frac{ds}{dt} = -\frac{\mu x s}{1+s} \tag{2.3.4}$$

$$\frac{dx}{dt} = \frac{\mu x s}{1+s} \tag{2.3.5}$$

$$\frac{d[O_2]}{dt} = -g(s,x,[O_2]) + k\left([O_2]^* - [O_2]\right), \tag{2.3.6}$$

with initial conditions $s(0) \geq 0$, $x(0) \geq 0$ and $0 \leq [O_2](0) \leq [O_2]^*$.

Notice that

$$s(t) + x(t) = c = s(0) + x(0) \tag{2.3.7}$$

for all $t \geq 0$. Solutions remain in the region $s(t) \geq 0$, $x(t) \geq 0$, $0 \leq [O_2] \leq [O_2]^*$ for all t.

The critical points are

$$(s, x, [O_2]) = (s, 0, [O_2]^*)$$

and

$$(s, x, [O_2]) = (0, x, [O_2]^*).$$

Using (2.3.7) to substitute for x in equation (2.3.4) gives

$$\frac{ds}{dt} = -\frac{\mu s}{1+s}(c-s),$$

a separable first order ODE. Solving, we obtain

$$e^{-\mu(t-t_0)} = \left(\frac{s(t)}{s(0)}\right)^{1/c}\left(\frac{c-s(0)}{c-s(t)}\right)^{1+1/c}. \tag{2.3.8}$$

Using (2.3.7) again, we have

$$\lim_{t\to\infty}\left(\frac{s(t)}{s(0)}\right)^{1/c}\left(\frac{x(0)}{x(t)}\right)^{1+1/c} = 0.$$

Since $\frac{dx}{dt} > 0$, the biomass is increasing, so $x(t)$ remains positive for any solution with initial conditions in the interior of the first octant. Furthermore, $x(t) \leq x(0) + s(0)$, so $x(t)$ is does not approach infinity. Thus $s(t) \to 0$ as $t \to \infty$, for any solution with positive initial conditions. Since $s(t)$ approaches zero and $g(0, x, [O_2]) = 0$, it follows that $[O_2](t)$ approaches saturation.

2.4 Convergence of the constants

Although the dynamics of the system of ordinary differential equations are relatively straightforward, the system with impulsive effect becomes more complicated. Throughout, we shall assume that all functions are continuous from the left at the impulse points, so $x(t_k^-) \equiv x(t_k)$, where t_k is the time of impulse in the kth cycle.

We shall denote the impulse points with a subscript for notational convenience. Thus, x_1 is the first impulse point, x_2 the next and so forth. This is done with the understanding that these points of impulse are occurring at times of impulse t_k. That is, $x_n = x(t_n^-)$ and $x_n^+ = x(t_n^+)$. The only exception to this is the initial conditions, where we shall have $x(0) = x(0^+)$, to ensure that there is no impulsive effect at the initial point, in accordance with impulsive theory.

Our analysis in the remainder of this chapter will involve the dimensionless system of impulsive differential equations given by (2.2.3).

When considering the impulsive effect, the practical upshot of this is that each cycle begins anew, with the same differential equations but a 'new' set of initial conditions (which are defined in relation to the set of final conditions for the previous cycle). This means that the relationship

$$x(t) + s(t) \;=\; c$$

is still true, except that the value of the constant will be different for each cycle. In particular, for all positive integers n,

$$x(t) + s(t) \;=\; x_n + s_n \;\equiv\; c_n \qquad\qquad t_{n-1} \;<\; t \;\leq\; t_n.$$

For the moment we shall assume that the impulsive effect always occurs and that there are an infinite number of moments of impulse. If the impulsive effect does not occur, or there are only a finite number of impulse times, then the nutrient runs down, as we have seen and the system halts (and in practice, the death rate would subsequently become non-negligible and the cells would die off). Some conditions are provided at the end of this chapter that guarantee indefinite cycling.

Since $x_n^+ = (1-r)x_n$ and $s_n^+ = (1-r)s_n + rs^i$, we have the recurrence relation

$$c_{n+1} \;=\; (1-r)c_n + rs^i$$

which has the solution

$$c_n \;=\; (1-r)^{n-1}c_1 + rs^i\left(1 + (1-r) + \cdots + (1-r)^{n-2}\right)$$

and thus, since $0 < r < 1$,

$$\lim_{n\to\infty} c_n = s^i,$$

which is independent of the emptying/refilling fraction r.

Furthermore,

$$\begin{aligned} c_{n+1} - c_n &= (1-r)c_n + rs^i - (1-r)c_{n-1} - rs^i \\ &= (1-r)(c_n - c_{n-1}) \\ &\vdots \\ &= (1-r)^{n-1}(c_2 - c_1) \\ &= (1-r)^{n-1}\left((1-r)c_1 + rs^i - c_1\right) \\ &= r(1-r)^{n-1}\left(s^i - c_1\right) \end{aligned}$$

and hence the sequence $\{c_n\}$ is increasing if $c_1 < s^i$ and decreasing if $c_1 > s^i$. We thus have monotone convergence of the constants.

2.5 Potential problems and numerical simulations

There are some serious problems that can arise from the oxygen-driven model for self-cycling fermentation. First, the function g given in Wincure, Cooper and Rey [38] by

$$g(s, x, [O_2]) = \frac{Y_0 \mu x s}{Y(K_s + s)} \tag{2.5.9}$$

is inappropriate for describing behaviour in the mathematical model. With this choice for g, model (2.2.3) predicts that the dissolved oxygen could become negative. For example, if $[O_2](0) = 0$ and $x(0)$ and $s(0)$ are sufficiently large, the model predicts that the dissolved oxygen level decreases and becomes negative. This is obviously unrealistic.

To overcome this problem, in the remainder of this section we assume that

$$g(s, x, [O_2]) = \frac{Y_0 \mu x s [O_2]}{Y(K_s + s)(a + [O_2])}.$$

With a suitably small choice of a, we have $\frac{[O_2]}{a+[O_2]} \approx 1$, except when $[O_2]$ is near zero. This choice of g approximates the function used in Wincure, Cooper and Rey

[38], but satisfies $g(s, x, 0) = 0$ and does not allow negative values of any variables. Other examples of oxygen transfer functions can be found in Grady and Lim [16] and Sundstrom and Klei [34].

Next we illustrate certain features of model (2.2.1) using numerical simulations. All simulations were run using ODE45 in MATLAB, with adjustments to incorporate the impulsive effect. The constants used in all simulations were taken from actual data used in Wincure, Cooper and Rey [38]. All simulations were run using the original (unscaled) equations (2.2.1).

Figure 2.1 shows a set of initial conditions and input data where the trajectory of (2.3.4)-(2.3.6) does not reach a dissolved oxygen minimum. The initial data used is $s(0) = 0.015$, $x(0) = 0.004$, $[O_2](0) = 0.0035$, with constants $r = \frac{1}{2}$, $[O_2]^* = 0.0078$, $K_s = 0.007$, $\mu = 0.01$, $Y = 0.73$, $Y_0 = 0.63$, $a = 0.00001$ and $k = 1.2$.

Figure 2.2 shows a trajectory which reaches a minimum once, but thereafter does not reach a minimum again. The initial data used is $s(0) = 0.2$, $x(0) = 0.03$, $[O_2](0) = 0.0055$, with constants $r = \frac{1}{2}$, $[O_2]^* = 0.0078$, $K_s = 0.007$, $\mu = 0.01$, $Y = 0.73$, $Y_0 = 0.63$, $a = 0.00001$, $k = 1.2$, $s^i = 0.04$ and $[O_2]^i = 0.004$.

Figure 2.3 shows an example of initial conditions and input data where we have a stable periodic orbit, with indefinite cycling. This is the situation most desirable for the SCF process. The initial data used is $s(0) = 0.35$, $x(0) = 0.95$, $[O_2](0) = 0.0075$, with constants $r = \frac{1}{2}$, $[O_2]^* = 0.0078$, $K_s = 0.007$, $\mu = 0.01$, $Y = 0.73$, $Y_0 = 0.63$, $a = 0.00001$, $k = 1.2$, $s^i = 0.8$ and $[O_2]^i = 0.0066$.

Simulations were also run using the oxygen transfer function (2.5.9) and similar behaviour was exhibited, as well as negative values of dissolved oxygen.

The fact that solutions may not undergo impulsive effect or may undergo impulsive effect a finite number of times raises questions about the practical application of the oxygen-driven SCF process. Conditions will be provided to ensure that these situations cannot occur, but the restrictions may be difficult to implement in practice, or may be violated following an unexpected disruption. Another approach for dealing with these problems will be given in the next chapter.

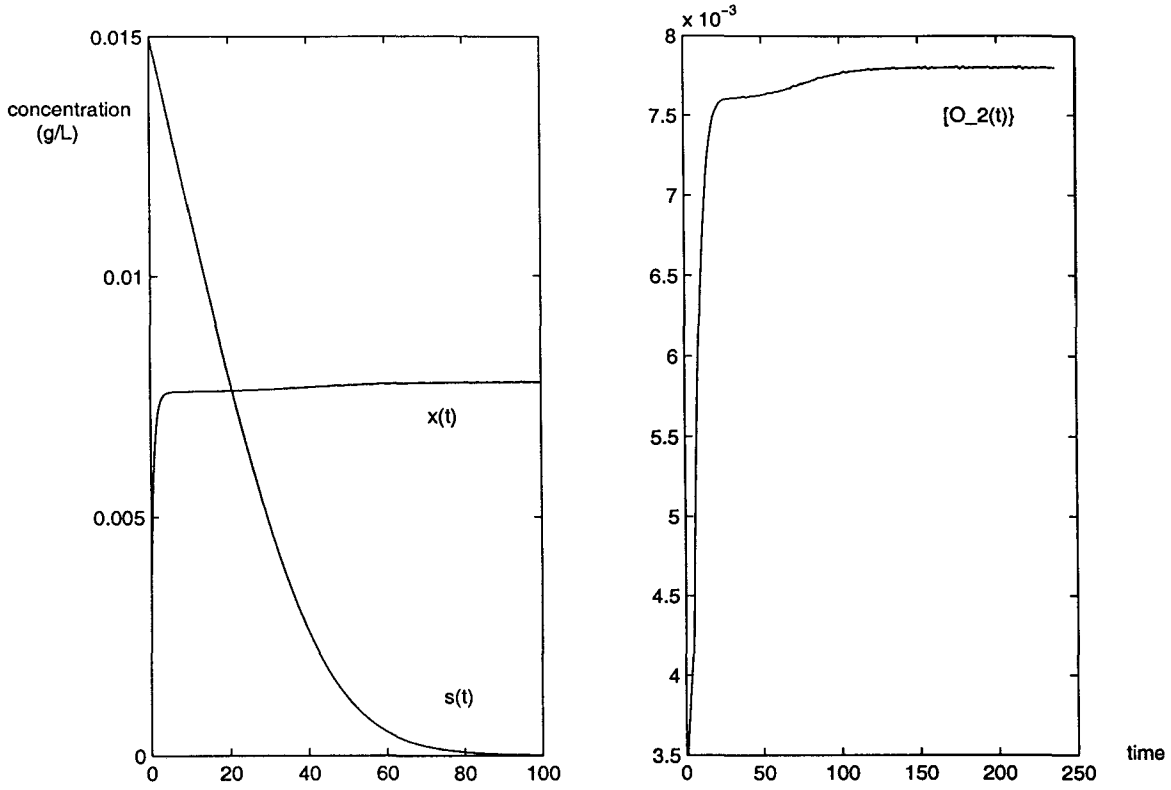

Figure 2.1: An example of initial conditions where the system does not undergo cycling. The oxygen is increasing to saturation, the nutrient approaches exhaustion and the microorganisms approach a constant value. We zoom in on the oxygen behaviour in the second part.

2.6 Conditions to guarantee indefinite cycling

In the previous section we explained one of the potential drawbacks of the oxygen-driven model of the SCF process. It is not clear how to predict that a given set of initial conditions will reach a dissolved oxygen minimum. Furthermore, even if such a minimum is reached, this does not necessarily guarantee that the next cycle will also reach a dissolved oxygen minimum. We would like to start with initial conditions so that a dissolved oxygen minimum is reached in finite time and use input conditions so that every subsequent cycle will also reach a dissolved oxygen minimum. We refer to such a scenario as *indefinite cycling*. This is still not an ideal solution, since in

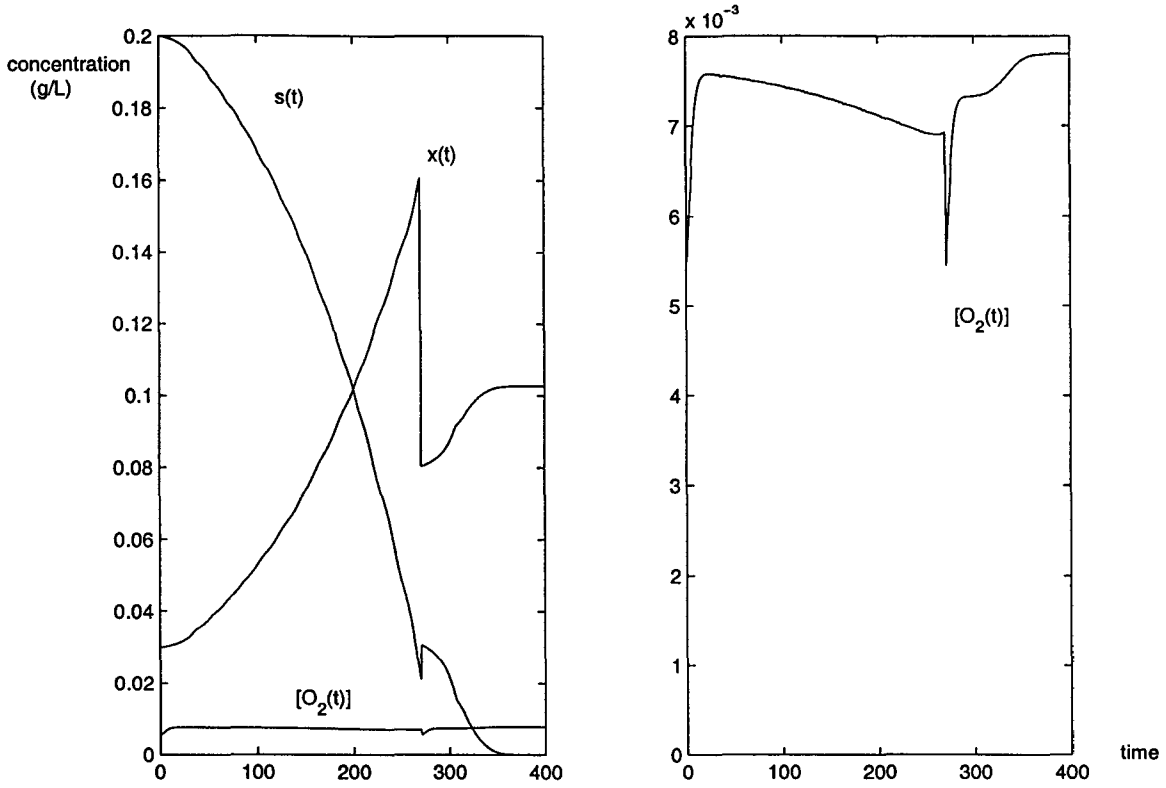

Figure 2.2: An example of initial conditions and input data where the system undergoes cycling only once. The oxygen reaches a minimum, so the system undergoes cycling, but trajectories are transported to a location where the oxygen is increasing to saturation, so there is no further cycling. We zoom in on the oxygen behaviour in the second part.

practice there may be disturbances in the system which could cause the process to halt.

It is somewhat distressing to realize that this question has not been addressed thus far. Self-cycling fermentation relies on computer monitoring and does not require the presence of an operator to oversee the process. If there is a real chance that the system could halt, then this is a cause for concern. It would be highly desirable to know in advance that a given set of initial and input conditions will guarantee indefinite cycling for the system.

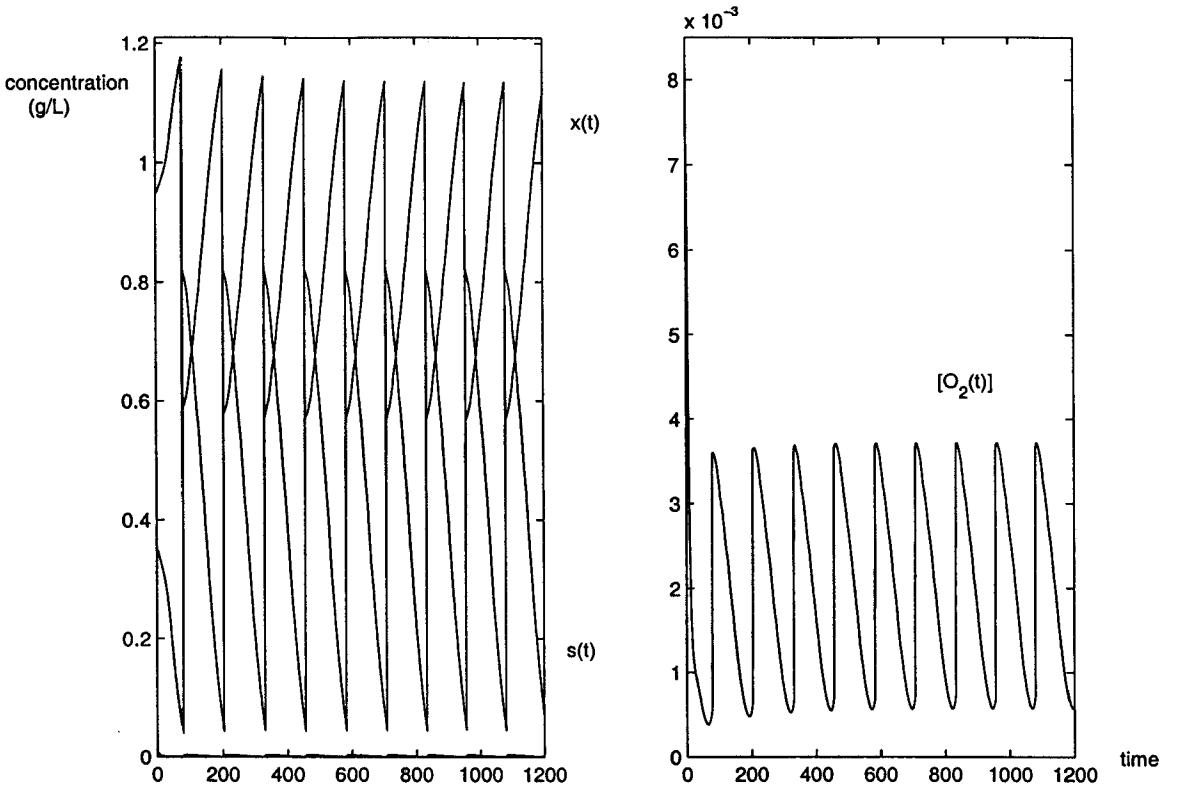

Figure 2.3: The system undergoes indefinite cycling.We have a stable periodic orbit, where the cycle time corresponds to the minimum doubling time of the microorganisms. This is the most desirable outcome of the SCF process, since a dissolved oxygen minimum is reached every time. The corresponding value of the nutrient at the end of each cycle is low and the biomass is quite high, so the output of every cycle is favourable. We zoom in on the oxygen behaviour in the second part.

A solution to the problem of not reaching a dissolved oxygen minimum is mentioned in Sheppard and Cooper [30]. We can set a predetermined period as the maximal allowable cycle time, meaning that if the system has not undergone impulsive effect by the end of this period, then we trigger the impulsive effect artificially.

The advantage of having a maximal allowable cycle time is that we will have indefinite cycling. The disadvantage is that we have lost the cycle time as a dependent variable. Determining an appropriate maximal period in advance requires knowledge of the characteristics of the species; such foreknowledge is ordinarily unnecessary in the SCF process.

Another way to ensure that we continue to reach a minimum in subsequent cycles, is to adjust the input to guarantee that after every impulse, solutions are transported to a suitable location from where they will be guaranteed to reach a minimum again.

Consider the oxygen content of the input. Since the fresh medium has presumably been prepared for some time, it is not unreasonable to suppose that the oxygen concentration of the input volume might be close to saturation. In fact, in Wincure, Cooper and Rey [38] the authors specifically make this assumption in their experiments.

That is,

$$[O_2]^i = [O_2]^*, \tag{2.6.10}$$

so

$$[O_2]_n^+ = (1-r)[O_2]_n + r[O_2]^*.$$

We similarly assume that the oxygen is at saturation at the start of the process. That is,

$$[O_2](0) = [O_2]^*. \tag{2.6.11}$$

This is not an unrealistic assumption, since it would be relatively easy to prepare the tank in advance and let the oxygen approach saturation before any microorganisms are introduced. If $x(0)$ and $s(0)$ are positive, then

$$\begin{aligned}\frac{d[O_2]}{dt}(s(0),x(0),[O_2](0)) &= k([O_2]^* - [O_2](0)) - g(s(0),x(0),[O_2](0)) \\ &= -g(s(0),x(0),[O_2]^*).\end{aligned}$$

Since g is increasing in $[O_2]$ and $g(s,x,0) = 0$, it follows that $g(s,x,[O_2]^*) \neq 0$. Therefore, we have

$$\frac{d[O_2]}{dt}(s(0),x(0),[O_2](0)) < 0.$$

Since the dissolved oxygen approaches saturation, we must reach a minimum in finite time.

Assume that a dissolved oxygen minimum is reached at least once and suppose condition (2.6.11) holds. Let $(s_n, x_n, [O_2]_n)$ be a point of impulse, with image $(s_n^+, x_n^+, [O_2]_n^+)$. We have

$$\begin{aligned} [O_2]^* - [O_2]_n^+ &= [O_2]^* - ((1-r)[O_2]_n + r[O_2]^*) \\ &= (1-r)\left([O_2]^* - [O_2]_n\right). \end{aligned}$$

Furthermore, since $\frac{d[O_2]}{dt} = 0$ at the minimum, we have

$$k\left([O_2]^* - [O_2]_n\right) = g(s_n, x_n, [O_2]_n).$$

Thus,

$$\begin{aligned} &\frac{d[O_2]}{dt}(s_n^+, x_n^+, [O_2]_n^+) = k\left([O_2]^* - [O_2]_n^+\right) - g(s_n^+, x_n^+, [O_2]_n^+) \\ &= (1-r)k\left([O_2]^* - [O_2]_n\right) - g((1-r)s_n + rs^i, (1-r)x_n, (1-r)[O_2]_n + r[O_2]^*) \\ &= (1-r)g(s_n, x_n, [O_2]_n) - (1-r)g((1-r)s_n + rs^i, x_n, (1-r)[O_2]_n + r[O_2]^*), \end{aligned}$$

since g is assumed linear in x.

Now, since $[O_2]_n \leq [O_2]^*$, we have

$$\begin{aligned} [O_2]_n &\leq [O_2]_n + r([O_2]^* - [O_2]_n) \\ &= (1-r)[O_2]_n + r[O_2]^*. \end{aligned}$$

If we have the initial condition

$$s(0) + x(0) < s^i, \tag{2.6.12}$$

then the constants c_n strictly increase to s^i, as shown in section 2.4. Hence, $s_n < c_n < s^i$. Thus

$$\begin{aligned} s_n &< s_n + r(s^i - s_n) \\ &= (1-r)s_n + rs^i. \end{aligned}$$

Therefore, since g is increasing in s and $[O_2]$,

$$g(s_n, x_n, [O_2]_n) < g((1-r)s_n + rs^i, x_n, (1-r)[O_2]_n + r[O_2]^*).$$

Thus

$$\frac{d[O_2]}{dt}(s_n^+, x_n^+, [O_2]_n^+) \ < \ 0.$$

It follows that the oxygen will reach a minimum in finite time.

Remarks. Instead of condition (2.6.12), we might impose the condition

$$s^i - s_n \ > \ 0,$$

except that we cannot guarantee anything about the end of nutrient cycle values s_n. However, in practice this revised condition is not an unreasonable one, since the value of the nutrient at the end of each cycle is usually much smaller than the input concentration. In the next chapter we will deal with this in more detail and impose a similar condition.

In terms of the original variables, condition (2.6.12) is

$$s(0) + \frac{x(0)}{Y} \ < \ s^i. \tag{2.6.13}$$

Thus, conditions (2.6.10), (2.6.11) and (2.6.13) guarantee that a dissolved oxygen minimum will be reached after every impulse point.

2.7 Stability of periodic orbits, if they exist

In the previous sections, we demonstrated that there may not be a periodic orbit in the oxygen-driven self cycling fermentation process. However, we can show that if a periodic orbit exists, then it is stable.

Suppose conditions (2.6.10), (2.6.11) and (2.6.12) hold. Since the constants converge to s^i, we can assume that c takes this value for the periodic orbit. Consider the two-dimensional impulsive differential equations under the assumption that the

input concentration of oxygen is at saturation.

$$\begin{aligned}
\frac{ds}{dt} &= -(s^i - s)\, f(s) && [O_2] \neq [O_2]_{\min} \\
\tfrac{d[O_2]}{dt} &= -g(s, s^i - s, [O_2]) + k([O_2]^* - [O_2]) && [O_2] \neq [O_2]_{\min} \\
\Delta s &= -rs + rs^i && [O_2] = [O_2]_{\min} \\
\Delta[O_2] &= -r[O_2] + r[O_2]^* && [O_2] = [O_2]_{\min}.
\end{aligned}$$

We assume $f(s) = \frac{\mu s}{1+s}$. However, for our argument we assume only that $f(s)$ is a differentiable function which is increasing in s and zero at the origin.

Let $s = \zeta(t)$, $[O_2] = \nu(t)$ be a T-periodic solution with one impulsive effect. Introduce the following notation:

$$\zeta_0 = \zeta(0^+), \nu_0 = \nu(0^+), \zeta_1 = \zeta(T), \nu_1 = \nu(T), \zeta_1^+ = \zeta(T^+), \nu_1^+ = \nu(T^+).$$

From the T-periodicity, $\zeta_1^+ = \zeta_0$ and $\nu_1^+ = \nu_0$. Then since $\Delta\zeta = -r\zeta + rs^i$ we have

$$\zeta_1^+ - \zeta_1 = \zeta_0 - \zeta_1 = -r\zeta_1 + rs^i$$

and so

$$\zeta_0 = (1-r)\zeta_1 + rs^i. \tag{2.7.14}$$

Thus,

$$\zeta_1 = \frac{1}{1-r}(\zeta_0 - rs^i) \tag{2.7.15}$$

and similarly, assuming (2.6.10),

$$\nu_1 = \frac{1}{1-r}(\nu_0 - r[O_2]^*). \tag{2.7.16}$$

Notice that from condition (2.6.12), we have $\zeta_0 + x(0) = \zeta_1 + x_1 < s^i$ and so $\zeta_1 < s^i$. Then from (2.7.14), we have

$$\zeta_0 = \zeta_1 + r(s^i - \zeta_1)$$

and thus $\zeta_0 > \zeta_1$.

Using the Floquet theory for two-dimensional impulsive differential equations (see Appendix B), we have

$$\begin{aligned} P &= -(s^i - s)f(s) & Q &= -g(s, s^i - s, [O_2]) + k([O_2]^* - [O_2]) \\ a &= -rs + rs^i & \phi &= -g(s, s^i - s, [O_2]) + k([O_2]^* - [O_2]) \\ b &= -r[O_2] + r[O_2]^*. \end{aligned}$$

Notice first that, since $\frac{d[O_2]}{dt}(T) = 0$,

$$k\left([O_2]^* - \nu_1\right) = g(\zeta_1, s^i - \zeta_1, \nu_1), \tag{2.7.17}$$

implying that $Q(\zeta_1, \nu_1) = 0$. Thus

$$\Delta_1 = (1-r)\frac{(s^i - \zeta_0)f(\zeta_0)\frac{\partial g}{\partial s} + \left(-g(\zeta_0, s^i - \zeta_0, \nu_0) + k\left([O_2]^* - \nu_0\right)\right)\left(\frac{\partial g}{\partial [O_2]} + k\right)}{(s^i - \zeta_1)f(\zeta_1)\frac{\partial g}{\partial s}}.$$

Note that Δ_1 is positive.

Now,

$$\frac{d^2[O_2]}{dt^2}(t) = -\frac{\partial g}{\partial s}\frac{ds}{dt} - \frac{\partial g}{\partial [O_2]}\frac{d[O_2]}{dt} - k\frac{d[O_2]}{dt},$$

so

$$\begin{aligned} \frac{d^2[O_2]}{dt^2}(T) &= -\frac{\partial g}{\partial s}\frac{ds}{dt} \\ &= (s^i - \zeta_1)f(\zeta_1)\frac{\partial g}{\partial s} > 0, \end{aligned}$$

since $[O_2](t)$ attains a minimum at T. It follows that the denominator of Δ_1 is positive.

Suppose $\nu_1 > \nu_0$. Then

$$\begin{aligned} \frac{1}{1-r}(\nu_0 - r[O_2]^*) &> \nu_0 \\ \nu_0 - r[O_2]^* &> \nu_0 - r\nu_0 \\ [O_2]^* &< \nu_0, \end{aligned}$$

which is a contradiction, since the oxygen is always below saturation. Thus $\nu_1 \leq \nu_0$.

Note also that

$$\begin{aligned} s^i - \zeta_1 &= s^i - \frac{1}{1-r}(\zeta_0 - rs^i) \\ &= \frac{1}{1-r}(s^i - \zeta_0). \end{aligned}$$

From (2.7.15), (2.7.16) and (2.7.17), we have

$$\begin{aligned} k\left([O_2]^* - \nu_1\right) &= g(\zeta_1, s^i - \zeta_1, \nu_1) \\ k\left([O_2]^* - \frac{1}{1-r}(\nu_0 - r[O_2]^*)\right) &= g(\zeta_1, s^i - \zeta_1, \nu_1) \\ \frac{1}{1-r}k\left([O_2]^* - \nu_0\right) &= g(\zeta_1, \frac{1}{1-r}(s^i - \zeta_0), \nu_1) \\ &= \frac{1}{1-r}g(\zeta_1, s^i - \zeta_0, \nu_1) \\ &< \frac{1}{1-r}g(\zeta_0, s^i - \zeta_0, \nu_0), \end{aligned}$$

since g is increasing in s and $[O_2]$ and we showed $\nu_1 \leq \nu_0$ and $\zeta_1 < \zeta_0$.

Thus

$$\begin{aligned} \Delta_1 &< (1-r)\frac{(s^i - \zeta_0)f(\zeta_0)\frac{\partial g}{\partial s} + (-g(\zeta_0, s^i - \zeta_0, \nu_0) + g(\zeta_0, s^i - \zeta_0, \nu_0))\left(\frac{\partial g}{\partial [O_2]} + k\right)}{(s^i - \zeta_1)f(\zeta_1)\frac{\partial g}{\partial s}} \\ &= (1-r)\frac{(s^i - \zeta_0)f(\zeta_0)}{(s^i - \zeta_1)f(\zeta_1)}. \end{aligned}$$

Furthermore,

$$\begin{aligned} \int_0^T \left(\frac{\partial P}{\partial s} + \frac{\partial Q}{\partial [O_2]}\right) dt &= \int_0^T \left(f(\zeta) - (s^i - \zeta)f'(\zeta) - \frac{\partial g}{\partial [O_2]} - k\right) dt \\ &= \int_0^T \left(-\frac{\zeta'}{s^i - \zeta} + \frac{f'(\zeta)}{f(\zeta)}\zeta' - \frac{\partial g}{\partial [O_2]} - k\right) dt \\ &< \int_{\zeta_0}^{\zeta_1} \left(-\frac{1}{s^i - \zeta} + \frac{f'(\zeta)}{f(\zeta)}\right) d\zeta \\ &= \ln\left(\frac{s^i - \zeta_1}{s^i - \zeta_0}\right) + \ln\left(\frac{f(\zeta_1)}{f(\zeta_0)}\right). \end{aligned}$$

Thus

$$\begin{aligned}\mu_2 &< (1-r)\frac{(s^i-\zeta_0)f(\zeta_0)}{(s^i-\zeta_1)f(\zeta_1)}\cdot\frac{(s^i-\zeta_1)f(\zeta_1)}{(s^i-\zeta_0)f(\zeta_0)}\\ &= 1-r,\end{aligned}$$

which is strictly less than one. Hence the periodic orbit, if it exists, is asymptotically stable.

2.8 Discussion

There is, of course, no guarantee that a periodic orbit exists. However, we can at least choose suitable initial and input conditions so that the system undergoes indefinite cycling. Condition (2.6.13) might be difficult to verify and is somewhat restrictive.

The possibility that the system may halt is a very real one, as Figures 2.1-2.2 demonstrate. Furthermore, the implication that the dissolved oxygen could be negative means that the model in Wincure, Cooper and Rey [38] loses biological relevance.

One of the advantages of the self-cycling fermentation process is that it does not require the presence of an operator and should, in theory, continue forever. The systems also reset themselves fairly quickly following an unexpected disturbance (for example, a power failure, as observed in Sheppard and Cooper [30]), but even if our initial conditions and input guarantee indefinite cycling, such a disturbance may potentially cause the system to cross over into the domain of attraction of a critical point.

In order to make sure this does not happen, the system would need at least regular monitoring (which may not be desirable and cancels out one of the advantages of such systems) or some sort of process control loop could be set up, but this may interfere with the property that cycle time is a dependent variable in the system. In order to retain many of the advantages of the oxygen-driven self-cycling fermentation process, especially knowing in advance that the conditions to begin cycling are met and whether we have continuous cycling, we shall propose an alternate means to

instigate the emptying/refilling process at the end of each cycle. Such an alternate method will be the topic of the next chapter.

Chapter 3

A Nutrient-Driven Self-Cycling Fermentation Process

3.1 Introduction

If we want to apply the self-cycling process specifically to the problem of sewage treatment, or any similar problem where the goal is to reduce nutrient levels below some threshold, there are potential problems. We have already seen that the oxygen-driven process may not begin cycling or cycling may not continue indefinitely. Even when the oxygen-driven process converges, the system takes a while to settle down into its steady, periodic state. This means that the first few cycles may release unacceptable levels of waste before the system settles down. Furthermore, if there is some sort of interruption to the system, there may again be a release of an unacceptable level of sewage immediately following this interruption, or the system may be sufficiently disturbed so that the oxygen level does not reach a minimum.

Although it is well known that the SCF process converges fairly quickly, either initially or after an interruption (see Wentworth and Cooper [36] for example), this may still be a cause for concern. When the goal of the SCF process is to clean up industrial pollutants, this may cause further difficulties, since the pollutants are often more toxic at medium concentrations than at their original levels. See Hughes and

Cooper [18] for example. It would thus be desirable to avoid this situation if possible, even for a few cycles of the process.

The Ontario Ministry of the Environment sets a Maximum Acceptable Concentration (MAC) standard and an Interim Maximum Acceptable (IMAC) standard for health-related parameters in drinking water (see Ontario Drinking Water Standards [25]). The MAC is a health related standard established for parameters present above a certain concentration, whereas the IMAC is a health related standard established for parameters for which is it infeasible, to establish a MAC either through insufficient toxicological data or for practical reasons.

Any treatment process which exceeds the MAC or IMAC, even for a few cycles, will not pass the guidelines. Furthermore, if we cannot guarantee in advance that the system will never exceed MAC or IMAC standards, then the SCF process cannot be implemented, even if the amount of waste is less than the MAC or IMAC level in practice.

In this chapter we suggest a modification to the process that avoids the problems in the oxygen-driven model and tailors the self-cycling fermentation process more specifically to nutrient minimizing problems such as sewage treatment.

One way to alter the SCF model is to use nutrient level as the triggering factor instead of a dissolved oxygen minimum. While the SCF model has many advantages, not least of which is its versatility, an adaptation such as this should maintain most of the advantages and tailor it to the particular case of reducing nutrient levels below some threshold.

Furthermore, one of the potential adjustments to the model, as seen in Sheppard and Cooper [30], is to trigger the impulsive effect early so as not to allow total nutrient depletion and hence biomass starvation. The nutrient-driven version of the model that we propose addresses this as well.

We shall also include the death rate $\bar{d}$ of the organisms, as a partial refinement of the oxygen-driven model. This is done with the understanding that we can simply assume $\bar{d} = 0$ if we wish to compare this model with the one in the previous chapter.

The idea is to choose some value $\bar{s}$ of nutrient (in practice fairly small but nonzero, although we will quantify allowable values later) and use that as the maximum value of nutrient allowable at the end of the cycle. That is, the impulsive effect only occurs when the nutrient level is definitely below $\bar{s}$. This allows us to set the guidelines for the system in advance. We call $\bar{s}$ the *tolerance*.

We can ignore the oxygen equation in this model, since the nutrient and biomass equations are independent of oxygen. We also consider a general uptake function $f(s)$, which is continuous, increasing and zero at the origin. Examples can be found in Sundstrom and Klei [34] and Grady and Lim [16]. We will use the specific form $f(s) = \frac{\mu s}{K_s+s}$ when running simulations.

3.2 The nutrient-driven model

Suppose the impulsive effect occurs when $s = \bar{s}$, rather than at a dissolved oxygen minimum. Using the notation of the previous chapter, $x = x_n$ and $s = \bar{s}$ at the nth moment of impulse. The image of the impulsive effect is the same as before, so that $x_n^+ = (1-r)x_n$ and $\bar{s}^+ = (1-r)\bar{s} + rs^i$, where s^i is the fixed concentration of nutrient coming in from the next input.

Model (2.2.1) is replaced by

$$\begin{aligned}
\frac{ds}{dt} &= -\frac{1}{Y}f(s)x & s &\neq \bar{s} \\
\frac{dx}{dt} &= -\bar{d}x + f(s)x & s &\neq \bar{s} \\
\Delta s &= -rs + rs^i & s &= \bar{s} \\
\Delta x &= -rx & s &= \bar{s},
\end{aligned} \tag{3.2.1}$$

where f satisfies:

$$\begin{aligned} &\text{i. } f : \mathbb{R} \to \mathbb{R}, \\ &\text{ii. } f \text{ is continuously differentiable,} \\ &\text{iii. } f(0) = 0, \text{ and} \\ &\text{iv. } f'(s) > 0, \end{aligned} \tag{3.2.2}$$

and we assume $\bar{d} \geq 0$.

We assume continuity from the left for the impulse points. We shall also assume that $s(0) \neq \bar{s}$, so there is no impulsive effect initially. Furthermore, we shall make the assumption that $s^i > \bar{s}$. Then for any $0 < r < 1$,

$$\bar{s}^+ = (1-r)\bar{s} + rs^i > \bar{s}.$$

Define λ to be the value of the nutrient that satisfies $f(\lambda) = \bar{d}$. If f is bounded below $\bar{d}$, then we define $\lambda = \infty$.

3.3 The associated system of ODEs

The associated system of ordinary differential equations is

$$\begin{aligned} \frac{ds}{dt} &= -\frac{1}{Y} f(s)x \\ \frac{dx}{dt} &= -\bar{d}x + f(s)x, \end{aligned} \tag{3.3.3}$$

with initial conditions satisfying $s(0) \geq 0$, $x(0) \geq 0$. Solutions with these initial conditions satisfy $s(t) \geq 0$, $x(t) \geq 0$ for all t.

Equilibria are of the form $(s^*, 0)$, where $s^* \geq 0$. The Jacobian matrix at $(s^*, 0)$ is

$$J(s^*, 0) = \begin{bmatrix} 0 & -\frac{f(s^*)}{Y} \\ 0 & f(s^*) - \bar{d} \end{bmatrix},$$

so $(s^*, 0)$ is unstable if $s^* > \lambda$.

If $s(0) > 0$ and $x(0) > 0$, then $s(t)$ is decreasing for all t. Furthermore, we have

$$x'' = x[f(s) - \bar{d}]^2 - \frac{1}{Y}x^2 f'(s)f(s).$$

When $s = \lambda$, $x' = 0$ and $x'' \leq 0$, since $f'(s) > 0$ for all s. Furthermore, $x'' = 0$ only when $x(0) = 0$. Thus x has a maximum value when $s = \lambda$ and $s(t) \leq s(0)$ for all t. Hence solutions are bounded.

Lemma 3.1. *If $s(0) > \lambda$, $x(0) > 0$ and $s \to s^*$, $x \to 0$ then $0 < s^* < \lambda$.*

Proof. Suppose $s(0) > \lambda$, $x(0) > 0$, $s \to s^*$ and $x \to 0$.

Assume $s \to s^* \geq \lambda$. Then, since $x \neq 0$ in the interior, we have the differential equation

$$\frac{dx}{ds} = Y\left(\frac{\bar{d}}{f(s)} - 1\right) \tag{3.3.4}$$

$$Y\int_{s(0)}^{s^*}\left(\frac{\bar{d}}{f(s)} - 1\right)ds = \int_{x(0)}^{0} 1dx$$

$$Y\int_{s(0)}^{s^*}\left(\frac{\bar{d}}{f(s)} - 1\right)ds = -x(0)$$

$$Y\int_{s^*}^{s(0)}\left(\frac{\bar{d}}{f(s)} - 1\right)ds = x(0). \tag{3.3.5}$$

Since $x(0) > 0$, the right hand side of (3.3.5) is positive.

If $s \to s^* \geq \lambda$, then $f(s) \geq f(s^*) \geq \bar{d}$ for $s \in [s^*, s(0)]$. Thus

$$Y\int_{s^*}^{s(0)}\left(\frac{\bar{d}}{f(s)} - 1\right)ds \leq 0,$$

so the left hand side of (3.3.5) is less than or equal to zero. This is a contradiction, so the assumption that $s^* \geq \lambda$ does not hold. Thus, $0 < s^* < \lambda$.

□

Theorem 3.1 (Poincaré-Bendixson Trichotomy). *Let $\gamma^+(y_0)$ be a positive semi-orbit of $y' = g(y)$ which remains in a closed and bounded subset K of $\mathbb{R}^2$ and suppose that K contains only a finite number of rest points. Then one of the following holds:*

i) $\omega(y_0)$ *is an equilibrium;*

ii) $\omega(y_0)$ *is a periodic orbit;*

iii) $\omega(y_0)$ *contains a finite number of equilibria and a set of trajectories whose alpha and omega limit sets consist of one of these equilibria.*

Since $s(t)$ is decreasing, there are no periodic orbits. For each y_0, let $K = \overline{\gamma(y_0)}$, the closure of the orbit through y_0. Then K is closed and bounded and contains two equilibria. Suppose $\bar{d} > 0$. If y_0 has initial conditions $s(0) > 0$, $x(0) > 0$, then one equilibrium $(s_1^*, 0)$ satisfies $s_1^* > s(0)$ and hence $(s_1^*, 0) \notin \omega(y_0)$, since s is decreasing. Furthermore, since s is decreasing, there cannot be a trajectory ψ such that $\psi \subseteq \omega(y_0)$ and $\omega(\psi) = \alpha(\psi) = (s_2^*, 0)$. Hence, by the Poincaré-Bendixson Trichotomy, solutions approach the equilibrium $(s_2^*, 0)$ satisfying $0 < s_2^* < \lambda$. If $s(0) = 0$, $x(0) > 0$ then $s' = 0$ for all t and $x' < 0$ so solutions approach $(0, 0)$.

If $\bar{d} = 0$, then $\lambda = 0$ and there are equilibria $(s^*, 0)$, $s^* \geq 0$ and $(0, x^*)$ where $x^* > 0$. In this case solutions are along lines $Ys + x = Ys(0) + x(0)$ and $x(t)$ is increasing. If y_0 has initial conditions $s(0) > 0$, $x(0) > 0$, then one equilibrium $(s^*, 0)$ satisfies $s^* > s(0)$ and hence $(s^*, 0) \notin \omega(y_0)$. Furthermore, since x is increasing, there cannot be a trajectory ψ such that $\psi \subseteq \omega(y_0)$ and $\omega(\psi) = \alpha(\psi) = (s^*, 0)$. Hence, by the Poincaré-Bendixson Trichotomy, solutions approach the equilibrium $(0, x^*)$ satisfying $x^* > 0$.

3.4 Conditions to ensure a positive, attracting periodic orbit

For a given species, we would like to be able to control some parameters in the SCF process to ensure indefinite cycling. Each species will have a predetermined death rate and monotone uptake function. The MAC or IMAC will determine the tolerance in advance. This gives the experimenter control over the choice of microorganism

in the tank and the emptying/refilling fraction r. There is some possibility that the experimenter could control s^i, but in most cases, s^i would represent the incoming level of contamination and hence would not be under the control of the experimenter.

Notice from the impulsive system (3.2.1) that $s(t)$ is decreasing between moments of impulse. Define

$$s_{\text{int}} \equiv Y \int_{\bar{s}}^{(1-r)\bar{s}+rs^i} \left(1 - \frac{\bar{d}}{f(s)}\right) ds.$$

Lemma 3.2. *a) If $\bar{s}^+ > \bar{s} \geq \lambda$ then $s_{int} > 0$.*

b) If $\bar{s} < \bar{s}^+ \leq \lambda$ then $s_{int} < 0$.

Proof.

a) Since $\bar{s} \geq \lambda$, $f(s) > f(\bar{s}) \geq \bar{d}$ for $s \in (\bar{s}, \bar{s}^+)$. Thus

$$Y \int_{\bar{s}}^{\bar{s}^+} \left(1 - \frac{\bar{d}}{f(s)}\right) ds > 0.$$

Hence $s_{\text{int}} < 0$.

b) Since $\bar{s}^+ < \lambda$, $f(s) < f(\bar{s}^+) < \bar{d}$ for $s \in (\bar{s}, \bar{s}^+)$. Thus

$$Y \int_{\bar{s}}^{\bar{s}^+} \left(1 - \frac{\bar{d}}{f(s)}\right) ds < 0.$$

Hence $s_{\text{int}} < 0$.

□

Proposition 3.1. *If $s(0) \geq \bar{s}^+ > \lambda > \bar{s}$, $x(0) > 0$ and $s_{int} \geq 0$, then solutions will reach $\bar{s}$ in finite time.*

Proof. Suppose $x \to 0$, $s \to s^* \geq \bar{s}$. Then from (3.3.5), we have

$$\begin{aligned} Y \int_{s^*}^{s(0)} \left(\frac{\bar{d}}{f(s)} - 1\right) ds &= x(0) \\ Y \int_{s^*}^{\bar{s}} \left(\frac{\bar{d}}{f(s)} - 1\right) ds + Y \int_{\bar{s}}^{\bar{s}^+} \left(\frac{\bar{d}}{f(s)} - 1\right) ds & \\ + Y \int_{\bar{s}^+}^{s(0)} \left(\frac{\bar{d}}{f(s)} - 1\right) ds &= x(0). \end{aligned}$$

Thus

$$\begin{aligned} Y\int_{s^*}^{\bar{s}}\left(\frac{\bar{d}}{f(s)}-1\right)ds - s_{\text{int}} &= x(0) - Y\int_{\bar{s}^+}^{s(0)}\left(\frac{\bar{d}}{f(s)}-1\right)ds \\ Y\int_{s^*}^{\bar{s}}\left(\frac{\bar{d}}{f(s)}-1\right)ds &= x(0) + s_{\text{int}} + Y\int_{\bar{s}^+}^{s(0)}\left(1-\frac{\bar{d}}{f(s)}\right)ds. \end{aligned} \tag{3.4.6}$$

We have $\lambda < \bar{s}^+ \leq s$ for all $s \in [\bar{s}^+, s(0)]$. Thus $f(s) \geq f(\bar{s}^+) > \bar{d}$, so

$$Y\int_{\bar{s}^+}^{s(0)}\left(1-\frac{\bar{d}}{f(s)}\right)ds \geq 0,$$

since $s(0) \geq \bar{s}^+$. Since $x(0) > 0$, the right hand side of (3.4.6) is positive.

If $s \to s^*$, then $s^* < \lambda$. Thus, since f is increasing, $f(s^*) < \bar{d}$. By assumption, $s^* \geq \bar{s}$, so $f(s) \leq f(s^*) < \bar{d}$ for $s \in [\bar{s}, s^*]$. Hence

$$Y\int_{\bar{s}}^{s^*}\left(1-\frac{\bar{d}}{f(s)}\right)ds \leq 0,$$

so the left hand side of (3.4.6) is less than or equal to zero. This is a contradiction, so the assumption that $s^* \geq \bar{s}$ does not hold. Thus, $s^* < \bar{s}$, so $\bar{s}$ is reached in finite time.

□

Remark. Solutions which have initial conditions satisfying $(s, x) = (\bar{s}^+, \epsilon)$ for any $\epsilon > 0$ will thus reach $\bar{s}$ in finite time. Solutions that reach $(s, x) = (\bar{s}, x_n)$, with $x_n > 0$, are transported under the impulsive effect to the location $(s, x) = (\bar{s}^+, (1-r)x_n)$, which are the new initial conditions for the next cycle. Since these new initial conditions satisfy the hypotheses of Proposition 3.1, they must therefore reach $(s, x) = (\bar{s}, x_{n+1})$ in finite time. Hence, if solutions reach the impulsive surface once, they will reach it infinitely often, when $s_{\text{int}} \geq 0$.

Theorem 3.2. *Assume $s_{int} > 0$. Then there exists a unique periodic orbit with exactly one impulse per period. This periodic orbit has the property of asymptotic phase.*

i) If $\bar{s} \geq \lambda$ then the periodic orbit attracts all solutions with initial conditions satisfying $s(0) > \bar{s}$ and $x(0) > 0$.

ii) If $\bar{s} < \lambda$ then the nontrivial periodic orbit attracts all solutions with initial conditions satisfying $Y \int_{\bar{s}}^{s(0)} \left(1 - \frac{\bar{d}}{f(s)}\right) ds \geq 0$ and $x(0) > 0$, or $Y \int_{\bar{s}}^{s(0)} \left(1 - \frac{\bar{d}}{f(s)}\right) ds < 0$, but $x(0)$ sufficiently large.

The periodic orbit satisfies

$$\begin{aligned} s_n &= \bar{s}, & s_n^+ &= (1-r)\bar{s} + rs^i, \\ x_n &= \tfrac{s_{int}}{r}, & x_n^+ &= (1-r)\tfrac{s_{int}}{r}, \end{aligned}$$

for all positive integers n. One of the following holds:

a) $x_n = \frac{s_{int}}{r}$ for all positive integers n; or

b) $x_n < \frac{s_{int}}{r}$, $x_n < x_{n+1}$ for all positive integers n and $x_n \to \frac{s_{int}}{r}$ as $n \to \infty$; or

c) $x_n > \frac{s_{int}}{r}$, $x_n > x_{n+1}$ for all positive integers n and $x_n \to \frac{s_{int}}{r}$ as $n \to \infty$.

iii) If $s(0) < \bar{s}$ or $s(0)$ satisfies $Y \int_{\bar{s}}^{s(0)} \left(1 - \frac{\bar{d}}{f(s)}\right) ds < 0$ and $x(0) > 0$ is sufficiently small, then there are no moments of impulse and $x(t) \to 0$, $s(t) \to s^*$, where $0 \leq s^* < \lambda$.

Proof. Suppose $s = \zeta(t)$, $x = \xi(t)$ is a T-periodic solution with one impulsive effect per period. We use the notation

$$\zeta_0 = \zeta(0^+),\ \zeta_1 = \zeta(T),\ \xi_0 = \xi(0^+),\ \xi_1 = \xi(T).$$

From the condition of T-periodicity, $\zeta_1^+ = \zeta_0$ and $\xi_1^+ = \xi_0$. The impulsive conditions give us

$$\begin{aligned} \zeta_0 &= (1-r)\bar{s} + rs^i \\ \zeta_1 &= \bar{s} \\ \xi_1 &= \frac{1}{1-r}\xi_0. \end{aligned}$$

From (3.3.4), we have

$$\begin{aligned} \int_{\xi_0}^{\xi_1} dx &= Y \int_{\zeta_0}^{\zeta_1} \left(\frac{\bar{d}}{f(s)} - 1 \right) ds \\ x\Big|_{\xi_0}^{\xi_0/(1-r)} &= Y \int_{(1-r)\bar{s}+rs^i}^{\bar{s}} \left(\frac{\bar{d}}{f(s)} - 1 \right) ds \\ \frac{r}{1-r}\xi_0 &= s_{\text{int}}. \end{aligned} \tag{3.4.7}$$

Thus a nontrivial periodic orbit exists if $s_{\text{int}} > 0$. The periodic orbit in x has initial point

$$\xi_0 = \frac{1-r}{r} s_{\text{int}} \tag{3.4.8}$$

and final point

$$\xi_1 = \frac{s_{\text{int}}}{r}.$$

We shall apply the impulsive Floquet theory (as described in Appendix B) to the two-dimensional system (3.2.1). If we calculate the nontrivial impulsive Floquet multiplier, as in Appendix B, we have

$$\begin{aligned} P &= -\frac{f(s)x}{Y}, & Q &= -\bar{d}x + f(s)x, \\ a &= -rs + rs^i, & b &= -rx, \\ \phi &= s - \bar{s}. \end{aligned}$$

Therefore,

$$\begin{aligned} \Delta_1 &= \frac{-f(\zeta_0)\xi_0(-r\cdot 1 - 0 + 1) + Y(-\bar{d}\xi_0 + f(\zeta_0)\xi_0)(-r\cdot 0 - 0 + 0)}{-f(\zeta_1)\xi_1 + Y(-\bar{d}\xi_1 + f(\zeta_1)\xi_1)(0)} \\ &= (1-r)^2 \frac{f(\zeta_0)}{f(\zeta_1)}, \end{aligned}$$

since $\xi_0 = (1-r)\xi_1 > 0$. Furthermore,

$$\int_0^T \left(\frac{\partial P}{\partial s} + \frac{\partial Q}{\partial x} \right) dt = \int_0^T \left(-\frac{f'(\zeta)\xi}{Y} - \bar{d} + f(\zeta) \right) dt$$

$$
\begin{aligned}
&= \int_0^T \left(\frac{f'(\zeta)\zeta'}{f(\zeta)} + \frac{\xi'}{\xi} \right) dt \\
&= \ln f(s)\Big|_{\zeta_0}^{\zeta_1} + \ln \xi \Big|_{\xi_0}^{\xi_1} \\
&= \ln \frac{f(\zeta_1)}{f(\zeta_0)} + \ln \frac{1}{1-r}.
\end{aligned}
$$

Then the nontrivial multiplier is

$$
\begin{aligned}
\mu_2 &= (1-r)^2 \frac{f(\zeta_0)}{f(\zeta_1)} \cdot \frac{f(\zeta_1)}{f(\zeta_0)} \cdot \frac{1}{1-r} \\
&= 1-r.
\end{aligned}
$$

Thus, the periodic orbit is orbitally asymptotically stable and has the property of asymptotic phase.

First we show that if the impulsive surface is reached once it is reached infinitely often.

i) Suppose $s \to s^*$, $x \to 0$. Then since, $s^* < \lambda \leq \bar{s}$, $\bar{s}$ is reached in finite time.

ii) Suppose $Y \int_{\bar{s}}^{s(0)} \left(1 - \frac{\bar{d}}{f(s)}\right) ds \geq 0$. Assume $x \to 0$ and $s \to s^* \geq \bar{s}$. From (3.3.5), we have

$$
\begin{aligned}
Y \int_{s^*}^{s(0)} \left(\frac{\bar{d}}{f(s)} - 1 \right) ds &= x(0) \\
Y \int_{s^*}^{\bar{s}} \left(\frac{\bar{d}}{f(s)} - 1 \right) ds + Y \int_{\bar{s}}^{s(0)} \left(\frac{\bar{d}}{f(s)} - 1 \right) ds &= x(0) \qquad (3.4.9)
\end{aligned}
$$

If $s \leq s^* < \lambda$, then $f(s) < \bar{d}$ for $s \in [\bar{s}, s^*]$. Hence

$$
Y \int_{\bar{s}}^{s^*} \left(1 - \frac{\bar{d}}{f(s)} \right) ds \leq 0.
$$

Then since $Y \int_{\bar{s}}^{s(0)} \left(\frac{\bar{d}}{f(s)} - 1 \right) ds < 0$, it follows that the left hand side of (3.4.9) is less than or equal to zero. This is a contradiction if $x(0) > 0$. Hence solutions will reach $\bar{s}$ in finite time.

Suppose $Y\int_{\bar{s}}^{s(0)}\left(1-\frac{\bar{d}}{f(s)}\right)ds<0$ and

$$x(0) \;>\; Y(\bar{s}^+ - s(0))\left(1-\frac{\bar{d}}{f(\bar{s}^+)}\right). \tag{3.4.10}$$

Assume $x\to 0$ and $s\to s^*\geq \bar{s}$. Then from (3.3.5), we have

$$\begin{aligned} Y\int_{s^*}^{s(0)}\left(\frac{\bar{d}}{f(s)}-1\right)ds &= x(0) \\ Y\int_{s^*}^{\bar{s}}\left(\frac{\bar{d}}{f(s)}-1\right)ds + Y\int_{\bar{s}}^{\bar{s}^+}\left(\frac{\bar{d}}{f(s)}-1\right)ds & \\ +Y\int_{\bar{s}^+}^{s(0)}\left(\frac{\bar{d}}{f(s)}-1\right)ds &= x(0) \end{aligned} \tag{3.4.11}$$

As above,

$$Y\int_{\bar{s}}^{s^*}\left(1-\frac{\bar{d}}{f(s)}\right)ds\leq 0.$$

If $s(0)\leq s\leq \bar{s}^+$, then $f(s)\leq f(\bar{s}^+)$ for $s\in[s(0),\bar{s}^+]$. Thus

$$1-\frac{\bar{d}}{f(s)}\leq 1-\frac{\bar{d}}{f(\bar{s}^+)}.$$

Hence

$$Y\int_{s(0)}^{\bar{s}^+}\left(1-\frac{\bar{d}}{f(s)}\right)ds\leq Y(\bar{s}^+-s(0))\left(1-\frac{\bar{d}}{f(\bar{s}^+)}\right).$$

Since $s_{\text{int}^*}>0$, it follows that the left hand side of (3.4.11) is less than

$$Y(\bar{s}^+-s(0))\left(1-\frac{\bar{d}}{f(\bar{s}^+)}\right).$$

This contradicts (3.4.10). Hence $\bar{s}$ is reached in finite time.

Solutions that reach $(s,x)=(\bar{s},x_n)$, with $x_n>0$, are transported under the impulsive effect to the location $(s,x)=(\bar{s}^+,(1-r)x_n)$, which is the new initial conditions for the next cycle. Since these new initial conditions satisfy the hypotheses of (i) or Proposition 3.1, they must therefore reach $(s,x)=(\bar{s},x_{n+1})$ in finite time. Hence, if solutions reach the impulsive surface once, they will reach it infinitely often.

Next we show that if the system cycles indefinitely, the convergence is monotone and all solutions that cycle indefinitely approach the periodic orbit.

From (3.3.4) we have

$$\begin{aligned} x_{n+1} &= x_n^+ + s_{\text{int}} \\ &= (1-r)x_n + s_{\text{int}}. \end{aligned} \tag{3.4.12}$$

This has the general solution

$$\begin{aligned} x_n &= (1-r)^{n-1}x_1 + s_{\text{int}}\left(1 + (1-r) + \cdots + (1-r)^{n-2}\right) \\ &= (1-r)^{n-1}x_1 + s_{\text{int}}\left(\frac{1-(1-r)^{n-1}}{r}\right). \end{aligned} \tag{3.4.13}$$

If $x_1 = \frac{s_{\text{int}}}{r}$, then

$$\begin{aligned} x_n &= (1-r)^{n-1}\frac{s_{\text{int}}}{r} + s_{\text{int}}\left(\frac{1-(1-r)^{n-1}}{r}\right) \\ &= \frac{s_{\text{int}}}{r} \end{aligned}$$

for all positive integers n.

If $x_1 < \frac{s_{\text{int}}}{r}$,then

$$\begin{aligned} x_n &< (1-r)^{n-1}\frac{s_{\text{int}}}{r} + s_{\text{int}}\left(\frac{1-(1-r)^{n-1}}{r}\right) \\ &= \frac{s_{\text{int}}}{r} \end{aligned} \tag{3.4.14}$$

for all positive integers n. Furthermore, from (3.4.12) we have

$$\begin{aligned} x_{n+1} - x_n &= (1-r)x_n + s_{\text{int}} - x_n \\ &= s_{\text{int}} - rx_n \\ &> s_{\text{int}} - r\left[\frac{s_{\text{int}}}{r}\right] \\ &= 0, \end{aligned}$$

since (3.4.14) holds for all positive integers n.

If $x_1 > \frac{s_{\text{int}}}{r}$,then

$$\begin{aligned} x_n &> (1-r)^{n-1}\frac{s_{\text{int}}}{r} + s_{\text{int}}\left(\frac{1-(1-r)^{n-1}}{r}\right) \\ &= \frac{s_{\text{int}}}{r} \end{aligned} \tag{3.4.15}$$

for all positive integers n. Furthermore, from (3.4.12) we have

$$\begin{aligned} x_{n+1} - x_n &= (1-r)x_n + s_{\text{int}} - x_n \\ &= s_{\text{int}} - rx_n \\ &< s_{\text{int}} - r\left[\frac{s_{\text{int}}}{r}\right] \\ &= 0, \end{aligned}$$

since (3.4.15) holds for all positive integers n.

Finally, note that from (3.4.13) we have, in all cases,

$$\lim_{n\to\infty} x_n = \frac{s_{\text{int}}}{r}.$$

iii) If $s(0) < \bar{s}$ then $\bar{s}$ is never reached, so there are no moments of impulse and $s \to s^*$, where $0 \le s^* \le s(0)$.

Suppose $s \to s^* < \bar{s}$. If $s(0)$ satisfies $Y\int_{\bar{s}}^{s(0)} \left(1 - \frac{\bar{d}}{f(s)}\right) ds = -\delta$, where $\delta > 0$, then from (3.3.5), we have

$$\begin{aligned} Y\int_{s^*}^{s(0)} \left(\frac{\bar{d}}{f(s)} - 1\right) ds &= x(0) \\ Y\int_{s^*}^{\bar{s}} \left(\frac{\bar{d}}{f(s)} - 1\right) ds + Y\int_{\bar{s}}^{s(0)} \left(\frac{\bar{d}}{f(s)} - 1\right) ds &= x(0) \\ Y\int_{s^*}^{\bar{s}} \left(\frac{\bar{d}}{f(s)} - 1\right) ds + \delta &= x(0). \end{aligned} \tag{3.4.16}$$

If $s^* \le s \le \bar{s} < \lambda$, then $f(s) < \bar{d}$ for $s \in [s^*, \bar{s}]$. Hence

$$Y\int_{s^*}^{\bar{s}} \left(\frac{\bar{d}}{f(s)} - 1\right) ds > 0.$$

Thus, the left hand side of (3.4.16) is greater than ϵ. Hence if we choose $0 < x(0) < \epsilon$, then we have a contradiction. Thus $\bar{s} \le s^* < \lambda$.

We shall now demonstrate that there are no periodic orbits with more than one impulse point per period, i.e. no higher order periodic orbits.

Suppose we have a T-periodic solution with k moments of impulse, at t_1, t_2, ..., t_{k-1}, T. Then

$$\begin{aligned} \zeta_i &= \zeta_1 = \bar{s} \\ \zeta_i^+ &= \zeta_0 = (1-r)\bar{s} + rs^i, \end{aligned}$$

for $i = 1, \ldots, k$; and

$$\begin{aligned} \xi_k^+ &= \xi_0 \\ (1-r)\xi_k &= \xi_0. \end{aligned} \tag{3.4.17}$$

From (3.4.7), we have the following. For $t \in (t_i, t_{i+1})$,

$$\int_{\xi_i^+}^{\xi_{i+1}} dx = s_{\text{int}},$$

and so

$$\xi_k - \xi_{k-1}^+ + (1-r)[\xi_{k-1} - \xi_{k-2}^+] + \cdots + (1-r)^{k-2}[\xi_2 - \xi_1^+] + (1-r)^{k-1}[\xi_1 - \xi_0]$$

$$= s_{\text{int}} + (1-r)s_{\text{int}} + \cdots + (1-r)^{k-2}s_{\text{int}} + (1-r)^{k-1}s_{\text{int}}.$$

Thus, since $\xi_i^+ = (1-r)\xi_i$, the interior values on the left hand side cancel, so we have

$$\xi_k - (1-r)^{k-1}\xi_0 = \frac{1-(1-r)^k}{r} s_{\text{int}}.$$

Hence, using (3.4.17),

$$\xi_k - (1-r)^{k-1}\xi_0 = \frac{1}{1-r}\xi_0 - (1-r)^{k-1}\xi_0,$$

so

$$\xi_0 = \frac{1-r}{r} s_{\text{int}}.$$

This is the same value of ξ_0 as for the first order period (from (3.4.8)). Since the ordinary differential equation with initial condition $(s(0), x(0)) = ((1-r)\bar{s} + rs^i, \xi_0)$ has a unique solution, it follows that $(\bar{s}, \xi_1)$ is the first point of impulse. However, from the results in the case of the single order period, $\xi_1^+ = \xi_0$. Hence there are no non-degenerate higher order periodic orbits.

□

Theorem 3.3. *Assume $s_{int} = 0$. Then there is no nontrivial periodic solution and*

$$\liminf_{t\to\infty} x(t) = 0.$$

If $s(0) \geq \bar{s}^+$ and $x(0) > 0$ or $s(0) > \bar{s}$ and $x(0)$ is sufficiently large, then there are an infinite number of impulses. If $s(0) < \bar{s}$ or $\bar{s} < s(0) < \bar{s}^+$ and $x(0) > 0$ is sufficiently small, there are no impulses and $s(t) \to s^*$, where $0 \leq s^* < \lambda$.

Proof. Since $s_{\text{int}} = 0$, we must have $\bar{s}^+ > \lambda$. Hence by Lemma 3.1, if $s(0) \geq \bar{s}^+$, $x(0) > 0$, then $\bar{s}$ is reached in finite time. The nature of the impulsive effect takes solutions at $(\bar{s}, x_n)$ to $(\bar{s}^+, (1-r)x_n)$, so if $\bar{s}$ is reached once, it is reached infinitely often. However, from (3.3.5), we have

$$\begin{aligned} Y\int_{\bar{s}^+}^{\bar{s}} \left(\frac{\bar{d}}{f(s)} - 1\right) ds &= \int_{x_n^+}^{x_{n+1}} 1 dx \\ 0 &= x_{n+1} - (1-r)x_n. \end{aligned}$$

Thus $x_{n+1} = (1-r)x_n < x_n$ for all n, so there is no nontrivial periodic orbit. Since $x_n = (1-r)^n x_1$ and $x_n^+ = (1-r)x_1^+$, $x_n \to 0$ and $x_n^+ \to 0$ as $n \to \infty$. Hence $\liminf_{t\to\infty} x(t) = 0$.

Suppose $\bar{s} < s(0) < \bar{s}^+$ and

$$x(0) > Y(\bar{s}^+ - s(0))\left(1 - \frac{\bar{d}}{f(\bar{s}^+)}\right).$$

Then, as in the proof of (ii) in Theorem 3.2, $\bar{s}$ is reached in finite time. Hence there are an infinite number of impulses if $x(0)$ is sufficiently large.

If $s(0) < \bar{s}$ then $\bar{s}$ is never reached, so there are no moments of impulse.

If $\bar{s} < s(0) < \bar{s}^+$ and $x(0)$ is sufficiently small, suppose $s \to s^* < \bar{s}$. There are two cases to consider. In the first case, if $\lambda \leq s(0)$, then by (3.3.5), we have

$$\begin{aligned} Y\int_{s^*}^{s(0)} \left(\frac{\bar{d}}{f(s)} - 1\right) ds &= x(0) \\ Y\int_{s^*}^{\bar{s}} \left(\frac{\bar{d}}{f(s)} - 1\right) ds + Y\int_{\bar{s}}^{\bar{s}^+} \left(\frac{\bar{d}}{f(s)} - 1\right) ds & \\ + Y\int_{\bar{s}^+}^{s(0)} \left(\frac{\bar{d}}{f(s)} - 1\right) ds &= x(0). \end{aligned} \tag{3.4.18}$$

If $s^* \leq s \leq \bar{s} < \lambda$, then $f(s) < \bar{d}$ for $s \in [s^*, \bar{s}]$. Hence

$$Y \int_{s^*}^{\bar{s}} \left(\frac{\bar{d}}{f(s)} - 1 \right) ds > 0.$$

If $\lambda \leq s(0) \leq s \leq \bar{s}^+$, then $f(s) \geq \bar{d}$ for $s \in [s(0), \bar{s}^+]$. Thus

$$Y \int_{s(0)}^{\bar{s}^+} \left(1 - \frac{\bar{d}}{f(s)} \right) ds \geq 0.$$

The left hand side of (3.4.18) is positive, say ϵ, so we can choose $0 < x(0) < \epsilon$. This is a contradiction, so $s^* \geq \bar{s}$ and hence we have $\bar{s} \leq s^* < \lambda$.

In the second case, if $s(0) < \lambda$, then by (3.3.5), we have

$$\begin{aligned} Y \int_{s^*}^{s(0)} \left(\frac{\bar{d}}{f(s)} - 1 \right) ds &= x(0) \\ Y \int_{s^*}^{\bar{s}} \left(\frac{\bar{d}}{f(s)} - 1 \right) ds + Y \int_{\bar{s}}^{s(0)} \left(\frac{\bar{d}}{f(s)} - 1 \right) ds &= x(0). \end{aligned} \tag{3.4.19}$$

As above,

$$Y \int_{s^*}^{\bar{s}} \left(\frac{\bar{d}}{f(s)} - 1 \right) ds > 0.$$

If $s \leq s(0) < \lambda$, then $f(s) < \bar{d}$ for $s \in [\bar{s}, s(0)]$. Thus

$$Y \int_{\bar{s}}^{s(0)} \left(\frac{\bar{d}}{f(s)} - 1 \right) ds > 0.$$

The left hand side of (3.4.19) is positive, say γ, so we can choose $0 < x(0) < \gamma$. This is a contradiction, so $s^* \geq \bar{s}$ and hence we have $\bar{s} \leq s^* < \lambda$.

□

Theorem 3.4. *Assume $s_{int} < 0$. Then there is no nontrivial periodic orbit. For any initial conditions, there are at most a finite number of impulses and eventually $s(t) \to s^*$ and $x(t) \to 0$, where $0 \leq s^* < \lambda$.*

Proof. Suppose $s_{\text{int}} < 0$. Note that we must have $\bar{s} < \lambda$. Suppose $s(0) = \bar{s}^+$, $0 < x(0) < -s_{\text{int}}$.

Assume $x \to 0$, $s \to s^* \leq \bar{s}$. Then from (3.3.5), we have

$$\begin{aligned} Y\int_{s^*}^{\bar{s}^+}\left(\frac{\bar{d}}{f(s)}-1\right)ds &= x(0) \\ Y\int_{s^*}^{\bar{s}}\left(\frac{\bar{d}}{f(s)}-1\right)ds + Y\int_{\bar{s}}^{\bar{s}^+}\left(\frac{\bar{d}}{f(s)}-1\right)ds &= x(0) \\ Y\int_{s^*}^{\bar{s}}\left(\frac{\bar{d}}{f(s)}-1\right)ds - s_{\text{int}} &= x(0) \\ Y\int_{s^*}^{\bar{s}}\left(\frac{\bar{d}}{f(s)}-1\right)ds &= x(0)+s_{\text{int}}. \end{aligned} \tag{3.4.20}$$

The right hand side is negative, by our choice of initial condition.

If $s \to s^* \leq \bar{s} < \lambda$, then $f(s) \leq f(\bar{s}) < \bar{d}$ for $s \in [s^*, \bar{s}]$. Hence

$$Y\int_{s^*}^{\bar{s}}\left(\frac{\bar{d}}{f(s)}-1\right)ds > 0,$$

so the left hand side of (3.4.20) is positive. This is a contradiction, so the assumption that $s^* \leq \bar{s}$ does not hold. Thus, $s \to s^* > \bar{s}$.

Assume we have initial conditions $s(0) = \bar{s}^+$, $x(0) > -s_{\text{int}}$ such that the solution has an infinite number of moments of impulse. However $x_{n+1} - x_n^+ < 0$, so $x_{n+1} < (1-r)x_n < x_n$. Hence $x_n \to m \geq 0$. If $m > 0$, then we have a periodic orbit with $x_{n+1} = x_n$ for all n. This is not possible with a strictly decreasing sequence of impulse points, so we must have $m = 0$.

If $x_n \to 0$ then $x_n^+ \to 0$. Hence there exists N such that

$$|x_n^+ - 0| < -s_{\text{int}}$$

whenever $n > N$. Thus $x_n^+ < -s_{\text{int}}$, so from the argument above, $s \to s^* > \bar{s}$. Thus there is no further moment of impulse, which is a contradiction. Hence there are at most a finite number of moments of impulse.

Thus, solutions with $s(0) = \bar{s}^+$, $x(0) > -s_{\text{int}}$ undergo k moments of impulse, until $0 < x_k^+ < -s_{\text{int}}$ and then $x \to 0$, $s \to s^* > \bar{s}$.

For any other initial conditions, either the impulsive surface is reached or it is not. If the surface is not reached, then there are no impulses and $\lim_{t\to\infty}(s(t), x(t)) =$

$(s^*, 0)$ where $s^* \geq 0$. If the surface is reached once, then the initial conditions for the next cycle satisfy $s(0) = \bar{s}^+$, $x(0) > 0$ and hence thereafter undergo only a finite number of impulses, by the above reasoning.

□

Remarks. When $f(s) = \frac{\mu s}{K_s + s}$, we have

$$\begin{aligned} s_{\text{int}} &= Y \int_{\bar{s}}^{(1-r)\bar{s}+rs^i} \left(1 - \frac{\bar{d}(K_s + s)}{\mu s}\right) ds \\ &= Y\left(1 - \frac{\bar{d}}{\mu}\right) r(s^i - \bar{s}) - \frac{Y\bar{d}K_s}{\mu} \ln \frac{(1-r)\bar{s} + rs^i}{\bar{s}}. \end{aligned}$$

Suppose $\bar{s} < \lambda < \bar{s}^+$. We have

$$\begin{aligned} \frac{\partial s_{\text{int}}}{\partial r} &= Y\left(1 - \frac{\bar{d}}{f(\bar{s}^+)}\right)(s^i - \bar{s}) \\ \frac{\partial s_{\text{int}}}{\partial s^i} &= Y\left(1 - \frac{\bar{d}}{f(\bar{s}^+)}\right) r \end{aligned}$$

If $\bar{s}^+ > \lambda$, then both $\frac{\partial s_{\text{int}}}{\partial r}$ and $\frac{\partial s_{\text{int}}}{\partial s^i}$ are positive. Thus s_{int} is increasing as r and s^i increase, so if $s_{\text{int}} \leq 0$, we may be able to increase the emptying/refilling fraction or the input until $s_{\text{int}} > 0$. In most practical applications, s^i will be fixed, so it is more likely that we would have control over r. However, it is interesting to note that increasing s^i and effectively increasing the amount of pollutant, may make the problem easier to solve.

3.5 Cycle times

One of the factors to consider in environmental cleanup processes is the amount of time the system takes to clean each batch. Explicitly determining the cycle times in impulsive systems can be quite difficult. However, we can make some estimates.

Lemma 3.3. *Suppose* $(s(t), x(t))$ *and* $(s_\epsilon(t), x_\epsilon(t))$ *are two solutions of system (3.3.3), with initial conditions* $(s(0), x(0))$ *and* $(s(0), x(0) + \epsilon)$ *respectively, for some* $\epsilon > 0$. *Then if* $s_\epsilon(t_2) = s(t_1)$, *it follows that* $x_\epsilon(t_2) = x(t_1) + \epsilon$.

Proof. Let $s(t_1)s_\epsilon(t_2) = s^*$. From (3.3.4), we have

$$\begin{aligned}\int_{s(0)}^{s^*}\left(\frac{\bar{d}}{f(s)}-1\right)ds &= \int_{x(0)}^{x(t_1)}dx\\ \int_{s^*}^{s(0)}\left(\frac{\bar{d}}{f(s)}-1\right)ds &= x(0)-x(t_1)\end{aligned}$$

and similarly

$$\begin{aligned}\int_{s(0)}^{s^*}\left(\frac{\bar{d}}{f(s)}-1\right)ds &= \int_{x(0)+\epsilon}^{x(t_2)}dx\\ \int_{s^*}^{s(0)}\left(\frac{\bar{d}}{f(s)}-1\right)ds &= x(0)+\epsilon-x(t_2).\end{aligned}$$

Thus

$$\begin{aligned}x(t_2) &= x(0)+\epsilon-\int_{s^*}^{s(0)}\left(\frac{\bar{d}}{f(s)}-1\right)ds\\ &= x(t_1)+\epsilon\end{aligned}$$

□

Theorem 3.5. *Suppose $(s(t),x(t))$ and $(s_\epsilon(t),x_\epsilon(t))$ are two solutions of system (3.3.3), with initial conditions $(s(0),x(0))$ and $(s(0),x(0)+\epsilon)$ respectively, for some $\epsilon > 0$. Then if $s_\epsilon(t_2) = s(t_1)$, it follows that $t_2 < t_1$.*

Proof. First consider $y(t) = s(t) - s_\epsilon(t)$. We have

$$\begin{aligned}y(0) &= s(0)-s_\epsilon(0) = 0\\ y'(t) &= -\frac{f(s(t))x(t)}{Y}+\frac{f(s_\epsilon(t))x_\epsilon(t)}{Y}\\ y'(0) &= -\frac{f(s(0))x(0)}{Y}+\frac{f(s_\epsilon(0))x_\epsilon(0)}{Y}\\ &= -\frac{f(s(0))x(0)}{Y}+\frac{f(s(0))x(0)}{Y}+\frac{f(s(0))\epsilon}{Y}\\ &> 0\end{aligned}$$

Thus $y(0) = 0$ and $y(t)$ is initially increasing. Suppose there exists $\tilde{t} > 0$ such that $y(t) > 0$ for $0 < t < \tilde{t}$, but $y(\tilde{t}) = 0$. This means that $y'(\tilde{t}) \leq 0$. However,

$$\begin{aligned}s(\tilde{t}) &= s_\epsilon(\tilde{t})\\ x(\tilde{t}) &= x_\epsilon(\tilde{t})-\epsilon\end{aligned}$$

by Lemma 3.3. Thus, at $\tilde{t}$, we have

$$\begin{aligned} s'(\tilde{t}) &= -\frac{x(\tilde{t})f(s(\tilde{t}))}{Y} \\ &= -\frac{x_\epsilon(\tilde{t})f(s(\tilde{t}))}{Y} + \epsilon\frac{f(s(\tilde{t}))}{Y} \\ &= s'_\epsilon(\tilde{t}) + \epsilon\frac{f(s(\tilde{t}))}{Y} \end{aligned}$$

Hence $y'(\tilde{t}) > 0$. This is a contradiction, so there does not exist $\tilde{t}$ such that $y(t) > 0$ for $0 < t < \tilde{t}$. Since $y(t)$ is initially increasing, we must therefore have $y(t) > 0$ for all t. That is,

$$s(t) > s_\epsilon(t) \qquad \text{for all } t > 0 \tag{3.5.21}$$

Suppose the time taken to travel from $(s(0), x(0))$ to some point (s^*, x^*) is t_1 and the time take to travel from $(s_\epsilon(0), x_\epsilon(0))$ to some point (s^*, x^*_ϵ) is t_2. We have

$$\begin{aligned} s(0) &= s_\epsilon(0) \\ x(0) &= x_\epsilon(0) - \epsilon \\ s(t_1) &= s_\epsilon(t_2) \\ x(t_1) &= x_\epsilon(t_2) - \epsilon \end{aligned}$$

by Lemma 3.3. Assume $t_2 \geq t_1$. Then, since $s_\epsilon(t)$ is decreasing, $s_\epsilon(t_2) \leq s_\epsilon(t_1)$. Thus,

$$s(t_1) = s_\epsilon(t_2) \leq s_\epsilon(t_1)$$

This contradicts (3.5.21). Hence $t_2 < t_1$.

□

Since $x_n^+ \to (1-r)\frac{s_{\text{int}}}{r}$ monotonically in Theorem 3.2, it follows that if x_n^+ is decreasing to $(1-r)\frac{s_{\text{int}}}{r}$, then the cycle times increase to the period T of the periodic orbit. Conversely, if x_n^+ is increasing to $(1-r)\frac{s_{\text{int}}}{r}$, then the cycle times decrease to the period T of the periodic orbit.

3.6 Numerical simulations

We demonstrate the various results in this chapter by means of numerical simulations. All simulations were run using ODE45 in MATLAB. All graphs were presented as subplots, with the graph on the left showing the behaviour of the nutrient and biomass with respect to time and the graph on the right showing the phase portrait in s-x space. The straight lines joining the endpoints of one cycle to the initial points of the next cycle are not actually part of the trajectories. Thus, in Figure 3.2 for example the periodic orbit in phase space consists of the curved part on the right and not the straight part on the left.

The five examples are

1. $s_{\text{int}} > 0$, $\bar{s} > \lambda$, $s(0) > \bar{s}$, $x(0) > 0$ to illustrate case (i) in Theorem 3.2. In this case the endpoints of each cycle were monotonically decreasing to the endpoint of the periodic orbit, thus illustrating (c). See Figure 3.1.

2. $s_{\text{int}} > 0$, $\bar{s} < \lambda < \bar{s}^+$, $s(0) = \bar{s}^+$, $x(0) = (1-r)\frac{s_{\text{int}}}{r}$ to illustrate the first part of case (i) in Theorem 3.2. In this case, the initial conditions were equal to the initial points of the periodic orbit, so the orbit was the periodic orbit, thus illustrating (a). See Figure 3.2.

3. $s_{\text{int}} > 0$, $\bar{s} < \lambda < \bar{s}$, $s(0) > \bar{s}$, $x(0) > Y(\bar{s}^+ - s(0)(1 - \frac{\bar{d}}{f(\bar{s}^+)})$ to illustrate the second part of case (ii) in Theorem 3.2. In this case the endpoints of each cycle were monotonically increasing to the endpoint of the periodic orbit, thus illustrating (b). See Figure3.3.

4. $s_{\text{int}} > 0$, $Y\int_{s(0)}^{\bar{s}^+}\left(1 - \frac{\bar{d}}{f(s)}\right)ds > s_{\text{int}}$, $x(0) > 0$ sufficiently small to illustrate case (iii) in Theorem 3.2. In this case, there was no impulsive effect and the solutions approached $(s^*, 0)$, where $s^* > \bar{s}$. See Figure 3.4.

5. $s_{\text{int}} < 0$, $s(0) = \bar{s}^+$, $x(0) > -s_{\text{int}}$ to illustrate Theorem 3.4. In this case there were a finite number of impulses and then the solutions approached $(s^*, 0)$, where $s^* > \bar{s}$. See Figure 3.5.

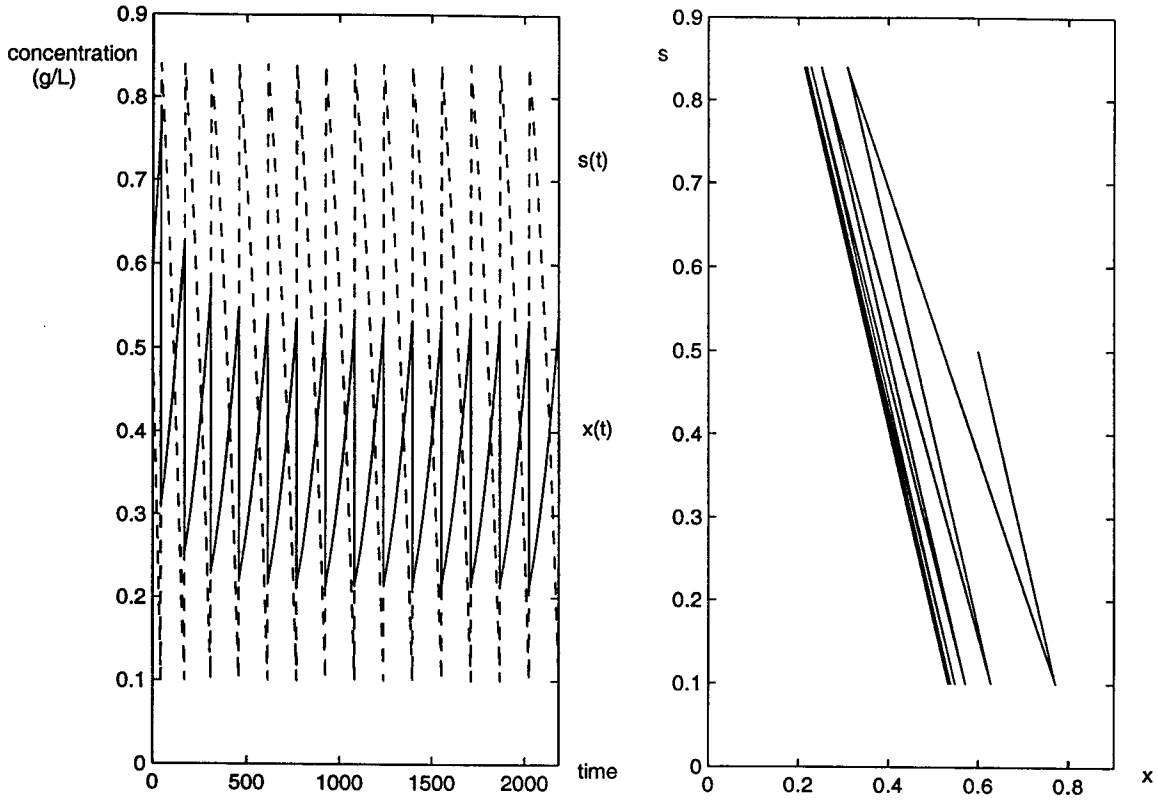

Figure 3.1: When $s_{\text{int}} > 0$, there is an orbitally stable positive periodic orbit with the property of asymptotic phase. In this case $s_{\text{int}} = 0.3197$, $\bar{s} > \lambda$, $s(0) > \bar{s}$, $x(0) > 0$ to illustrate case (i) in Theorem 3.2. The endpoints of each cycle were monotonically decreasing to the endpoint of the periodic orbit.

The case $s_{\text{int}} = 0$ was not illustrated, due to the knife-edge effect of such a condition.

The monotone uptake function used was $f(s) = \frac{\mu s}{K_s + s}$. The constants used in all simulations were $s^i = 1.333$, $\bar{s} = 0.1$, $r = 0.6$, $\mu = 0.01$, $K_s = 0.007$, $Y = 0.73$. These last three values were taken from actual constants used in Wincure, Cooper and Rey [38].

The initial conditions and the death rates for each simulation were as follows:

1. $s(0) = 0.5$, $x(0) = 0.6$, $\bar{d} = 0.004$. In this case $s_{\text{int}} = 0.8398$.

2. $s(0) = 0.8398$, $x(0) = 0.01295$, $\bar{d} = 0.00945$. In this case $s_{\text{int}} = 0.01943$.

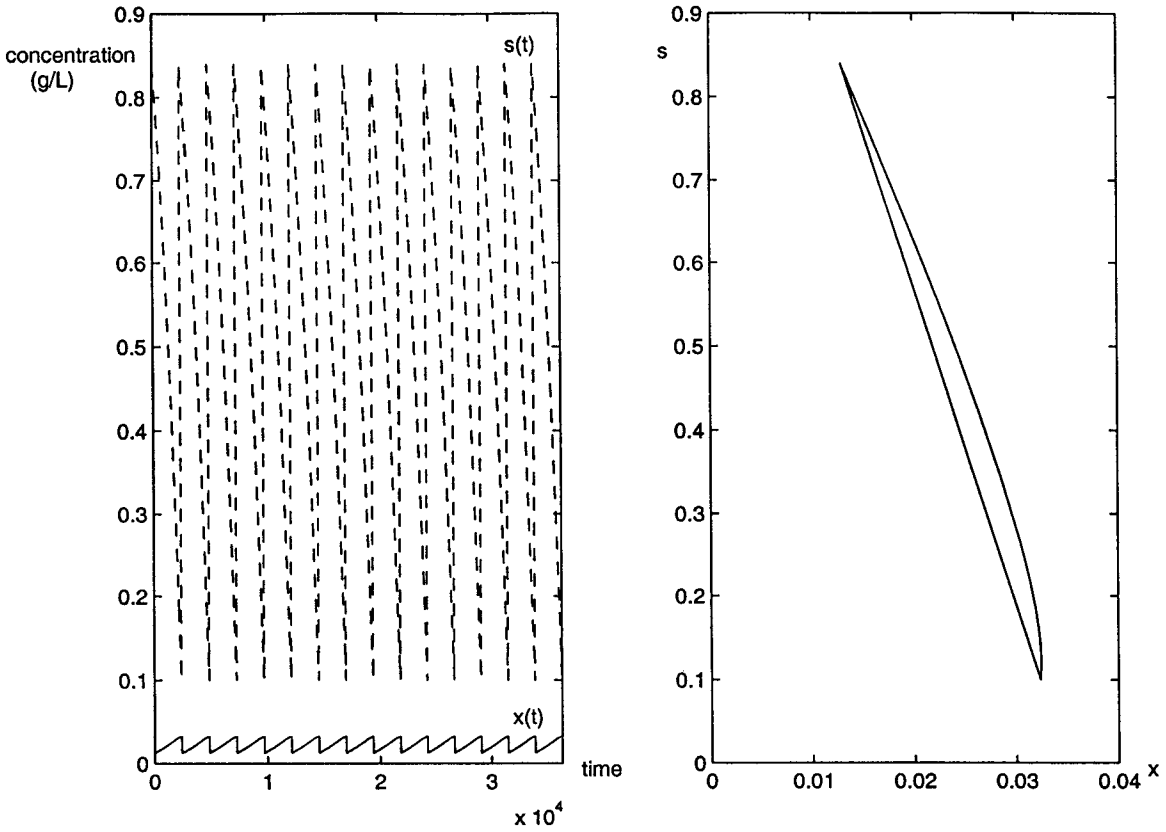

Figure 3.2: When $s_{\text{int}} > 0$, there is an orbitally stable positive periodic orbit with the property of asymptotic phase. In this case $s_{\text{int}} = 0.01943$, $\bar{s} < \lambda < \bar{s}^+$, $s(0) = \bar{s}^+$, $x(0) = (1-r)\frac{s_{\text{int}}}{r}$ to illustrate the first part of case (i) in Theorem 3.2. In this case, the initial conditions were equal to the initial points of the periodic orbit, so the orbit was the periodic orbit.

3. $s(0) = 0.5$, $x(0) = 0.002$, $\bar{d} = 0.00945$. In this case $s_{\text{int}} = 0.01943$.

4. $s(0) = 0.135$, $x(0) = 0.00001$, $\bar{d} = 0.00945$. In this case $s_{\text{int}} = 0.01943$.

5. $s(0) = 0.8398$, $x(0) = 0.4$, $\bar{d} = 0.00986$. In this case $s_{\text{int}} = -0.00316$.

3.7 Discussion

The Ontario Ministry of the Environemnt sets a maximum acceptable concentration (or interim maximal acceptable concentration) of contaminants in the water and this

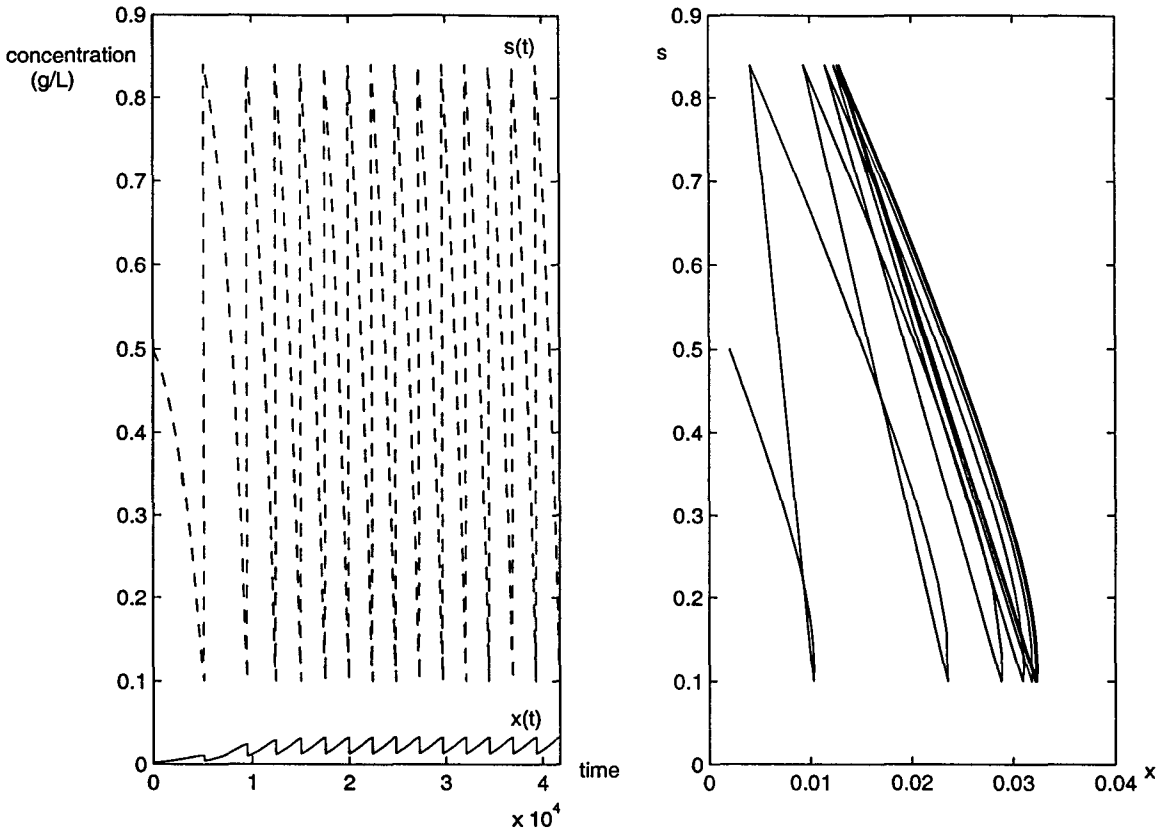

Figure 3.3: When $s_{\text{int}} > 0$, there is an orbitally stable positive periodic orbit with the property of asymptotic phase. In this case $s_{\text{int}} = 0.01943$, $\bar{s} < \lambda < \bar{s}$, $s(0) > \bar{s}$, $x(0) > Y(\bar{s}^+ - s(0)(1 - \frac{d}{f(\bar{s}^+)})$ to illustrate the second part of case (ii) in Theorem 3.2. In this case the endpoints of each cycle were monotonically increasing to the endpoint of the periodic orbit.

value would make an ideal choice for $\bar{s}$. With this value, we are guaranteed not to be releasing batches of water that are anything less than the maximal acceptable concentration (as opposed to the oxygen-driven SCF model). Furthermore, since s_{int} is increasing as $\bar{s}$ increases, this means that we are more likely to ensure that $s_{\text{int}} > 0$. Furthermore, if s_{int} was already positive, a higher value of $\bar{s}$ will result in a higher value of the endpoint of the periodic orbit and thus a higher yield of microorganisms in each cycle.

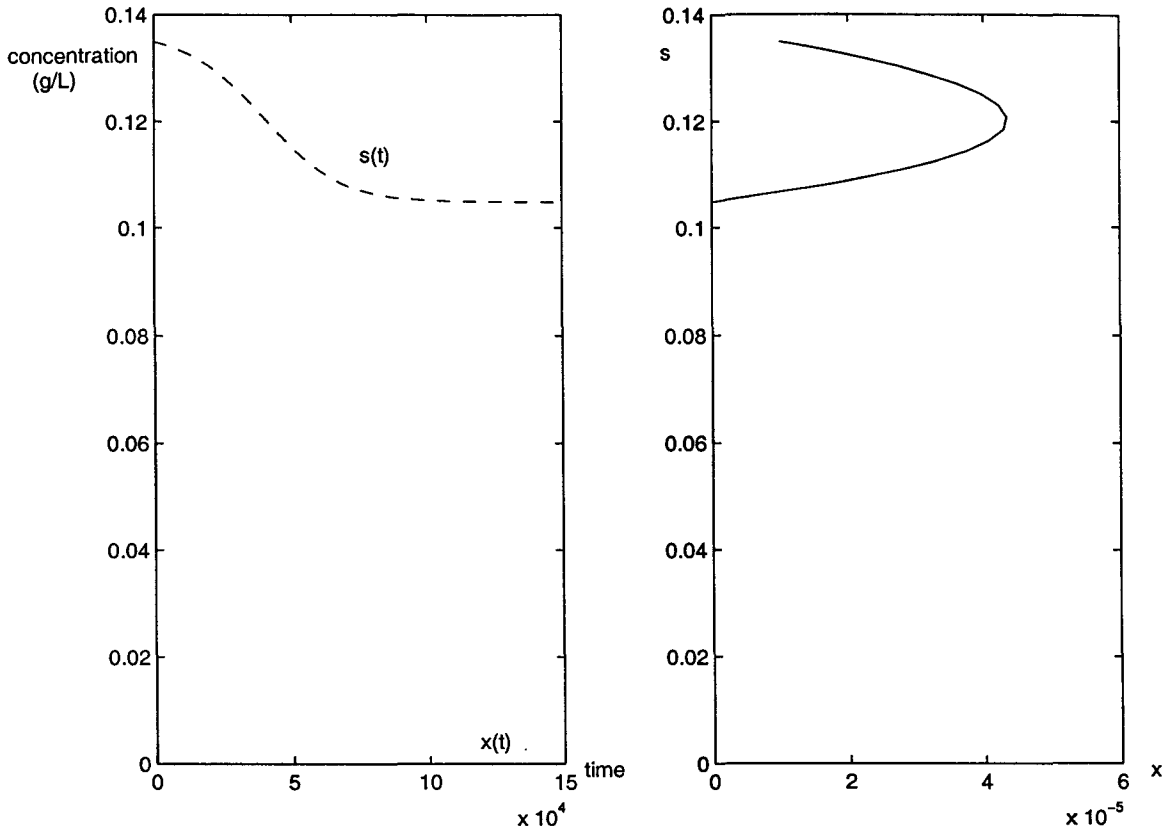

Figure 3.4: $s_{\text{int}} = 0.01943$, $Y\int_{s(0)}^{\bar{s}^+}\left(1-\frac{\bar{d}}{f(s)}\right)ds > s_{\text{int}}$, $x(0) > 0$ sufficiently small to illustrate case (iii) in Theorem 3.2. There was no impulsive effect and the solutions approached $(s^*, 0)$, where $s^* > \bar{s}$.

We require

$$\bar{s} \;<\; s^i$$

for the system to run. This is not an unreasonable restriction, since if $s^i < \bar{s}$ then the input is already below the MAC or IMAC, so there is no need to clean it up. The 'knife-edge' case, $\bar{s} = s^i$ means that $\bar{s} = (1-r)\bar{s}+rs^i$, so the nutrient is at an impulsive equilibrium of instantaneous impulsive effect. However, the microorganisms are being continually depleted, so they are being reduced by a fraction r at every instant and thus approach extinction. This case does not arise in reality.

With control over the choice of microorganism or the emptying/refilling fraction,

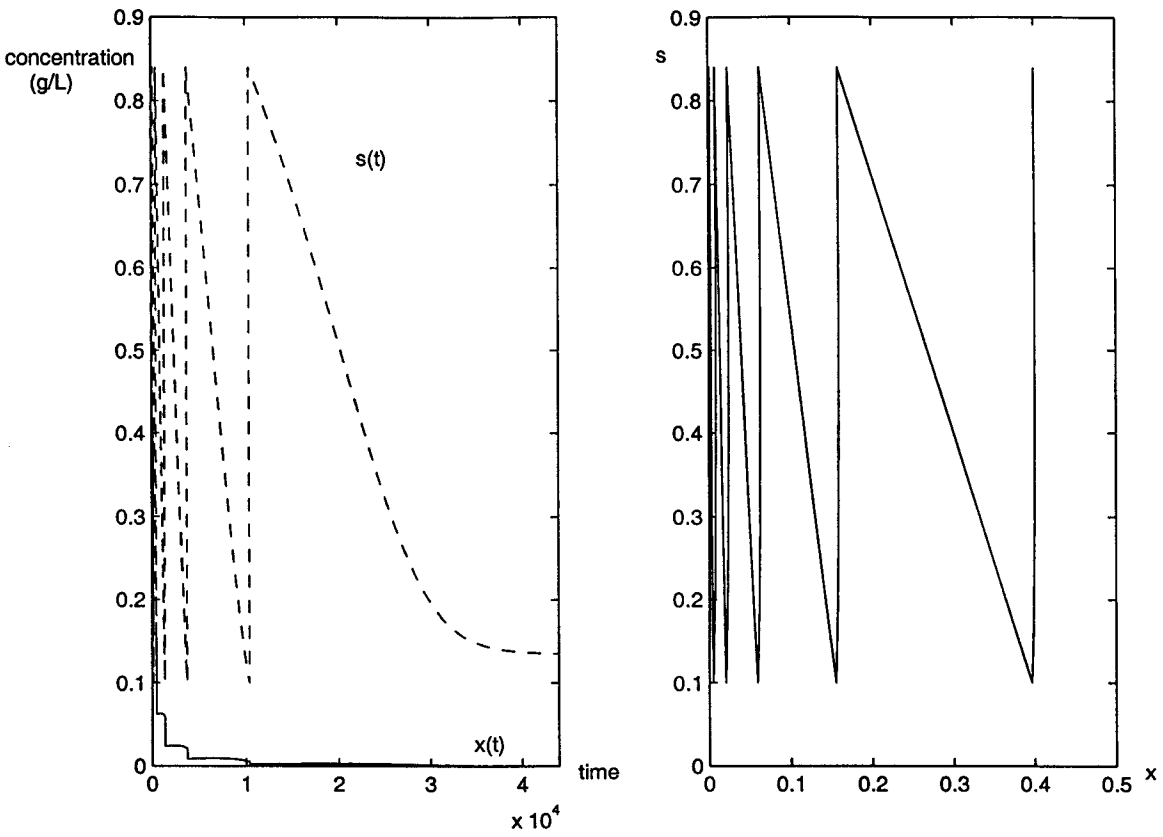

Figure 3.5: When $s_{\text{int}} < 0$, there is no nontrivial periodic orbit and solutions undergo at most a finite number of impulses. In this case $s_{\text{int}} = -0.00316$, $s(0) = \bar{s}^+$, $x(0) > -s_{\text{int}}$ to illustrate Theorem 3.4. In this case there were a finite number of impulses and then the solutions approached $(s^*, 0)$, where $s^* > \bar{s}$.

we can determine s_{int}. There is a unique positive periodic orbit with the property of asymptotic phase if and only if $s_{\text{int}} > 0$.

If $s_{\text{int}} > 0$ and $\bar{s} \geq \lambda$, where λ is the value of s such that $f(\lambda) = \bar{d}$ (or $\lambda = \infty$ if $f(s) < \bar{d}$ for all s) then the nontrivial periodic orbit attracts all solutions with initial conditions satisfying $s(0) > \bar{s}$ and $x(0) > 0$. If $s_{\text{int}} > 0$ and $\bar{s} < \lambda$ then the nontrivial periodic orbit attracts all solutions with initial conditions satisfying $s(0) \geq (1-r)\bar{s} + rs^i$ and $x(0) > 0$, or $s(0) > \bar{s}$ but $x(0)$ sufficiently large. The endpoints of each cycle in x will approach the endpoint of the periodic orbit monotonically. Furthermore, the cycle times will monotonically approach the period of the periodic

orbit.

If $s_{\text{int}} > 0$ and $s(0) < \bar{s}$ or $s(0)$ satisfies $Y \int_{s(0)}^{(1-r)\bar{s}+rs^i} \left(1 - \frac{d}{f(s)}\right) ds > s_{\text{int}}$ and $x(0) > 0$ is sufficiently small, then there are no moments of impulse and $x(t) \to 0$, $s(t) \to s^*$, where $\bar{s} \leq s^* < \lambda$.

If $s_{\text{int}} = 0$, then there is no nontrivial periodic solution and

$$\liminf_{t\to\infty} x(t) = 0.$$

If $s_{\text{int}} < 0$, then there is no nontrivial periodic orbit and solutions undergo at most a finite number of impulses and eventually $s(t) \to s^*$ and $x(t) \to 0$, where $\bar{s} \leq s^* < \lambda$.

Impulsive theory requires that $s(0) \neq \bar{s}$ so that we do not undergo cycling immediately. The initial condition $s(0) = s^i > (1-r)\bar{s} + rs^i$ is a reasonable one in practice, since the first batch to clean is presumably as polluted as the others. This means that we can measure s_{int} in advance, or choose an appropriate microorganism and emptying/refilling fraction so that $s_{\text{int}} > 0$. We will thus be guaranteed to cycle indefinitely for appropriate initial conditions. This is the most desirable situation.

We can also force the microorganism to wash out for appropriate constants or initial conditions, should this be desirable. An example where this might occur is if the microorganism x is a pest that is eating a neutral nutrient s until this nutrient is depleted below some value $\bar{s}$. If the microorganism switches nutrient at $\bar{s}$ to a nutrient that is valuable, it would be desirable to gradually eliminate the microorganism, without letting the neutral nutrient fall below $\bar{s}$. If we can choose an emptying/refilling fraction r such that $s_{\text{int}} < 0$, then the population will decrease over each cycle without causing the microorganism to switch nutrients and eventually we will have $s(t) \to s^* > \bar{s}$ and $x(t) \to 0$ as $t \to \infty$.

The biggest potential problem with the nutrient-driven model is the practicality of detecting the nutrient. However, in Sheppard and Cooper [30], the computer is programmed to cycle the nutrient (nitrogen in this case) at the precise time of nutrient exhaustion, suggesting that detection of the nutrient levels by a computer is viable, at least for some choices of limiting nutrient.

It is possible that detection may not be possible at low nutrient levels. However,

if $\tilde{s} > \bar{s}$ is the lowest value of nutrient that the computer can detect, we can program the computer to delay the moment of impulsive for a fixed period after detecting the level $\tilde{s}$. This is not an ideal solution, but it should provide a reasonable approximation to $\bar{s}$.

The oxygen-driven SCF process may be better if the goal is maximizing biomass or examining the evolutionary aspects of cells in response to nutrients. It is also possible that setting the computer to monitor nutrient levels may affect the life-cycle of the organisms, so it should be noted that we are assuming this effect is negligible for the purposes of this model. Comparison with the oxygen-driven model when $\bar{d} = 0$ shows that we are guaranteed to cycle indefinitely for any initial conditions with $s(0) > \bar{s}$ and $x(0) > 0$.

The nutrient-driven model retains many of the advantages of the SCF process. Cycle time is still a dependent variable, which was the main advantage of self-cycling fermentation over batch fermentation and other techniques. No cycle time needs to be specified in advance. There are also two identical batches at the end of each cycle.

There is a further advantage the nutrient-driven model has over the oxygen-driven one. In practice, a computer will never trigger the impulsive effect at a dissolved oxygen minimum, since there is a small time delay between the detection of the dissolved oxygen minimum and the emptying/refilling process. See Figure 2.3 for example. This delay corresponds to a time when the oxygen begins to rise rapidly. There is also a delay in triggering the nutrient-driven model, but in this case it is to the advantage of the system. Our aim with the nutrient-driven model is to improve efficiency of systems where the goal is to reduce the nutrient below some threshold, so this means that the nutrient level will only be smaller. Furthermore, if we know in advance that the delay corresponds to an amount ϵ of nutrient, then we can instruct the computer to detect the nutrient level at $\bar{s} + \epsilon$, on the assumption that the delay in the system means that we will actually be emptying the tank when the nutrient is at level $\bar{s}$.

For the remainder of this thesis we shall consider the nature of impulsive effect to

be nutrient-driven. The next questions that arise concern the size of the microorganisms and the nature of reproduction. We shall address such concerns in the context of impulsive differential equations in the next chapter.

Chapter 4

A Size-Structured Model for the Nutrient-Driven Self-Cycling Fermentation Process

4.1 Introduction

With the process of self-cycling fermentation, it is possible that some cells in the tank may continue to grow in size indefinitely. Although we are regularly removing a fraction the contents of the tank at the end of each cycle, there is still the distinct possibility that some cells may not get removed and may instead grow to relatively large sizes. It becomes necessary to consider what effect this will have on the process.

Size consideration has been a factor in practice. In Wentworth and Cooper [36], it was observed that after the exhaustion of the limiting nutrient, the cells continued to increase in size, but the total number of cells did not change.

In previous chapters, only the average mass of the organisms was considered. Some of the cells may be much larger than others, or there might be a greater number of small cells. Measuring biomass does not reflect the physical properties of the tank if we consider the effects of growth. In order to accommodate this, we will

examine population density, length, surface area and the number of cells. A model that accounts for individual variations in one or more characteristics, such as size, is called a structured population model.

The last part of this chapter takes a more realistic approach to modelling cell reproduction. The existing model is adapted to include impulsive effects, so it describes a model of self-cycling fermentation that accounts for cell division.

Some of the work in the first part of this chapter follows the approach of Cushing [12], although we have adapted the model to accommodate impulsive effects. The model in the last part is from Metz and Diekmann [22], and is also adapted to include impulsive effects. As in the previous chapter, the impulsive effect is driven by the nutrient reaching a predetermined tolerance $\bar{s}$.

4.2 Development of the model

Suppose an individual in the population is characterized by its length l. We assume all individuals have the same length l_b at birth and they do not shrink, so $l_b \leq l$.

We assume that the rate of nutrient uptake is proportional to the superficial surface area. For example, filter feeding species such as *Daphnia* absorb nutrient in this way. Although the actual cell surface area may be quite complex, the superficial surface area is approximately spherical. For an individual of length l the rate of uptake is given by $l^2 f(s)$, where $f(s)$ is the uptake rate per unit surface area. We assume that f satisfies the conditions in (3.2.2).

Some sources require $\lim_{s\to\infty} f(s) < \infty$ to ensure that the uptake function does not lose biological relevance for large values of s. However, since the nutrient levels in the SCF process are between fixed values, unbounded uptake functions do not pose a problem for our system.

Suppose a fraction κ of energy derived from ingested nutrient is used for growth, and $1 - \kappa$ is used for reproduction. The energy required for maintenance of the organism is assumed to be insignificant in comparison and is neglected. Let ϖ be the

conversion factor relating nutrient to biomass and ω be the conversion factor relating nutrient units to weight of offspring.

The growth rate of the organism is

$$\frac{d(l^3)}{dt} = \frac{\kappa l^2}{\varpi} f(s),$$

or

$$\frac{dl}{dt} = \frac{\kappa}{3\varpi} f(s).$$

The remaining fraction of uptake is $(1-\kappa)l^2 f(s)$. This is used for reproduction. Each offspring requires ωl_b^3 units of resource. Thus the birth rate for individuals of length l is

$$\text{birth rate} = \frac{1-\kappa}{\omega l_b^3} f(s) l^2.$$

Let $\rho(t,l)$ be the density of individuals of size l at time t. ρ has units in grams per litre. The number of individuals with length $a \leq l \leq b$, at time t, is given by $\int_a^b \rho(t,l)dl$.

Consider individuals of length $a \leq l \leq b$ at a fixed time $t_0 > 0$. At time $t > t_0$, this group of individuals occupies size range $a(t) \leq l \leq b(t)$, where

$$a(t) = a + \int_{t_0}^{t} \frac{\kappa}{3\varpi} f(s(r))dr \tag{4.2.1}$$

$$b(t) = b + \int_{t_0}^{t} \frac{\kappa}{3\varpi} f(s(r))dr. \tag{4.2.2}$$

During each cycle, the number of individuals in this group can only change due to mortality, so

$$\frac{d}{dt}\int_{a(t)}^{b(t)} \rho(t,l)dl = -\bar{d}\int_{a(t)}^{b(t)} \rho(t,l)dl \qquad s \neq \bar{s}, \tag{4.2.3}$$

where $\bar{d}$ is the death rate, which we assume to be constant and independent of l. Each cycle is defined in the same manner as the previous chapter, so the tolerance $\bar{s}$ is assumed to satisfy $\bar{s} < s^i$.

For the impulsive effect, we have to consider the difference between the population at time t_k^- and time t_k^+, where t_k is the time at which the nutrient reaches the tolerance level $\bar{s}$. Note firstly that

$$\begin{aligned} a(t_k^+) &= a + \int_{t_0}^{t_k^+} \frac{\kappa}{3\varpi} f(s(r))dr \\ &= a + \int_{t_0}^{t_k^-} \frac{\kappa}{3\varpi} f(s(r))dr \\ &= a(t_k^-), \end{aligned}$$

since the integral is not affected by the impulsive effect. Similarly, $b(t_k^+) = b(t_k^-)$. Now at the end of each cycle, the number of individuals of size l (and hence the density of individuals of size l) is reduced by a fraction r. That is,

$$\begin{aligned} \Delta\rho(t_k, l) &\equiv \rho(t_k^+, l) - \rho(t_k^-, l) \\ &= -r\rho(t_k^-, l) \qquad\qquad s = \bar{s}. \end{aligned} \tag{4.2.4}$$

Turning now to the number of individuals at the impulse point, we have

$$\begin{aligned} \Delta \int_{a(t_k)}^{b(t_k)} \rho(t_k, l)dl &= \int_{a(t_k^+)}^{b(t_k^+)} \rho(t_k^+, l)dl - \int_{a(t_k^-)}^{b(t_k^-)} \rho(t_k, l)dl \\ &= \int_{a(t_k)}^{b(t_k)} \Delta\rho(t_k, l)dl \\ &= -r \int_{a(t_k)}^{b(t_k)} \rho(t_k, l)dl \qquad\qquad s = \bar{s}. \end{aligned}$$

Without impulsive effect, we have, using the Leibniz rule applied to Equation (4.2.3),

$$\int_{a(t)}^{b(t)} \frac{\partial\rho(t,l)}{\partial t}dl + b'(t)\rho(t, b(t)) - a'(t)\rho(t, a(t) = -\bar{d}\int_{a(t)}^{b(t)} \rho(t, l)dl$$

for $t \neq t_k$.

Now, by the fundamental theorem of calculus applied to (4.2.1)-(4.2.2), $b'(t) = a'(t) = \frac{\kappa}{3\varpi} f(s(t))$, so we have

$$\int_{a(t)}^{b(t)} \frac{\partial\rho(t,l)}{\partial t}dl + \frac{\kappa}{3\varpi} f(s(t))\left[\rho(t, b(t)) - \rho(t, a(t)\right] + \bar{d}\int_{a(t)}^{b(t)} \rho(t, l)dl = 0,$$

or

$$\int_{a(t)}^{b(t)} \left[\frac{\partial \rho(t,l)}{\partial t} + \frac{\kappa}{3\varpi} f(s(t)) \frac{\partial \rho(t,l)}{\partial l} + \bar{d}\rho(t,l) \right] dl \;=\; 0.$$

We can take the (length) limits to be a and b such that $l_b < a < b$. Suppose the integrand is not identically zero as a function of l for any fixed t_0 with $t_0 \neq t_k$. Then there is a point l_0 where it is (say) positive and hence a range of lengths around l_0 where it would be positive (since continuous in l). Taking a and b to be the endpoints of such an interval leads to a contradiction. Thus the integrand must be identically zero. Hence, for $t \neq t_k$,

$$\frac{\partial \rho}{\partial t} + \frac{\kappa}{3\varpi} f(s(t)) \frac{\partial \rho}{\partial l} \;=\; -\bar{d}\rho \tag{4.2.5}$$

for $l_b < l$ and $s \neq \bar{s}$.

At time $t = 0$,

$$\rho(0,l) \;=\; \rho_0(l) \tag{4.2.6}$$

for $l \geq l_b$, where ρ_0 is the initial density of the population.

The number of offspring born in the time interval $(t, t+\delta t)$, where $\delta t > 0$ is small, is obtained by adding the individual contribution of each size class. This is given by

$$\frac{1-\kappa}{\omega l_b^3} f(s(t)) \int_{l_b}^{\infty} l^2 \rho(t,l) dl \; \delta t.$$

We choose δt small so that offspring born of offspring in this period can be neglected. We allow unbounded sizes, but we shall see later that the number of such individuals is negligible. See section 4.5.

At time $t+\delta t$, the length of the offspring that were born at time t is approximately

$$l_{\delta t} \;=\; l_b + \frac{\kappa}{3\varpi} f(s(t)) \delta t.$$

The newborns occupy the size range $l_b \leq l \leq l_{\delta t}$ at time $t + \delta t$, so an expression for the number of individuals at time $t + \delta t$, is given by

$$\int_{l_b}^{l_{\delta t}} \rho(t+\delta t, l) dl \;=\; \frac{1-\kappa}{\omega l_b^3} f(s(t)) \int_{l_b}^{\infty} l^2 \rho(t,l) dl \; \delta t,$$

or

$$\frac{3\varpi}{\kappa f(s(t))\delta t}\int_{l_b}^{l_{\delta t}}\rho(t+\delta t,l)dl \;=\; \frac{3\varpi(1-\kappa)}{\kappa\omega l_b^3}\int_{l_b}^{\infty}l^2\rho(t,l)dl.$$

Let $\delta t \to 0$. Then

$$\rho(t,l_b) \;=\; \frac{3\varpi(1-\kappa)}{\kappa\omega l_b^3}\int_{l_b}^{\infty}l^2\rho(t,l)dl \qquad t\neq t_k, \tag{4.2.7}$$

giving us a boundary condition at $l = l_b$. When $t = t_k$, the boundary condition becomes,

$$\rho(t_k^+,l_b) \;=\; \frac{3\varpi(1-\kappa)}{\kappa\omega l_b^3}\int_{l_b}^{\infty}l^2(1-r)\rho(t_k^-,l)dl. \tag{4.2.8}$$

The rate of consumption of nutrient by an individual of length l is proportional to the surface area and the uptake function. Thus

$$\frac{ds}{dt} \;=\; -f(s(t))\int_{l_b}^{\infty}l^2\rho(t,l)dl \qquad s\neq\bar{s}, \tag{4.2.9}$$

where we determine the rate of uptake of nutrient at time t by summing over individuals of all sizes.

The impulsive effect for nutrient is to reduce the amount of nutrient remaining at the end of a cycle by a fraction r and then to add in an equal volume of fresh medium. This gives us the conditions

$$s(0) \;=\; s^0 \tag{4.2.10}$$

$$\Delta s \;=\; -rs+rs^i \qquad s=\bar{s}. \tag{4.2.11}$$

In summary, the ordinary and partial differential equations for nutrient and population density are given by

$$\frac{ds}{dt} \;=\; -f(s(t))\int_{l_b}^{\infty}l^2\rho(t,l)dl \qquad s\neq\bar{s}$$

$$\frac{\partial\rho}{\partial t}+\frac{\kappa}{3\varpi}f(s(t))\frac{\partial\rho}{\partial l} \;=\; -\bar{d}\rho \qquad s\neq\bar{s}$$

$$\Delta s \;=\; -rs+rs^i \qquad s=\bar{s}$$

$$\Delta\rho(t_k,l) \;=\; -r\rho(t_k^-,l) \qquad s=\bar{s},$$

with boundary conditions

$$\begin{aligned}\rho(t,l_b) &= \frac{3\varpi(1-\kappa)}{\kappa\omega l_b^3}\int_{l_b}^{\infty} l^2\rho(t,l)dl \qquad\qquad t\neq t_k\\ \rho(t_k^+,l_b) &= \frac{3\varpi(1-\kappa)}{\kappa\omega l_b^3}\int_{l_b}^{\infty} l^2(1-r)\rho(t_k^-,l)dl,\end{aligned}$$

and initial conditions

$$\begin{aligned}s(0) &= s^0\\ \rho(0,l) &= \rho_0(l).\end{aligned}$$

Remark. We shall see shortly that both the average individual length and the standard deviation in length approach a constant value as $t\to\infty$. Thus, while some individuals may grow unnaturally large, they represent a negligible fraction of the total population. This is partly due to the fact that the tank is assumed to be well-stirred and so the cells are removed uniformly. We also expect $\rho_0(l)=0$ for $l\geq l_m$. This implies

$$\rho(t,l) \equiv 0$$

for $l\geq l_m(t)$, where

$$l_m(t) = l_m+\int_0^t \frac{\kappa}{3\varpi}f(s(r))dr.$$

4.3 Reduction to a system of impulsive ordinary differential equations

Let

$$\begin{aligned}A(t) &= \frac{1}{l_b^2}\int_{l_b}^{\infty}\rho(t,l)l^2dl\\ L(t) &= \frac{1}{l_b}\int_{l_b}^{\infty}\rho(t,l)ldl\\ P(t) &= \int_{l_b}^{\infty}\rho(t,l)dl.\end{aligned}$$

$A(t)$ represents the total surface area of the population at time t, $L(t)$ the total length and $P(t)$ the total number of individuals. Our aim is to derive a system of impulsive ordinary differential equations for these new variables.

Notice first that

$$A'(t) = \frac{1}{l_b^2}\int_{l_b}^{\infty}\frac{\partial \rho}{\partial t}l^2 dl.$$

From (4.2.5), we have

$$\begin{aligned}\frac{l^2}{l_b^2}\frac{\partial \rho}{\partial t} &= -\frac{\kappa l^2}{3\varpi l_b^2}f(s(t))\frac{\partial \rho}{\partial l} - \frac{l^2\bar{d}}{l_b^2}\rho \\ \frac{1}{l_b^2}\int_{l_b}^{\infty} l^2\frac{\partial \rho}{\partial t}dl &= -\frac{\kappa f(s(t))}{3\varpi l_b^2}\int_{l_b}^{\infty} l^2\frac{\partial \rho}{\partial l}dl - \frac{\bar{d}}{l_b^2}\int_{l_b}^{\infty} l^2\rho dl.\end{aligned}$$

Therefore,

$$\begin{aligned}A'(t) + \frac{\kappa}{3\varpi l_b^2}f(s(t))\int_{l_b}^{\infty} l^2\frac{\partial \rho}{\partial l}dl &= -\bar{d}A(t) \\ A'(t) + \frac{\kappa}{3\varpi l_b^2}f(s(t))l^2\rho(t,l)\Big|_{l=l_b}^{\infty} - \frac{\kappa}{3\varpi l_b^2}f(s(t))\int_{l_b}^{\infty} 2l\rho dl &= -\bar{d}A(t).\end{aligned}$$

Now, ρ vanishes for large lengths, so we can take $l^2\rho(t,l) \to 0$ as $l \to \infty$. Thus,

$$A'(t) = \frac{2\kappa}{3\varpi l_b}f(s(t))L(t) - \bar{d}A(t) + \frac{\kappa}{3\varpi}f(s(t))\rho(t,l_b).$$

From (4.2.7), $\rho(t,l_b) = \frac{3\varpi(1-\kappa)}{\kappa\omega l_b}A(t)$, so we have

$$A'(t) = \frac{2\beta}{3l_b}f(s(t))L(t) + \frac{\alpha}{l_b}f(s(t))A(t) - \bar{d}A(t) \qquad s \neq \bar{s}.$$

where $\alpha = \frac{1-\kappa}{\omega}$ and $\beta = \frac{\kappa}{\varpi}$. When $s = \bar{s}$, we have

$$\begin{aligned}\Delta A(t_k) &= \frac{1}{l_b^2}\int_{l_b^2}^{\infty}\rho(t_k^+,l)l^2dl - \frac{1}{l_b^2}\int_{l_b^2}^{\infty}\rho(t_k^-,l)l^2dl \\ &= \frac{1}{l_b^2}\int_{l_b^2}^{\infty}\Delta\rho(t_k,l)l^2dl \\ &= -\frac{r}{l_b^2}\int_{l_b}^{\infty}\rho(t_k^-,l)l^2dl \\ &= -rA(t_k^-).\end{aligned}$$

Using (4.2.6), at time $t = 0$, we have

$$\begin{aligned} A(0) &= \frac{1}{l_b^2}\int_{l_b}^{\infty} \rho(0,l)dl \\ &= \frac{1}{l_b^2}\int_{l_b}^{\infty} \rho_0(l)dl \\ &\equiv A_0. \end{aligned}$$

We now look at the length equation.

$$\begin{aligned} L'(t) &= \frac{1}{l_b}\int_{l_b}^{\infty} \frac{\partial \rho(t,l)}{\partial t} l dl \\ &= \frac{1}{l_b}\int_{l_b}^{\infty} \left(-\frac{\kappa}{3\varpi} f(s(t)) \frac{\partial \rho(t,l)}{\partial l} l - \bar{d}\rho(t,l)l \right) dl \\ &= -\frac{\kappa}{3\varpi l_b} f(s(t)) \int_{l_b}^{\infty} l \frac{\partial \rho(t,l)}{\partial l} dl - \bar{d}L(t) \\ &= -\frac{\kappa}{3\varpi l_b} f(s(t)) l\rho(t,l)\Big|_{l=l_b}^{\infty} + \frac{\kappa}{3\varpi l_b} f(s(t)) \int_{l_b}^{\infty} \rho(t,l)dl - \bar{d}L(t) \\ &= \frac{\kappa}{3\varpi} f(s(t))\rho(t,l_b) + \frac{\kappa}{3\varpi l_b} f(s(t))P(t) - \bar{d}L(t) \\ &= \frac{1-\kappa}{\omega l_b} f(s(t))A(t) + \frac{\kappa}{3\varpi l_b} f(s(t))P(t) - \bar{d}L(t), \end{aligned}$$

using (4.2.7). Hence we have

$$L'(t) = \frac{\alpha}{l_b} f(s(t))A(t) + \frac{\beta}{3l_b} f(s(t))P(t) - \bar{d}L(t) \qquad s \neq \bar{s}.$$

When $s = \bar{s}$, we have

$$\begin{aligned} \Delta L(t_k) &= \frac{1}{l_b}\int_{l_b}^{\infty} \Delta\rho(t_k,l) l dl \\ &= -\frac{r}{l_b}\int_{l_b}^{\infty} \rho(t_k^-,l) l dl \\ &= -rL(t_k^-) \end{aligned}$$

and at $t = 0$, we have

$$\begin{aligned} L(0) &= \frac{1}{l_b}\int_{l_b}^{\infty} \rho(0,l) l dl \\ &= \frac{1}{l_b}\int_{l_b}^{\infty} \rho_0(l) l dl \\ &\equiv L_0. \end{aligned}$$

Finally, we turn to the population equation.

$$\begin{aligned} P'(t) &= \int_{l_b}^{\infty} \frac{\partial \rho(t,l)}{\partial t} dl \\ &= \int_{l_b}^{\infty} \left(-\frac{\kappa}{3\varpi} f(s(t)) \frac{\partial \rho(t,l)}{\partial l} - \bar{d}\rho(t,l) \right) dl \\ &= -\frac{\kappa}{3\varpi} f(s(t)) \int_{l_b}^{\infty} \frac{\partial \rho(t,l)}{\partial l} dl - \bar{d}P(t) \\ &= -\frac{\kappa}{3\varpi} f(s(t)) \rho(t,l)\Big|_{l=l_b}^{\infty} - \bar{d}P(t) \\ &= \frac{\kappa}{3\varpi} f(s(t)) \rho(t,l_b) - \bar{d}P(t) \\ &= \frac{1-\kappa}{\omega l_b} f(s(t)) A(t) - \bar{d}P(t), \end{aligned}$$

using (4.2.7). Hence we have

$$P'(t) = \frac{\alpha}{l_b} f(s(t)) A(t) - \bar{d}P(t) \qquad s \neq \bar{s}.$$

When $s = \bar{s}$, we have

$$\begin{aligned} \Delta P(t_k) &= \int_{l_b}^{\infty} \Delta \rho(t_k, l) dl \\ &= -r \int_{l_b}^{\infty} \rho(t_k^-, l) dl \\ &= -r P(t_k^-) \end{aligned}$$

and at $t = 0$, we have

$$\begin{aligned} P(0) &= \int_{l_b}^{\infty} \rho(0,l) dl \\ &= \int_{l_b}^{\infty} \rho_0(l) dl \\ &\equiv P_0. \end{aligned}$$

We have thus reduced the problem to a system of impulsive ordinary differential equations

$$
\begin{aligned}
s' &= -f(s)l_b^2 A && s \neq \bar{s} \\
A' &= -\bar{d}A + \frac{\alpha}{l_b} f(s)A + \frac{2\beta}{3l_b} f(s)L && s \neq \bar{s} \\
L' &= -\bar{d}L + \frac{\alpha}{l_b} f(s)A + \frac{\beta}{3l_b} f(s)P && s \neq \bar{s} \\
P' &= -\bar{d}P + \frac{\alpha}{l_b} f(s)A && s \neq \bar{s} \\
\Delta s &= -rs + rs^i && s = \bar{s} \\
\Delta A &= -rA && s = \bar{s} \\
\Delta L &= -rL && s = \bar{s} \\
\Delta P &= -rP && s = \bar{s}.
\end{aligned}
\tag{4.3.12}
$$

4.4 Further developments

If we let

$$
\vec{p} = \begin{pmatrix} A \\ L \\ P \end{pmatrix} \quad \text{and} \quad H = \begin{pmatrix} \alpha & \alpha & \alpha \\ \frac{2}{3}\beta & 0 & 0 \\ 0 & \frac{1}{3}\beta & 0 \end{pmatrix},
$$

then the impulsive system is

$$
\begin{aligned}
s' &= -f(s)l_b^2 A && s \neq \bar{s} \\
\vec{p}\,' &= -\bar{d}\vec{p} + \frac{f(s)}{l_b} H^t \vec{p} && s \neq \bar{s} \\
\Delta s &= -rs + rs^i && s = \bar{s} \\
\Delta \vec{p} &= -r\vec{p} && s = \bar{s}.
\end{aligned}
$$

If we make the change of variable $\vec{q} = T^t\vec{p}$, where T is a nonsingular matrix, then

$$
\begin{aligned}
\vec{q} &= -\bar{d}\vec{q} + \frac{f(s)}{l_b} (T^{-1}HT)^t \vec{q} && s \neq \bar{s} \\
\Delta \vec{q}^{-} &= -r\vec{q} && s = \bar{s}.
\end{aligned}
\tag{4.4.13}
$$

Using Lemma 1 (page 845) of Cushing [12], H has a positive eigenvalue $\bar{\mu}$. From Lemma 9.3.1 (page 216) of Smith and Waltman [32], H has a corresponding eigenvector

$$\vec{v} = \begin{pmatrix} \frac{9}{2}\left(\frac{\bar{\mu}}{\beta}\right)^2 \\ \frac{3\mu}{\beta} \\ 1 \end{pmatrix},$$

where $\bar{\mu} = \bar{\mu}(\alpha, \beta)$ is smooth and strictly increasing in α and β, with $\bar{\mu}(\alpha, 0) = \alpha$ and $\bar{\mu}(0, \beta) = 0$.

The characteristic polynomial of H is

$$\lambda^3 - \alpha\lambda^2 - \frac{2}{3}\alpha\beta\lambda - \frac{2}{9}\alpha\beta^2 = 0. \tag{4.4.14}$$

Corresponding to the eigenvalue $\bar{\mu}$, H^t also has a positive eigenvector $\vec{w}$, which satisfies $\vec{w} \cdot \vec{v} = 1$ and which has first component

$$w_1 = \frac{2\bar{\mu}\beta^2}{9\bar{\mu}^3 + 6\alpha\beta\bar{\mu} + 4\alpha\beta^2}.$$

The remaining eigenvalues of H are $\gamma \pm i\nu$, where $\gamma < 0$ and $\nu > 0$. There is a nonsingular matrix T such that

$$T^{-1}HT = \begin{pmatrix} \bar{\mu} & 0 & 0 \\ 0 & \gamma & \nu \\ 0 & -\nu & \gamma \end{pmatrix}.$$

The first column of T is the eigenvector $\vec{v}$ and the first row of T^{-1} is $\vec{w}^t$. $\bar{\mu}$ is the *physiological efficiency coefficient* of the population, reflecting both reproductive and growth efficiency.

In the new variables, we have

$$\vec{q} = \begin{pmatrix} x \\ y \\ z \end{pmatrix},$$

where

$$x = \vec{v}\cdot\vec{p} = \frac{9}{2}\left(\frac{\bar{\mu}}{\beta}\right)^2 A + \frac{3\bar{\mu}}{\beta}L + P > 0$$

is a weighted average of A, L and P that serves as a measure of population size. Note that

$$A = \vec{c}\cdot\vec{q} = w_1 x + c_2 y + c_3 z,$$

where

$$c = \begin{pmatrix} w_1 \\ c_2 \\ c_3 \end{pmatrix}$$

is the first column of T^{-1}, containing the first component $w_1 > 0$ of the positive eigenvector $\vec{w}$. Consequently, from (4.4.13), the impulsive differential equations are

$$\begin{aligned}
s' &= -f(s)l_b^2(w_1 x + c_2 y + c_3 z) && s \neq \bar{s} \\
x' &= -\bar{d}x + \frac{\bar{\mu}}{l_b}f(s)x && s \neq \bar{s} \\
y' &= -\bar{d}y + \frac{f(s)}{l_b}(\gamma y - \nu z) && s \neq \bar{s} \\
z' &= -\bar{d}z + \frac{f(s)}{l_b}(\nu y + \gamma z) && s \neq \bar{s} \\
\Delta s &= -rs + rs^i && s = \bar{s} \\
\Delta x &= -rx && s = \bar{s} \\
\Delta y &= -ry && s = \bar{s} \\
\Delta z &= -rz && s = \bar{s}.
\end{aligned} \tag{4.4.15}$$

Proposition 4.1. *Consider model (4.4.15). Let $u = y + iz$. Then $u(t) \to 0$ as $t \to \infty$.*

Proof. For $s \neq \bar{s}$, we have

$$\begin{aligned}
\frac{d|u|^2}{dt} &= 2yy' + 2zz' \\
&= 2y\left[-\bar{d}y + \frac{\gamma}{l_b}g(s)y - \frac{\nu}{l_b}g(s)z\right] + 2z\left[-\bar{d}z + \frac{\nu}{l_b}g(s)y + \frac{\gamma}{l_b}g(s)z\right]
\end{aligned}$$

$$
\begin{aligned}
&= 2\left[-\bar{d}+\frac{\gamma}{l_b}g(s(t))\right](y^2+z^2) \\
&= 2\left[-\bar{d}+\frac{\gamma}{l_b}g(s(t))\right]|u|^2 \\
&\leq -2\bar{d}|u|^2 \qquad (4.4.16)
\end{aligned}
$$

since $\gamma < 0$.

Either (4.4.16) holds for all t sufficiently large, or there exists a sequence $\{t_k\}_{k=1}^{\infty}$ with $t_k \to \infty$ as $k \to \infty$ such that $s(t_k^-) = \bar{s}$. In the first case, $|u|^2 \to 0$ as $t \to \infty$. Otherwise

$$
\frac{d|u|^2}{dt} \leq -2\bar{d}|u|^2, \qquad t \neq t_k.
$$

Since $\Delta y(t_k) = y(t_k^+) - y(t_k^-) = -ry(t_k^-)$, it follows that $y(t_k^+) + y(t_k^-) = (2-r)y(t_k^-)$. Thus $y^2(t_k^+) - y^2(t_k^-) = -r(2-r)y^2(t_k^-)$. Similarly $z^2(t_k^+) - z^2(t_k^-) = -r(2-r)z^2(t_k^-)$. Hence $\Delta|u|^2(t_k) = \left(y^2(t_k^+) + z^2(t_k^+)\right) - \left(y^2(t_k^-) + z^2(t_k^-)\right) = -r(2-r)|u|^2(t_k^-)$.

With (4.4.16), we obtain the impulsive differential inequality

$$
\begin{aligned}
\frac{d}{dt}|u|^2 &\leq -2\bar{d}|u|^2 \qquad && t \neq t_k \\
\Delta|u|^2 &= -r(2-r)|u|^2 \qquad && t = t_k.
\end{aligned}
$$

We thus have

$$
\begin{aligned}
|u|^2(t) &\leq |u|^2(t_k^+)e^{-2\bar{d}(t-t_k)} \qquad && t_k < t < t_{k+1} \\
|u|^2(t_{k+1}^-) &\leq |u|^2(t_k^+)e^{-2\bar{d}(t_{k+1}-t_k)}
\end{aligned}
$$

Now, $|u|^2(t_k^+) - |u|^2(t_k^-) = -r(2-r)|u|^2(t_k^-)$, so $|u|^2(t_k^+) = (1-r)^2|u|^2(t_k^-)$. Thus, for $t_k < t < t_{k+1}$,

$$
\begin{aligned}
|u|^2(t) &\leq (1-r)^2|u|^2(t_k^-)e^{-2\bar{d}(t-t_k)} \\
&\leq (1-r)^2\left[(1-r)^2|u|^2(t_{k-1}^-)e^{-2\bar{d}(t_k-t_{k-1})}\right]e^{-2\bar{d}(t-t_k)} \\
&= (1-r)^4|u|^2(t_{k-1}^-)e^{-2\bar{d}(t-t_{k-1})} \\
&\vdots \\
&\leq (1-r)^{2k}|u|^2(t_1^-)e^{-2\bar{d}(t-t_1)} \\
&\leq (1-r)^{2k}|u|^2(0^+)e^{-2\bar{d}(t-t_0)}.
\end{aligned}
$$

Now, $0 < r < 1$. Therefore, as $t \to \infty$, $k \to \infty$, $\lim_{t\to\infty} |u|^2(t) = 0$.

□

By Proposition 4.1, it follows immediately that in model (4.4.15) we have

$$\lim_{t\to\infty} y(t) = \lim_{t\to\infty} z(t) = 0.$$

Therefore, the omega limit set of (4.4.15) is contained in the set $\{(s,x,y,z) \in \mathbb{R}^4_+ : s \geq \bar{s}, y = z = 0\}$.

Next, we study the dynamics of (4.4.15) with initial conditions restricted to this set, giving the autonomous impulsive system

$$\begin{aligned} s' &= -g(s)l_b^2 w_1 x & s &\neq \bar{s} \\ x' &= -\bar{d}x + \bar{\mu} l_b^{-1} g(s)x & s &\neq \bar{s} \\ \Delta s &= -r\bar{s} + rs^i & s &= \bar{s} \\ \Delta x &= -rx(t_k^-) & s &= \bar{s}. \end{aligned} \tag{4.4.17}$$

$$s(0) > \bar{s},\ x(0) \geq 0.$$

Define

$$s_{\text{intsize}} \equiv \int_{\bar{s}}^{(1-r)\bar{s}+rs^i} \left(\frac{\bar{\mu}}{l_b^3 w_1} - \frac{\bar{d}}{g(s)l_b^2 w_1} \right) ds.$$

In the notation of Theorem 1,

$$\begin{aligned} s_{\text{int}} &= s_{\text{intsize}} \\ f(s) &= \frac{\bar{\mu} g(s)}{l_b}, \\ Y &= \frac{\bar{\mu}}{l_b^3 w_1}. \end{aligned}$$

By Theorem 3.2, if $s_{\text{intsize}} > 0$, then there exists a periodic orbit with one impulse per period, and solutions with $s(0) \geq (1-r)\bar{s} + rs^i$ and $x(0) > 0$ approach this periodic orbit as $t \to \infty$. The periodic orbit cycles between $((1-r)\bar{s} + rs^i, \frac{1-r}{r} s_{\text{intsize}})$ and $(\bar{s}, \frac{1}{r} s_{\text{intsize}})$. If $s_{\text{intsize}} < 0$, then $x(t) \to 0$ as $t \to \infty$. If $s_{\text{intsize}} = 0$, then $\liminf_{t\to\infty} x(t) = 0$.

Thus, in order to control the fermentor, one needs to understand how to manipulate s_{intsize}. Define

$$\begin{aligned} l_{b_0} &\equiv \frac{\bar{\mu} r(s^i - \bar{s})}{\bar{d} \int_{\bar{s}}^{(1-r)\bar{s}+rs^i} [g(s)]^{-1} ds}, \\ \bar{\mu}_0 &\equiv \frac{\bar{d} l_b \int_{\bar{s}}^{(1-r)\bar{s}+rs^i} [g(s)]^{-1} ds}{r(s^i - \bar{s})}. \end{aligned}$$

It follows that if $l_b < l_{b_0}$ or equivalently if $\bar{\mu} > \bar{\mu}_0$, then $s_{\text{intsize}} > 0$. That is, if the size at birth is sufficiently small, or the physiological efficiency coefficient is sufficiently large, then the population of microorganisms will survive in the self-cycling fermentation process. Otherwise, $s_{\text{intsize}} \leq 0$, and so the population will be eliminated.

4.5 Average Cell Size

Consider model (4.3.12). Let $\bar{A}(t) = \frac{A(t)}{P(t)}$ and $\bar{L}(t) = \frac{L(t)}{P(t)}$ denote the average surface area and the average length of the population at time t.

Either A, L, and P are continuous for all sufficiently large t, or there exists a sequence $\{t_k\}_{k=1}^{\infty}$ with $t_k \to \infty$ as $k \to \infty$ such that $s(t_k^-) = \bar{s}$.

When $t = t_k$, $\Delta\bar{A}(t_k) = \frac{A(t_k^+)}{P(t_k^+)} - \frac{A(t_k^-)}{P(t_k^-)}$. From model (4.3.12), it follows that $A(t_k^+) = (1-r)A(t_k^-)$, $P(t_k^+) = (1-r)P(t_k^-)$ and $L(t_k^+) = (1-r)L(t_k^-)$. Therefore, $\Delta\bar{A}(t_k) = 0$. Similarly $\Delta\bar{L}(t_k) = 0$.

Differentiating $\bar{A}$ and $\bar{L}$ and using (4.3.12), it follows that

$$\begin{aligned} \frac{d\bar{A}}{dt} &= l_b^{-1} g(s(t)) \left[\frac{1-\kappa}{\omega} \bar{A} + \frac{2\kappa}{3\varpi} \bar{L} - \frac{1-\kappa}{\omega} \bar{A}^2 \right] && t \neq t_k \\ \frac{d\bar{L}}{dt} &= l_b^{-1} g(s(t)) \left[\frac{1-\kappa}{\omega} \bar{A} + \frac{\kappa}{3\varpi} - \frac{1-\kappa}{\omega} \bar{A}\bar{L} \right] && t \neq t_k \qquad (4.5.18) \\ \Delta\bar{A} &= 0 && t = t_k \\ \Delta\bar{L} &= 0 && t = t_k. \end{aligned}$$

Thus, there is no discontinuity, and $\bar{A}$ and $\bar{L}$ satisfy the first two equations for all

$t > 0$. This seems reasonable, since the tank is well-stirred and the harvesting is applied uniformly.

Define

$$\tau \equiv \frac{1-\kappa}{\omega l_b}\int_0^t g(s(r))dr, \qquad k \geq 1,$$

with the understanding that τ is evaluated piecewise over the values t_k.

Equations (4.5.18) can thus be transformed into the system of ordinary differential equations (without jump discontinuities)

$$\begin{aligned} \frac{d\bar{A}}{d\tau} &= \bar{A} + \frac{2\kappa}{3\varpi(1-\kappa)}\bar{L} - \bar{A}^2 \\ \frac{d\bar{L}}{d\tau} &= \bar{A} + \frac{\kappa}{3\varpi(1-\kappa)} - \bar{A}\bar{L} \\ \bar{A}(0) > 0,\ \bar{L}(0) &> 0. \end{aligned} \tag{4.5.19}$$

The following theorem is an immediate consequence of results in Smith and Waltman [32] (Chapter 9).

Theorem 4.1. *For any solution of (4.3.12) with $A(0), L(0), P(0) > 0$,*

$$\lim_{t\to\infty}\left(\bar{A}(t), \bar{L}(t)\right) = \left(\frac{\bar{\mu}\omega}{1-\kappa}, 1 + \frac{\kappa}{3\bar{\mu}\varpi}\right).$$

Furthermore, the standard deviation, given by $\sigma(t) = l_b\left[\bar{A}(t) - \bar{L}^2(t)\right]^{\frac{1}{2}}$ satisfies $\lim_{t\to\infty}\sigma(t) = \frac{l_b\kappa}{3\bar{\mu}\varpi}$.

4.6 Numerical Simulations

Numerical simulations were run on model (4.3.12), using a Michaelis-Menten uptake function, $g(s) = \frac{ms}{K+s}$. In this case

$$\begin{aligned} l_{b_0} &= \frac{\bar{\mu}mr(s^i - \bar{s})}{\bar{d}}\left[K\ln\left(\frac{(1-r)\bar{s} + rs^i}{\bar{s}}\right) + r(s^i - \bar{s})\right]^{-1} \\ \bar{\mu}_0 &= \frac{\bar{d}l_b}{mr(s^i - \bar{s})}\left[K\ln\left(\frac{(1-r)\bar{s} + rs^i}{\bar{s}}\right) + r(s^i - \bar{s})\right]. \end{aligned}$$

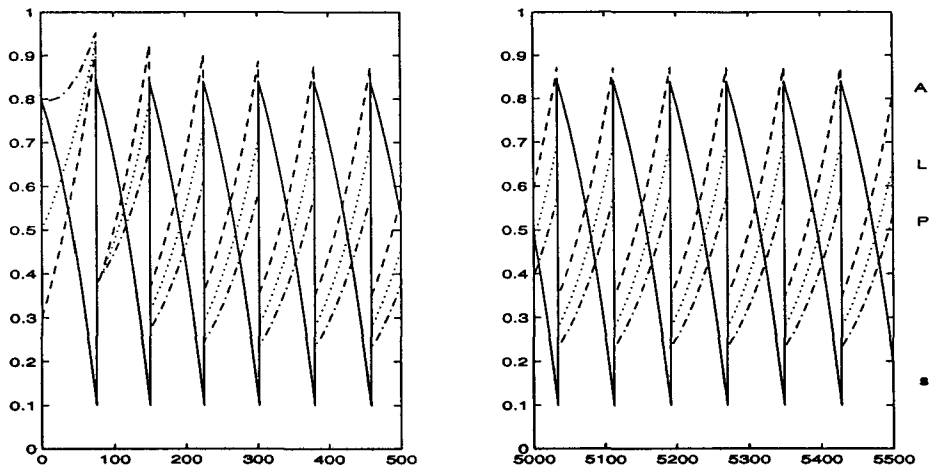

Figure 4.1: The dynamics of the nutrient concentration, surface area, length and total population for model (4.3.12). The surface area, length and population approach a periodic orbit.

Simulations were carried out in MATLAB using ODE45 with the appropriate events option to calculate the moment of impulsive effect. We set $s^i = 1.333$, $\bar{s} = 0.1$, $m = 0.0167$, $K = 0.007$, $\bar{d} = 0.005$, $r = 0.6$, $l_b = 1$, $\omega = 0.822$, $\kappa = 0.45$ and $\varpi = 0.7$. This produced corresponding values of $w_1 = 0.6409$ and $\bar{\mu} = 1.6123$. The calculated value of s_{intsize} was 3.598, $\bar{\mu}_0$ was 0.377 and l_{b_0} was 3.314. Note that $\bar{\mu} > \bar{\mu}_0$ and $l_b < l_{b_0}$. The initial conditions used were $s(0) = 0.8$, $A(0) = 0.3$, $L(0) = 0.5$, $P(0) = 0.8$. See Figure 4.1.

Figure 4.2 was obtained by dividing the curves $A(t)$ and $L(t)$ in Figure 4.1 by $P(t)$ and thus shows the corresponding average surface area and average length. These exhibited no discontinuities and the curves equilibrated, as predicted.

4.7 A model for a cell population reproducing by unequal fission

A drawback with the model of Cushing [12], is that simplyfing assumptions are made about reproduction. Bacteria undergo cell division, with a mother cell dividing into

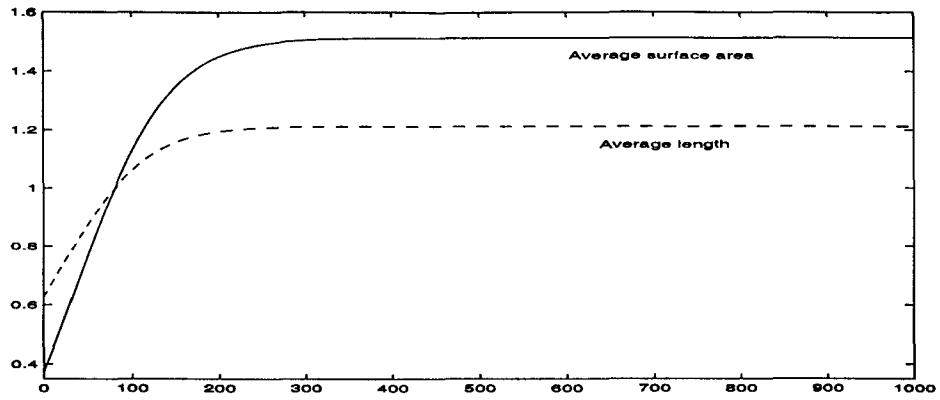

Figure 4.2: The dynamics of the average surface area of the population and the average length of the population for model (4.3.12), demonstrating equilibrating values and no discontinuities.

two daughter cells. In this section, we take this process into account, in order to demonstrate that the impulsive effect can be applied to more realistic models of cell behaviour.

We consider a model for the growth of a cell population that reproduces by unequal fission and is subject to impulsive effect. We adapt the model from Metz and Diekmann [22], so that the impulsive effect is triggered when the nutrient reaches a tolerance level $\bar{s}$.

We assume that a cell is fully characterized by its size x. Fission (asexual reproduction, in which a mother cell divides into two independent daughter cells) will not necessarily result in cells of equal size.

There is a ratio χ between the birth size of a daughter and the size of her mother at division. We consider χ to be a random variable, described by a smooth probability density function $\rho(\chi)$ which does not depend on the division size of the mother. ρ is symmetric around $\chi = \frac{1}{2}$, since size is conserved at division. Furthermore, $\int_0^1 \rho(\chi)d\chi = 1$.

The equations for reproduction by unequal fission, when $s \neq \bar{s}$, are

$$\frac{\partial n}{\partial t}(t,x) + f(s(t))\frac{\partial}{\partial x}(\underline{x}n(t,x)) = -\bar{d}n(t,x) - b(x)n(t,x) +$$

$$2\int_0^1 \frac{\rho(\chi)}{\chi} b\left(\frac{x}{\chi}\right) n\left(t, \frac{x}{\chi}\right) d\chi \qquad (4.7.20)$$

$$\frac{ds(t)}{dt} = -\frac{1}{Y} f(s(t)) \int_{x_{\min}}^1 x n(t,x) dx, \qquad (4.7.21)$$

where

- x is the size of the cells,
- $n(t,x)$ is the size distribution per unit volume of cells of size x,
- $s(t)$ is the concentration of limiting nutrient,
- $\bar{d}$ is the death rate of the cells, assumed constant
- $b(x)$ is the division rate,
- Y is the yield constant,
- $x_{\min}$ is the minimum size and
- f is the uptake rate of nutrient.

We now wish to add in the impulsive effect corresponding to the emptying and refilling of the tank. As before, when the nutrient level reaches the tolerance $\bar{s}$, the size distribution per unit volume of cells of size x is reduced by a fraction r. Thus

$$\begin{aligned} \Delta s(t_k) &= -rs(t_k) + rs^i \\ \Delta n(t_k, x) &\equiv n(t_k^+, x) - n(t_k, x) \\ &= -rn(t_k, x) \qquad s = \bar{s}. \end{aligned} \qquad (4.7.22)$$

The growth rate is $V = f(s(t))x$.

Our aim is to reduce the model of partial differential equations to one of ordinary differential equations with impulsive effect.

We make the following assumptions:

(H1) $f(0) = 0$, f is continuous and $\lim_{s\to\infty} f(s) \equiv F$ exists and is finite,

(H2) $\rho(\chi) > 0$, $\chi \in (\frac{1}{2} - \gamma, \frac{1}{2} + \gamma)$ and $\rho(\chi) = 0$ outside this interval. $\rho(\chi)$ is symmetric about $\chi = \frac{1}{2}$, $\int_0^1 \rho(\chi) d\chi = 1$ and ρ is continuously differentiable on $[\frac{1}{2} - \gamma, \frac{1}{2} + \gamma]$, and

(H3) b is continuous on $[0, 1)$, $b(x) > 0$, for $x \in (a, 1)$, $b(x) = 0$, for $x \leq a$,

$$\lim_{x \uparrow 1} \int_a^x b(\xi) d\xi = \infty,$$

and the function

$$g(x) = \frac{b(x)}{Fx} \exp\left[- \int_a^x \frac{b(\xi)}{F\xi} d\xi \right]$$

is bounded.

Remarks. We extend the definition of b and n so that $b(\frac{x}{\chi}) n(t, \frac{x}{\chi}) = 0$ if $\frac{x}{\chi} > 1$, as in Heijmans [17], so that equation (4.7.20) is well-defined.

Metz and Diekmann [22] postulate that each cell has a stochastically predetermined size at which fission has to occur, provided the cells do not die before reaching that size. The function $g(x)$ in assumption (H3) is the probability density of the "size at division precluding death".

In accordance with accepted biological wisdom, we assume that there exists a maximal size $x_{\max}$ in the sense that cells will divide with probability one before reaching $x_{\max}$. By scaling, we can set $x_{\max} = 1$. Assumptions (H1)-(H3) ensure that all cells will divide before reaching maximal size, so there is no size distribution for cells of maximal size. Thus

$$n(t, 1) = 0. \tag{4.7.23}$$

Note that this is not a boundary condition for the partial differential equations, but rather a statement of fact that coincides with the assumptions above.

The minimum size for division is a and the minimum possible division ratio is $\frac{1}{2} - \gamma$, so

$$x_{\min} = \left(\frac{1}{2} - \gamma \right) a.$$

From (H2), we assume that there are no cells with division rate actually equal to $\frac{1}{2} - \gamma$, so this gives us a lower bound on the size and hence the boundary condition

$$n(t, x_{\min}) = 0. \tag{4.7.24}$$

We also have the initial conditions

$$n(0, x) = n^0(x) \geq 0 \tag{4.7.25}$$

$$s(0) = s^0 \geq 0. \tag{4.7.26}$$

For a function ϕ, define

$$W[\phi] = \int_{x_{\min}}^{1} x\phi(x)dx.$$

This quantity can be interpreted as the biomass of a population with size distribution described by the function ϕ.

Define $W(t) = W[n(t, x; s^0, n^0)]$ whenever a solution

$$\left(s(t; s^0, n^0),\ n(t, x; s^0, n^0)\right)$$

of (4.7.20), (4.7.21), (4.7.24), (4.7.25), (4.7.26) exists.

Theorem 4.2. *$W(t)$, $s(t)$ obey the impulsive differential equations*

$$\begin{aligned}
\frac{ds}{dt} &= -\frac{1}{Y}f(s)W && s \neq \bar{s} \\
\frac{dW}{dt} &= -\bar{d}W + f(s)W && s \neq \bar{s} \\
\Delta s &= -rs + rs^i && s = \bar{s} \\
\Delta W &= -rW && s = \bar{s},
\end{aligned} \tag{4.7.27}$$

with initial conditions $W(0) = W[n^0]$ and $s(0) = s^0$.

Proof. The differential equation in s follows easily from (4.7.21). We also have the initial condition $W(0) = W[n(0,x;s^0,n^0)] = W[n^0]$.

Differentiating $W(t)$ gives us

$$\begin{aligned} W'(t) &= \int_{x_{\min}}^1 x\frac{\partial n}{\partial t}(t,x)dx \\ &= \int_{x_{\min}}^1 \left[-xf(s)\frac{\partial}{\partial x}\left(xn(t,x)\right) - \bar{d}xn(t,x)\right. \\ &\qquad \left. -xb(x)n(t,x) + 2\int_0^1 x\frac{\rho(\chi)}{\chi}b\left(\frac{x}{\chi}\right)n\left(t,\frac{x}{\chi}\right)d\chi\right]dx \end{aligned}$$

from (4.7.20). Integrating by parts, we have

$$\begin{aligned} W'(t) &= -x^2f(s)n(t,x)\Big|_{x_{\min}}^1 + f(s)\int_{x_{\min}}^1 xn(t,x)dx - \int_{x_{\min}}^1 \bar{d}xn(t,x)dx \\ &\quad - \int_{x_{\min}}^1 xb(x)n(t,x)dx + 2\int_{x_{\min}}^1\int_0^1 \frac{x}{\chi}\rho(\chi)b\left(\frac{x}{\chi}\right)n\left(t,\frac{x}{\chi}\right)d\chi dx \\ &= -x^2f(s)n(t,x)\Big|_{x_{\min}}^1 + f(s)W(t) - \bar{d}\int_{x_{\min}}^1 xn(t,x)dx \\ &\quad - \int_{x_{\min}}^1 xb(x)n(t,x)dx + 2\int_0^1 \chi\rho(\chi)\int_{\frac{1}{\chi}x_{\min}}^{\frac{1}{\chi}} yb(y)n(t,y)dyd\chi, \end{aligned}$$

where we make the change of variable $y = \frac{x}{\chi}$ in the last integral.

Now $\chi^* \in \left(\frac{1}{2}-\gamma, \frac{1}{2}+\gamma\right)$, so $\frac{1}{\chi} > 1$. Furthermore, $x_{\min} = \left(\frac{1}{2}-\gamma\right)a$, so $x_{\min} < a\chi$, or in other words $\frac{1}{\chi}x_{\min} < a$. Thus

$$\int_{\frac{1}{\chi}x_{\min}}^{\frac{1}{\chi}} yb(y)n(t,y)dy = \int_a^1 yb(y)n(t,y)dy,$$

since $b(y) = 0$ outside the interval $(a,1)$. Hence

$$\begin{aligned} W'(t) &= -x^2f(s)n(t,x)\Big|_{x_{\min}}^1 + f(s)W(t) - \bar{d}W(t) \\ &\quad - \int_a^1 xb(x)n(t,x)dx + 2\int_0^1 \chi\rho(\chi)d\chi\int_a^1 yb(y)n(t,y)dy \\ &= -x^2f(s)n(t,x)\Big|_{x_{\min}}^1 + f(s)W(t) - \bar{d}W(t), \end{aligned}$$

since $\int_0^1 \chi\rho(\chi)d\chi$ is the expected value of the probability density function, which equals $\frac{1}{2}$, by symmetry. Then, since $n(t, x_{\min}) = n(t, 1) = 0$, from (4.7.23) and (4.7.24), we have

$$W'(t) = -\bar{d}W(t) + f(s)W(t).$$

When $s = \bar{s}$, we have, using (4.7.22),

$$\begin{aligned}
\Delta W(t_k) &= W(t_k^+) - W(t_k) \\
&= \int_{x_{\min}}^1 xn(t_k^+, x)dx - \int_{x_{\min}}^1 xn(t_k, x)dx \\
&= \int_{x_{\min}}^1 x\Delta n(t_k, x)dx \\
&= -r\int_{x_{\min}}^1 xn(t_k, x)dx \\
&= -rW(t_k).
\end{aligned}$$

□

Equations (4.7.27) are analogous to equations (3.2.1), so we can apply Theorem 3.2. That is, if

$$s_{\text{intfission}} \equiv Y\int_{(1-r)\bar{s}+rs^i}^{\bar{s}} \left(\frac{\bar{d}}{f(s)} - 1\right) ds$$

satisfies $s_{\text{intfission}} > 0$, then there there exists a unique periodic orbit with one impulse per period and this periodic orbit has the property of asymptotic phase.

4.8 Discussion

The size of individuals is an important factor in controlling the outcome of the self-cycling fermentation process. The approach of Cushing [12], who included size in his model of the chemostat, was modified to produce a size-structured model for self-cycling fermentation.

Our model resulted in a system of impulsive ordinary and partial differential equations. It was possible to reduce this model to one in which we could apply the results for the nonstructured model of self-cycling fermentation. Thus, we determined a threshold s_{intsize} that depends on the uptake function $g(s)$ and biologically relevant parameters r, $\bar{s}$, s^i as in the unstructured model, as well as the size of the microorganisms at birth and the physiological efficiency coefficient.

If the size at birth is small enough, or the physiological efficiency coefficient is large enough, then s_{intsize} will be positive and hence the population will survive in the form of an impulsive periodic orbit. This mirrors a result in Cushing [12]. He showed that survival in the chemostat depended on the parameters in a similar fashion. However, in that case, the survival is in terms of a globally asymptotically stable fixed point in the interior, instead of a periodic orbit. On the other hand, we showed that the average length and surface area of the microorganisms always equilibrates and that the standard deviation approaches a constant value. Thus, as for the chemostat, if some cells in the self-cycling fermentation process grow unnaturally large, they still form a negligible fraction of the overall population.

As in the original model of Cushing, the most serious deficiency of this model is the description of the reproduction process. However, the analysis of a model that treats cell division more realistically and at the same time treats growth and consumption as discussed here would be very difficult.

To counterpoint this, we considered a model that treated reproduction more realistically. This model followed the approach of Metz and Diekmann [22] and adapted the chemostat model to an impulsive one. The ratio of the division size between the mother and daughter cell was considered to be a random variable. The problem was reduced to the same problem as the one considered in Chapter 3.

We shall now turn to the question of competition in the self-cycling fermentation process.

Chapter 5

Competition in the Nutrient-Driven SCF Process

5.1 Introduction

We now turn to competition in the self-cycling fermentation process, with a fixed nutrient level still determining the impulsive effect. That is, the organisms in the tank compete with one another by consuming a single nonreproducing limiting nutrient. When the nutrient level reaches a certain tolerance, the impulsive effect is triggered and a fraction of the volume of the tank is removed and replaced with fresh growth medium.

There are many interesting issues to resolve. Can more than one population coexist, and if so, can we predict this outcome in advance? If not, can we determine which population excludes the others and is the outcome initial condition dependent?

We consider the model with $r = \frac{1}{2}$ throughout. In this chapter we use the specific uptake function $f_i(s) = \frac{\mu_i s}{K_i + s}$, $i = 1, 2$ and ignore the death rates to simplify the calculations. We generalize model (3.2.1) to multiple species in the obvious way. We shall first analyse two-species competition in depth and then look at an example of three-species competition.

5.2 Two-species competition in the SCF process

Once again, we use the notation introduced for model (2.2.1) in Chapter 2. The model for two-species competition in the self-cycling fermentation process is

$$\begin{aligned}
\frac{ds}{dt} &= -\frac{xf_1(s)}{Y_1} - \frac{yf_2(s)}{Y_2} && s \neq \bar{s} \\
\frac{dx}{dt} &= xf_1(s) && s \neq \bar{s} \\
\frac{dy}{dt} &= yf_2(s) && s \neq \bar{s} \\
\Delta s &= -\frac{s}{2} + \frac{s^i}{2} && s = \bar{s} \\
\Delta x &= -\frac{x}{2} && s = \bar{s} \\
\Delta y &= -\frac{y}{2} && s = \bar{s},
\end{aligned} \tag{5.2.1}$$

where

$$f_i(s) = \frac{\mu_i s}{K_i + s}, \qquad i = 1, 2,$$

μ_i is the maximum specific growth rate and K_i is the half saturation constant for each species.

Proposition 5.1. *All solutions of system (5.2.1) with initial conditions satisfying*

$$s(0) > \bar{s},\ x(0) \geq 0,\ y(0) \geq 0,\ x(0) + y(0) \neq 0,$$

cycle indefinitely and approach the plane $s + \frac{x}{Y_1} + \frac{y}{Y_2} = s^i$ *asymptotically.*

Proof. First note that solutions with

$$s(0) > \bar{s},\ x(0) \geq 0,\ y(0) \geq 0,\ x(0) + y(0) \neq 0,$$

reach $s(t) = \bar{s}$ in finite time. Suppose not. Then $x(t)$ and $y(t)$ increase and $s(t)$ decreases. If

$$\lim_{t\to\infty} s(t) = s^* > \bar{s}$$

then

$$s'(t) < -\frac{x(0)}{Y_1} f_1(s^* + \epsilon) - \frac{y(0)}{Y_2} f_2(s^* + \epsilon)$$

for any $\epsilon > 0$ and all sufficiently large t. But then $s(t) \to -\infty$ as $t \to \infty$, a contradiction.

Hence, if such solutions reach $s = \bar{s}$ once, they will be transported to the new location $s = \frac{s^i}{2} + \frac{\bar{s}}{2}$ which satisfies $s > \bar{s}$ (for $s^i > \bar{s}$), so solutions will reach $s = \bar{s}$ again. Thus such solutions will cycle indefinitely.

We have the condition $(s + \frac{x}{Y_1} + \frac{y}{Y_2})'(t) = 0$ within each cycle and so

$$s(t) + \tfrac{x(t)}{Y_1} + \tfrac{y(t)}{Y_2} = c_n \qquad t_{n-1} < t \leq t_n.$$

Then, since $x_n^+ = \frac{x_n}{2}$ and $y_n^+ = \frac{y_n}{2}$, we have the recurrence relation

$$c_{n+1} = \frac{c_n}{2} + \frac{s^i}{2},$$

which has general solution

$$c_n = \frac{c_1}{2^{n-1}} + s^i \sum_{i=1}^{n-1} \frac{1}{2^i}.$$

Thus

$$\lim_{n\to\infty} c_n = s^i.$$

Hence solutions approach $s(t) + \frac{x(t)}{Y_1} + \frac{y(t)}{Y_2} = s^i$ asymptotically.

□

Remark. The portion of the plane $s(t) + x(t) + y(t) = s^i$ in the first octant is positively invariant under (5.2.1).

Suppose the two uptake functions $f_1(s)$ and $f_2(s)$ are not identical. Either $f_1(s)$ and $f_2(s)$ do not intersect for any $s > 0$ or there exists a unique $s^* > 0$ where $f_1(s^*) = f_2(s^*)$. In this case $\mu_1 \neq \mu_2$ and

$$s^* = \frac{\mu_1 K_2 - \mu_2 K_1}{\mu_2 - \mu_1}.$$

Suppose the two functions are tangent at s^*. Then

$$\begin{aligned} f_1'(s^*) &= f_2'(s^*) \\ \frac{\mu_1 K_1}{(K_1 + s^*)^2} &= \frac{\mu_2 K_2}{(K_2 + s^*)^2} \\ \frac{\mu_1 K_1 (\mu_2 - \mu_1)^2}{\mu_1^2 (K_2 - K_1)^2} &= \frac{\mu_2 K_2 (\mu_2 - \mu_1)^2}{\mu_2^2 (K_2 - K_1)^2} \\ \mu_1 K_2 &= \mu_2 K_1, \end{aligned}$$

which is a contradiction since $s^* > 0$ by assumption. Hence the two functions actually cross at s^*.

If $f_1(s) > f_2(s)$ for $\bar{s} < s < \frac{s^i}{2} + \frac{\bar{s}}{2}$, then

$$\begin{aligned} \frac{dy}{dx} &= \frac{y f_2(s)}{x f_1(s)} \\ &< \frac{y}{x} \end{aligned}$$

for positive values of x and y.

Suppose we have a positive periodic orbit. Then in xy space, the trajectory starts on the line $\frac{x_{n-1}^+}{Y_1} + \frac{y_{n-1}^+}{Y_2} = \frac{1}{2}s^i - \frac{1}{2}\bar{s}$ and travels to the line $\frac{x_n}{Y_1} + \frac{y_n}{Y_2} = s^i - \bar{s}$, whereupon it returns to the first line along the ray $y = x$. However, since $\frac{dy}{dx} < \frac{y}{x}$ for all $s \in (\bar{s}, \frac{1}{2}s^i + \frac{1}{2}\bar{s})$, the trajectory cannot return to the same point on the first line. Instead we have $y_{n+1} < y_n$ and $x_{n+1} > x_n$ for all n. Thus, the trajectories can only head to the periodic orbit on the x axis and hence the extinction of y.

If $f_2(s) > f_1(s)$ for $\bar{s} < s < \frac{s^i}{2} + \frac{\bar{s}}{2}$, then, using similar reasoning, trajectories approach a periodic orbit on the y axis in xy space and extinction of x results.

Thus, if one uptake function dominates the other in the range $\bar{s} < s < \frac{s^i}{2} + \frac{\bar{s}}{2}$, then the competitor with the dominant uptake function wins the competition.

Remark. If the two uptake functions are equal, then

$$\frac{dy}{dx} = \frac{y}{x},$$

so solutions are along the lines

$$y = \frac{y_n^+}{x_n^+}x.$$

However, if we consider the lines of impulsive effect, joining (x_n, y_n) to (x_n^+, y_n^+), we have

$$\begin{aligned} y - y_n &= \frac{y_n - y_n^+}{x_n - x_n^+}(x - x_n) \\ &= \frac{y_n/2}{x_n/2}(x - x_n), \end{aligned}$$

since $(x_n^+, y_n^+) = (\frac{x_n}{2}, \frac{y_n}{2})$. Thus

$$\begin{aligned} y - y_n &= \frac{y_n}{x_n}(x - x_n) \\ y - y_n &= \frac{y_n}{x_n}x - y_n \\ y &= \frac{y_n}{x_n}x, \end{aligned}$$

so solutions when the functions are equal are along the line of impulsive effect. Thus, if the two uptake functions are equal, then there are an infinite number of periodic orbits, depending on initial conditions.

Consider the impulsive differential equations (5.2.1). There is a periodic orbit on each of the boundaries $x = 0$ and $y = 0$. These periodic orbits have initial points

$$(s, x, y) = \left(\frac{s^i}{2} + \frac{\bar{s}}{2}, Y_1\left(\frac{s^i}{2} - \frac{\bar{s}}{2}\right), 0\right)$$

and

$$(s, x, y) = \left(\frac{s^i}{2} + \frac{\bar{s}}{2}, 0, Y_2\left(\frac{s^i}{2} - \frac{\bar{s}}{2}\right)\right),$$

and final points

$$(s, x, y) = \left(\bar{s}, Y_1(s^i - \bar{s}), 0\right)$$

and

$$(s, x, y) = \left(\bar{s}, 0, Y_2(s^i - \bar{s})\right).$$

Consider the periodic orbit when $y = 0$. Denote this periodic orbit by $(\zeta(t), \xi(t), 0)$, where

$$\begin{aligned}
\zeta_0 &= \frac{s^i}{2} + \frac{\bar{s}}{2} \\
\zeta_1 &= \bar{s} \\
\xi_0 &= Y_1\left(\frac{s^i}{2} - \frac{\bar{s}}{2}\right) \\
\xi_1 &= Y_1(s^i - \bar{s}).
\end{aligned}$$

In particular,

$$\xi_1 = 2\xi_0$$

and we have the relationship

$$\zeta(t) + \frac{\xi(t)}{Y_1} = s^i. \tag{5.2.2}$$

We have the two dimensional system

$$\begin{aligned}
\frac{ds}{dt} &= -x f_1(s) - \left(s^i - s - \tfrac{x}{Y_1}\right) f_2(s) && s \neq \bar{s} \\
\frac{dx}{dt} &= x f_1(s) && s \neq \bar{s} \\
\Delta s &= -\frac{s}{2} + \frac{s^i}{2} && s = \bar{s} \\
\Delta x &= -\frac{x}{2} && s = \bar{s}.
\end{aligned} \tag{5.2.3}$$

Using impulsive Floquet theory and (5.2.2), we have

$$\begin{aligned}
P &= -2\xi_0 f_1(\bar{s}) & P_+ &= -\xi_0 f_1\left(\frac{s^i}{2}+\frac{\bar{s}}{2}\right)\\
Q &= 2\xi_0 f_1(\bar{s}) & Q_+ &= \xi_0 f_1\left(\frac{s^i}{2}+\frac{\bar{s}}{2}\right)\\
\frac{\partial b}{\partial x} &= -\frac{1}{2} & \frac{\partial \phi}{\partial s} &= 1\\
\frac{\partial b}{\partial s} &= 0 & \frac{\partial \phi}{\partial x} &= 0\\
\frac{\partial a}{\partial s} &= -\frac{1}{2} & \frac{\partial a}{\partial x} &= 0.
\end{aligned}$$

Thus

$$\begin{aligned}
\Delta_1 &= \frac{-\xi_0 f_1\left(\frac{s^i}{2}+\frac{\bar{s}}{2}\right)\left(-\frac{1}{2}\cdot 1-0\cdot 0+1\right)+\xi_0 f_1\left(\frac{s^i}{2}+\frac{\bar{s}}{2}\right)(0\cdot 0-0\cdot 1+0)}{-2\xi_0 f_1(\bar{s})+2\xi_0 f_1(\bar{s})(0)}\\
&= \frac{f_1\left(\frac{s^i}{2}+\frac{\bar{s}}{2}\right)}{4f_1(\bar{s})}.
\end{aligned}$$

Then, using (5.2.2), we have

$$\begin{aligned}
&\int_0^T \left[\frac{\partial P}{\partial s}(\zeta(t),\xi(t))+\frac{\partial Q}{\partial x}(\zeta(t),\xi(t))\right]dt\\
&= \int_0^T \left[-\xi f_1'(\zeta)+f_2(\zeta)-\left(s^i-\zeta-\frac{\xi}{Y_1}\right)f_2'(\zeta)+f_1(\zeta)\right]dt\\
&= \int_0^T \left[-\xi f_1'(\zeta)+f_1(\zeta)+f_2(\zeta)\right]dt\\
&= \int_0^T \left[\frac{f_1'(\zeta)}{f_1(\zeta)}\zeta'+\frac{\xi'}{\xi}+f_2(\zeta)\right]dt\\
&= \int_{\frac{s^i}{2}+\frac{3}{2}}^{\bar{s}} \frac{f_1'(\zeta)}{f_1(\zeta)}d\zeta+\int_{\xi_0}^{2\xi_0}\frac{d\xi}{\xi}+\int_0^T f_2(\zeta)dt\\
&= \ln\left(\frac{f_1(\bar{s})}{f_1\left(\frac{s^i}{2}+\frac{\bar{s}}{2}\right)}\right)+\ln 2+\int_0^T f_2(\zeta)dt.
\end{aligned}$$

Now

$$\begin{aligned}
\int_0^T f_2(\zeta)dt &= \int_0^T \frac{f_2(\zeta)}{-\xi f_1(\zeta)}\zeta' dt \\
&= -\int_{\frac{s^i}{2}+\frac{\bar{s}}{2}}^{\bar{s}} \frac{f_2(\zeta)}{f_1(\zeta)(s^i-\zeta)}d\zeta \\
&= \int_{\bar{s}}^{\frac{s^i}{2}+\frac{\bar{s}}{2}} \frac{\mu_2(K_1+\zeta)}{\mu_1(K_2+\zeta)(s^i-\zeta)}d\zeta \\
&= \frac{\mu_2}{\mu_1}\int_{\bar{s}}^{\frac{s^i}{2}+\frac{\bar{s}}{2}} \left[\frac{K_1+s^i}{(K_2+s^i)(s^i-\zeta)} + \frac{K_1-K_2}{(s^i+K_2)(K_2+\zeta)}\right]d\zeta,
\end{aligned}$$

using partial fraction decomposition. Therefore

$$\begin{aligned}
\int_0^T f_2(\zeta)dt &= -\frac{\mu_2(K_1+s^i)}{\mu_1(K_2+s^i)}\ln(s^i-\zeta)\Big|_{\bar{s}}^{\frac{s^i}{2}+\frac{\bar{s}}{2}} + \frac{\mu_2(K_1-K_2)}{\mu_1(s^i+K_2)}\ln(K_2+\zeta)\Big|_{\bar{s}}^{\frac{s^i}{2}+\frac{\bar{s}}{2}} \\
&= -\frac{\mu_2(K_1+s^i)}{\mu_1(K_2+s^i)}\ln\left(\frac{\frac{s^i}{2}-\frac{\bar{s}}{2}}{s^i-\bar{s}}\right) + \frac{\mu_2(K_1-K_2)}{\mu_1(s^i+K_2)}\ln\left(\frac{K_2+\frac{s^i}{2}+\frac{\bar{s}}{2}}{K_2+\bar{s}}\right) \\
&= \frac{\mu_2(K_1+s^i)}{\mu_1(K_2+s^i)}\ln 2 + \frac{\mu_2(K_1-K_2)}{\mu_1(s^i+K_2)}\ln\left(\frac{K_2+\frac{s^i}{2}+\frac{\bar{s}}{2}}{K_2+\bar{s}}\right).
\end{aligned}$$

Denote the non-trivial Floquet multiplier for the periodic orbit on the x-axis by μ_{2x} and the one on the y-axis by μ_{2y}. We thus have

$$\begin{aligned}
\mu_{2x} &= \frac{f_1\left(\frac{s^i}{2}+\frac{\bar{s}}{2}\right)}{4f_1(\bar{s})}\cdot\frac{f_1(\bar{s})}{f_1\left(\frac{s^i}{2}+\frac{\bar{s}}{2}\right)}\cdot 2\cdot 2^{\frac{\mu_2(K_1+s^i)}{\mu_1(K_2+s^i)}}\cdot\left(\frac{K_2+\frac{s^i}{2}+\frac{\bar{s}}{2}}{K_2+\bar{s}}\right)^{\frac{\mu_2(K_1-K_2)}{\mu_1(K_2+s^i)}} \\
&= 2^{\frac{\mu_2(K_1+s^i)}{\mu_1(K_2+s^i)}-1}\cdot\left(\frac{K_2+\frac{s^i}{2}+\frac{\bar{s}}{2}}{K_2+\bar{s}}\right)^{\frac{\mu_2(K_1-K_2)}{\mu_1(K_2+s^i)}}. \qquad (5.2.4)
\end{aligned}$$

By an identical process applied to the orbit $(\zeta(t), 0, \nu(t))$, we have the two dimensional system

$$\begin{aligned}
\frac{ds}{dt} &= -\left(s^i - s - \tfrac{y}{Y_2}\right) f_1(s) - y f_2(s) && s \neq \bar{s} \\
\frac{dy}{dt} &= y f_2(s) && s \neq \bar{s} \\
\Delta s &= -\frac{s}{2} + \frac{s^i}{2} && s = \bar{s} \\
\Delta y &= -\frac{y}{2} && s = \bar{s},
\end{aligned} \tag{5.2.5}$$

and hence the symmetric result

$$\mu_{2y} = 2^{\frac{\mu_1(K_2+s^i)}{\mu_2(K_1+s^i)}-1} \cdot \left(\frac{K_1 + \frac{s^i}{2} + \frac{\bar{s}}{2}}{K_1 + \bar{s}}\right)^{\frac{\mu_1(K_2-K_1)}{\mu_2(K_1+s^i)}}. \tag{5.2.6}$$

The periodic orbit on the x-axis is stable if $\mu_{2x} < 1$ and unstable if $\mu_{2x} > 1$. The periodic orbit on the y-axis is stable if $\mu_{2y} < 1$ and unstable if $\mu_{2y} > 1$. One suspects that it is possible to have a stable positive periodic orbit, and hence coexistence, if the multipliers satisfy $\mu_{2x} > 1$ and $\mu_{2y} > 1$. We shall prove that in this case the system is persistent in both x and y in section 5.4. In light of this, we shall refer to this case, when $\mu_{2x} > 1$ and $\mu_{2y} > 1$, as the central region of coexistence.

5.3 Numerical simulations

To analyse the behaviour of competitors, we fixed s^i, $\bar{s}$ and $f_2(s)$ and let μ_1 and K_1 vary. Figure 5.1 shows the various states in μ_1-K_1 space. The other constants are $Y_1 = Y_2 = 1$, $\mu_2 = 1$, $K_2 = 1$, $s^i = 20$ and $\bar{s} = 0.1$.

In the upper grey region, $f_2(s) > f_1(s)$ for $\bar{s} < s < \frac{s^i}{2} + \frac{\bar{s}}{2}$, so y wins the competition. In the lower grey region $f_1(s) > f_2(s)$ for $\bar{s} < s < \frac{s^i}{2} + \frac{\bar{s}}{2}$, so x wins the competition.

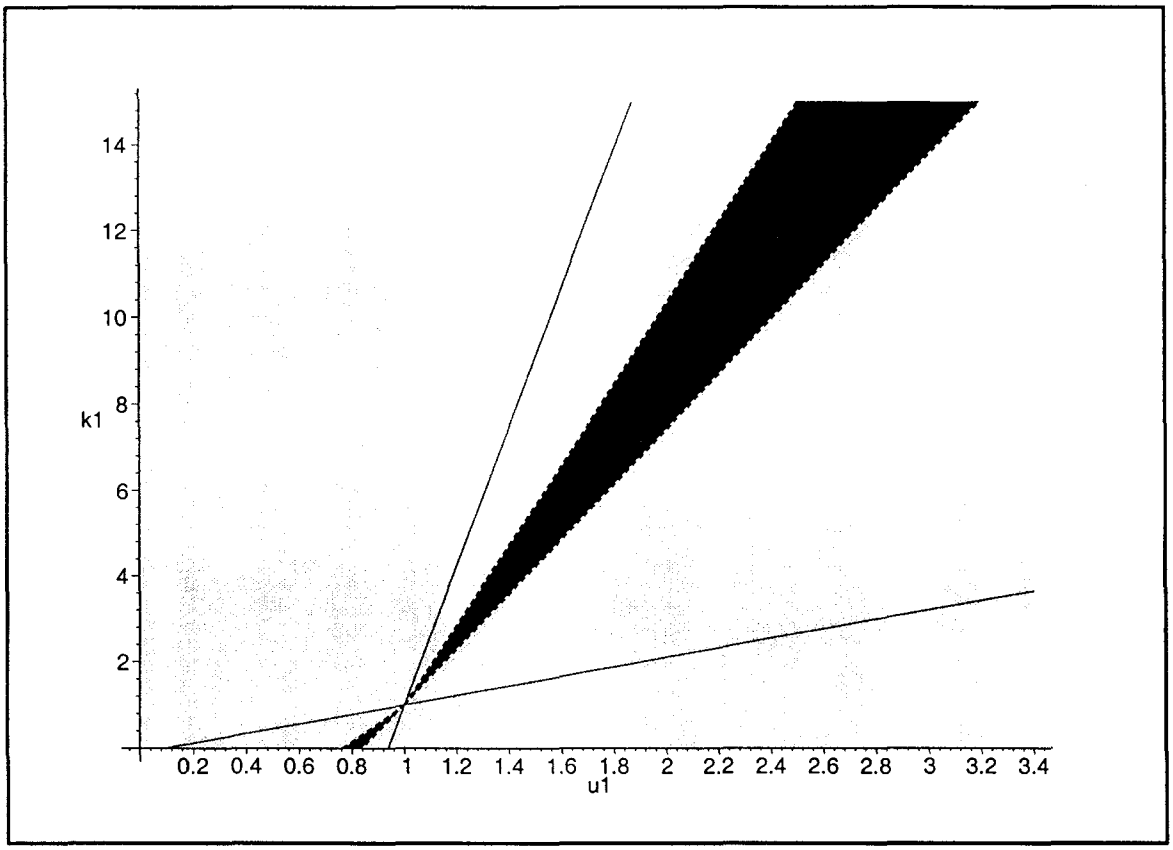

Figure 5.1: In the dark region in the centre, the nontrivial Floquet multipliers are greater than one, suggesting coexistence in this region. In the grey area above the central region of coexistence, species y wins the competition. In the grey region below the central region of coexistence, species x wins the competition. At the point $(1, 1)$, the two uptake functions are identical.

The two dotted curves correspond to the case when the nontrivial Floquet multipliers equal one. Numerical simulations seem to indicate that coexistence may be possible in the central dark region between the two lines, in the form of a periodic orbit with one impulse per period. We prove that the two species coexist in this central region in the next section.

In the grey area immediately above the central region of coexistence, the two uptake functions cross, but y still wins the competition. In the grey region immediately below the central region of coexistence, the uptake functions also cross, but x wins the competition.

The point $(1,1)$ corresponds to the case when the two uptake functions are identical and both multipliers are equal to one. The two curves do not actually cross at this point. They are tangent to one another. This area is magnified in Figure 5.2.

System 5.2.1 was modelled in MATLAB using constants chosen from the central region of coexistence in Figure 5.1. We chose $\mu_1 = 2$ and $K_1 = 6.33$, with $\mu_2 = 1$, $K_2 = 1$, $s^i = 20$ and $\bar{s} = 0.1$. This gave multipliers of $\mu_{2x} = 1.0348$ and $\mu_{2y} = 1.0345$. The initial conditions used were $s(0) = 10$, $x(0) = 2$, $y(0) = 0.7$. Solutions converged to a periodic orbit. See Figure 5.3. The first part of Figure 5.3 shows the first 30 iterations. The second part shows iterations 200 through 230. The third part shows iterations 500 through 530.

5.4 Persistence

Consider the following definitions for maps, from Freedman and So [15]. In the following, X is a metric space with metric d, and $f : X \to X$. Let $f^n(x)$ denote the nth iterate of x under f.

Definition 5.1. *Let Y be a subspace of X and f satisfy $f(Y) \subset Y$ and $f(X\backslash Y) \subset X\backslash Y$. We say that f is persistent (with respect to Y) if for all $x \in X\backslash Y$,*

$$\liminf_{n\to\infty} d(f^n(x), Y) \;>\; 0.$$

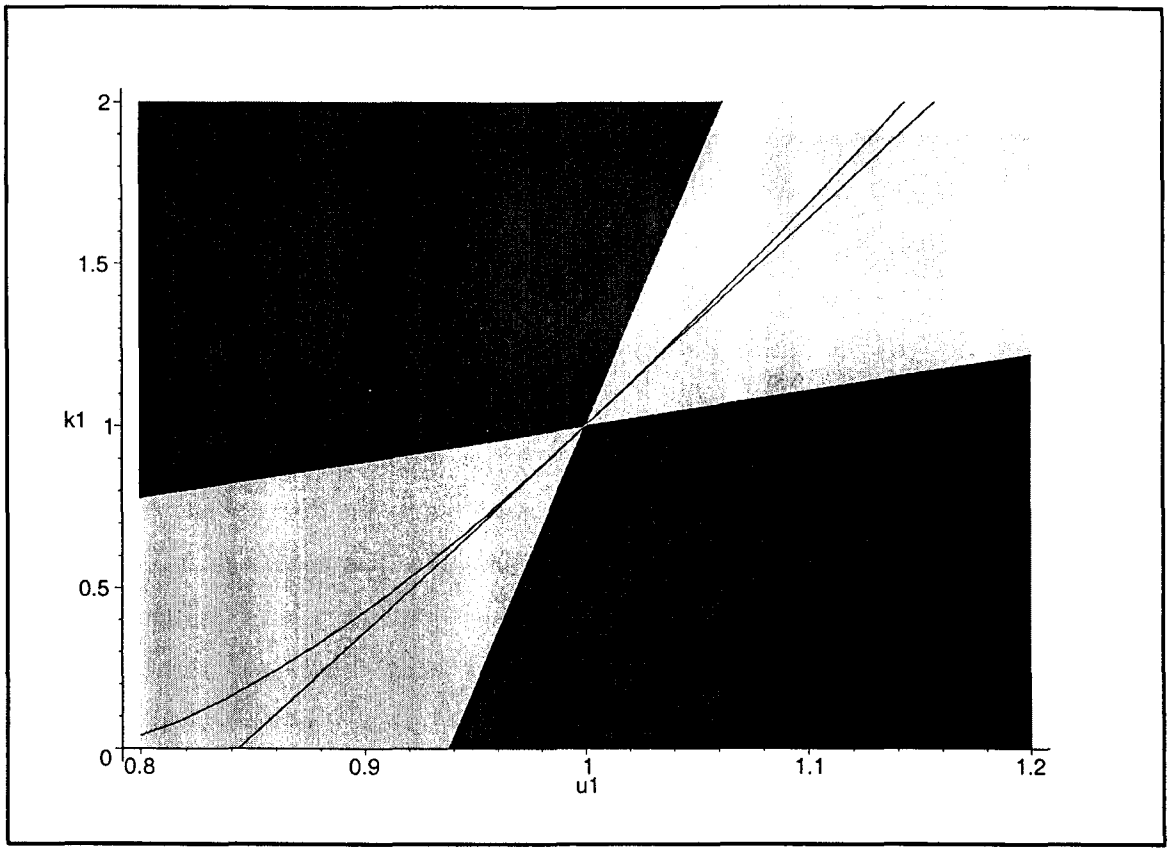

Figure 5.2: The area around $\mu_1 = 1$, $K_1 = 1$ in Figure 5.1 magnified about the tangential curves. In the upper dark region, $f_2(s) > f_1(s)$ for $\bar{s} < s < \frac{s'}{2} + \frac{\bar{s}}{2}$, so y wins the competition. In the lower dark region $f_1(s) > f_2(s)$ for $\bar{s} < s < \frac{s'}{2} + \frac{\bar{s}}{2}$, so x wins the competition. Along the two lines in the grey region, the nontrivial Floquet multipliers equal one. These two lines are tangent to one another at the point $(1, 1)$ and hence do not cross. Coexistence is possible in the central region between the two lines. In the grey area above the central region of coexistence, the two uptake functions cross, but y still wins the competition. In the grey region below the central region of coexistence, the uptake functions also cross, but x wins the competition. At the point $(1, 1)$, the two uptake functions are identical.

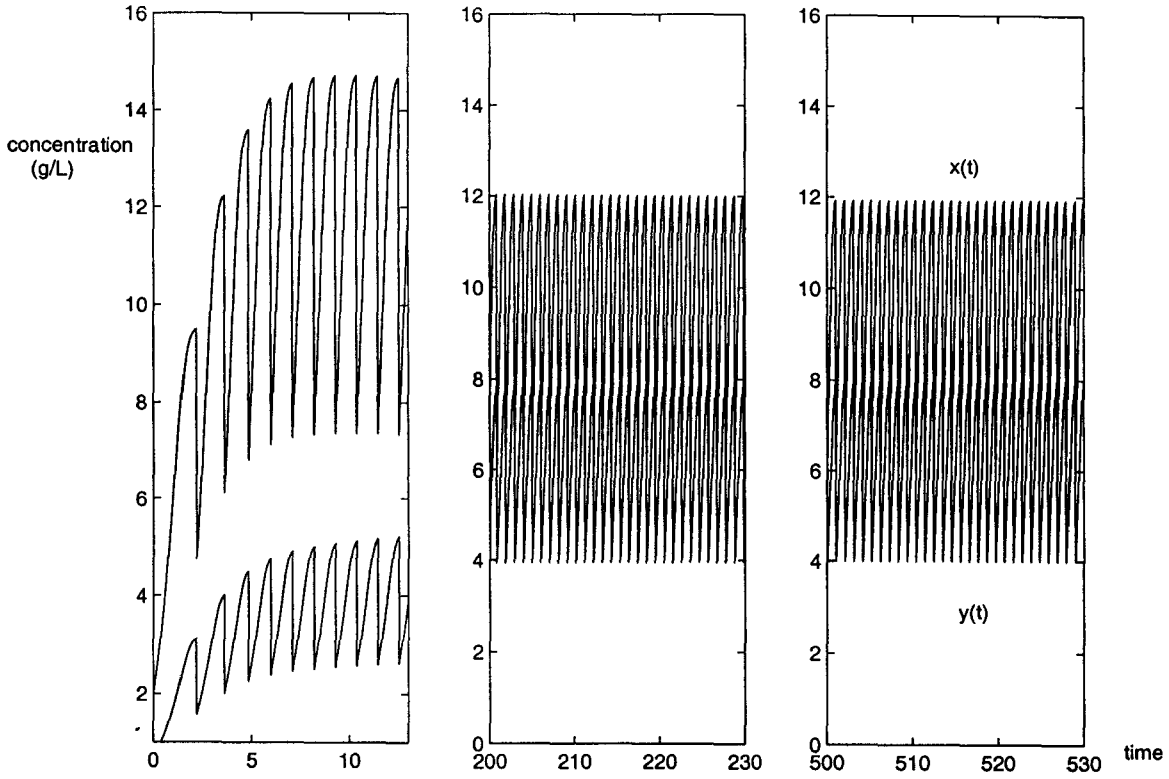

Figure 5.3: Coexistence of two microorganisms in the SCF process. The data used here was taken from the central region of coexistence in Figure 5.1. The graph on the left shows two species converging to what appears to be a stable periodic orbit. The graphs in the middle and on the right show the dynamics after the system has run for a long period of time and appears to have settled at a periodic orbit. Neither species is diminishing over time, suggesting coexistence.

Definition 5.2. *Let $x \in X$. Let $\mathbb{Z}$ denote the set of integers and let $\mathbb{Z}_+$ denote the set of nonnegative integers. A sequence $\{x_n\}_{n\in\mathbb{Z}_+}$ of points in X is called a* positive orbit *through x if $x_0 = x$ and $f(x_n) = x_{n+1}$ for all $n \in \mathbb{Z}_+$. A sequence $\{x_{-n}\}_{n\in\mathbb{Z}_+}$ of points in X is called a* negative orbit *through x if $x_0 = x$ and $f(x_{-n-1}) = x_{-n}$ for all $n \in \mathbb{Z}_+$. A sequence $\{x_n\}_{n\in\mathbb{Z}}$ of points in X is called an* orbit *through x if $x_0 = x$ and $f(x_n) = x_{n+1}$ for all $n \in \mathbb{Z}$.*

Definition 5.3. *Given a topological space X, a subset E of X is* precompact *if its closure is compact.*

Definition 5.4. *A positive orbit $\{x_n\}_{n\in\mathbb{Z}_+}$ through x (respectively, a negative orbit $\{x_{-n}\}_{n\in\mathbb{Z}_+}$ through x) is said to be* compact *if, when considered as a subset of X, it is precompact.*

Definition 5.5. *1. Let $\{x_n\}_{n\in\mathbb{Z}_+}$ be a positive orbit. The* omega limit set *of $\{x_n\}_{n\in\mathbb{Z}_+}$ is the set $\omega(\{x_n\}_{n\in\mathbb{Z}_+}) = \{y \in X : y = \lim_{n\to\infty} x_{i_n}$ for some subsequence $\{x_{i_n}\}_{n\in\mathbb{Z}_+}$ of $\{x_n\}_{n\in\mathbb{Z}_+}\}$.*

2. Let $\{x_{-n}\}_{n\in\mathbb{Z}_+}$ be a negative orbit. The alpha limit set *of $\{x_{-n}\}_{n\in\mathbb{Z}_+}$ is the set $\alpha(\{x_{-n}\}_{n\in\mathbb{Z}_+}) = \{y \in X : y = \lim_{n\to\infty} x_{-i_n}$ for some subsequence $\{x_{-i_n}\}_{n\in\mathbb{Z}_+}$ of $\{x_{-n}\}_{n\in\mathbb{Z}_+}\}$.*

Definition 5.6. *Let $M \subset X$. M is* positively invariant *(respectively,* negatively invariant, *or* invariant*) if $f(M) \subset M$ (respectively, $M \subset f(M)$, or $f(M) = M$).*

Definition 5.7. *A nonempty, closed, invariant subset M of X is an* isolated invariant set *if it is the maximal invariant set in some neighbourhood of itself.*

Definition 5.8. *Let $M \subset X$ be an isolated invariant set.*

1. A compact positive orbit $\{x_n\}_{n\in\mathbb{Z}_+}$ is in the stable set *of M (under f) if $\omega(\{x_n\}_{n\in\mathbb{Z}_+}) \subset M$. We denote the stable set by $W^+(M)$.*

2. A compact negative orbit $\{x_{-n}\}_{n\in\mathbb{Z}_+}$ is in the unstable set *of M (under f) if $\alpha(\{x_{-n}\}_{n\in\mathbb{Z}_+}) \subset M$. We denote the unstable set by $W^-(M)$.*

3. *A compact positive orbit* $\{x_n\}_{n\in\mathbb{Z}_+}$ *is in the* weakly stable set *of* M *(under* f*) if* $\omega(\{x_n\}_{n\in\mathbb{Z}_+}) \cap M \neq \emptyset$. *We denote the weakly stable set by* $W^+_{\mathrm{W}}(M)$.

4. *A compact negative orbit* $\{x_{-n}\}_{n\in\mathbb{Z}_+}$ *is in the* weakly unstable set *of* M *(under* f*) if* $\alpha(\{x_{-n}\}_{n\in\mathbb{Z}_+}) \cap M \neq \emptyset$. *We denote the weakly unstable set by* $W^-_{\mathrm{W}}(M)$.

The following theorem is the analogue of the Butler-McGehee theorem for maps, from Freedman and So [15].

Theorem 5.1. *Let* X *be a metric space with metric* d. *Let* $f : X \to X$ *be continuous and let* M *be an isolated invariant set in* X. *If* $\{x_n\}_{n\in\mathbb{Z}_+}$ *is a compact positive orbit and* $\{x_n\}_{n\in\mathbb{Z}_+} \in W^+_{\mathrm{W}}(M)\backslash W^+(M)$, *then*

1. *there exists a positive orbit* $\{y_n\}_{n\in\mathbb{Z}_+}$ *in* $\omega(\{x_n\}_{n\in\mathbb{Z}_+})$ *such that* $y_0 \notin M$ *and* $\{y_n\}_{n\in\mathbb{Z}_+} \in W^+(M)$, *and*

2. *there exists a negative orbit* $\{z_{-n}\}_{n\in\mathbb{Z}_+}$ *in* $\omega(\{x_n\}_{n\in\mathbb{Z}_+})$ *such that* $z_0 \notin M$ *and* $\{z_{-n}\}_{n\in\mathbb{Z}_+} \in W^-(M)$.

The following theorem is from Miller and Michel [23].

Theorem 5.2. *Let* F *be continuous, let* $F_w = \frac{\partial F}{\partial w} = \left[\frac{\partial F_i}{\partial w_j}\right]$ *exist and let* F_w *be continuous. If* $\phi(t,\tau,\xi)$ *is the solution of* $w' = F(t,w)$ *such that* $\phi(\tau,\tau,\xi) = \xi$, *then* ϕ *is continuous and has continuous first partial derivatives in* (t,τ,ξ).

Lemma 5.1. *The function* $\phi = \phi(t,\tau,\xi)$ *that solves the associated system of ordinary differential equations (5.2.1) with initial condition* $\phi(\tau,\tau,\xi) = \xi$ *is continuous in* (t,τ,ξ).

Proof. We have

$$\begin{pmatrix} s' \\ x' \\ y' \end{pmatrix} = \begin{pmatrix} -\frac{x}{Y_1}f_1(s) - \frac{y}{Y_2}f_2(s) \\ xf_1(s) \\ yf_2(s) \end{pmatrix} = F(t,w)$$

where $w = (s, x, y)$. Then

$$F_w = \begin{bmatrix} -\frac{x}{Y_1}f_1'(s) - \frac{y}{Y_2}f_2'(s) & -\frac{1}{Y_1}f_1(s) & -\frac{1}{Y_2}f_2(s) \\ xf_1'(s) & f_1(s) & 0 \\ yf_2'(s) & 0 & f_2(s) \end{bmatrix}$$

Each function f_i, $i = 1, 2$ satisfies conditions (3.2.2), so F and F_w are continuous. Hence $\phi(t, \tau, \xi)$ is continuous in (t, τ, ξ) by Theorem 5.2.

□

Remark. In our case we have $f_1(s)$ and $f_2(s)$ explicitly, but Lemma 5.1 holds for any monotone uptake functions.

Theorem 5.3. *Consider system (5.2.1) with uptake functions $f_1(s)$ and $f_2(s)$ satisfying the conditions in (3.2.2). Suppose also that the nontrivial Floquet multiplier for (5.2.3) is denoted μ_{2x} and satisfies $\mu_{2x} > 1$ and the nontrivial Floquet multiplier for (5.2.5) satisfies $\mu_{2y} > 1$. Then solutions of (5.2.1) with initial conditions*

$$s(0) > \bar{s}, \quad x(0) > 0, \quad y(0) > 0$$

satisfy

$$\liminf_{t\to\infty} x(t) > 0, \quad \liminf_{t\to\infty} y(t) > 0.$$

Proof. Consider any initial point $(s(0), x(0), y(0))$ where

$$s(0) > \bar{s}, \quad x(0) > 0, \quad y(0) > 0.$$

By Proposition 5.1 there exists a first time t_1 such that solutions of (5.2.1) satisfy

$$s(t_1) = \bar{s}, \quad x(t_1) > 0, \quad y(t_1) > 0.$$

Then if t_n denotes the time of the nth impulse point, we have for for $t_{n-1} < t \leq t_n$

$(n > 1)$,

$$\begin{aligned} \bar{s} \quad &\leq \quad s(t) \quad < \quad \frac{s^i}{2} + \frac{\bar{s}}{2} \\ 0 \quad < \quad \frac{x(t_{n-1})}{2} \quad &< \quad x(t) \quad \leq \quad x(t_n) \\ 0 \quad < \quad \frac{y(t_{n-1})}{2} \quad &< \quad y(t) \quad \leq \quad y(t_n) \end{aligned}$$

Therefore, it suffices to consider the sequence of impulse points $(\bar{s}, x(t_n), y(t_n))$ and to show that

$$\liminf_{n\to\infty} x(t_n) > 0 \quad \text{and} \quad \liminf_{n\to\infty} y(t_n) > 0.$$

Define the map $f : X \to X$ where

$$X = \{(x, y) : x \geq 0, y \geq 0, x + y \neq 0\},$$

in the following way:

$$f(x(t_n), y(t_n)) = (x(t_{n+1}), y(t_{n+1}))$$

where $(\bar{s}, x(t_n), y(t_n))$ and $(\bar{s}, x(t_{n+1}), y(t_{n+1}))$ are impulse points for system (5.2.1).

First we show that f is continuous on X by showing that f is a composition $g \circ h : X \to X$ of two continuous functions,

$$h : X \to X \qquad \text{and} \qquad g : X \to X.$$

Define

$$h(x, y) = \left(\frac{x}{2}, \frac{y}{2}\right)$$

and

$$g(x, y) = (u(x, y), v(x, y)),$$

where $u(x, y) = x(\bar{t})$ and $v(x, y) = y(\bar{t})$ such that $(s(t), x(t), y(t))$, $0 \leq t \leq \bar{t}$ is the solution of the associated ODE of (5.2.1) with initial conditions

$$s(0) = \frac{s^i}{2} + \frac{\bar{s}}{2}, \quad x(0) = x, \quad y(0) = y$$

and $\bar{s} < s(t) < \frac{s^i}{2} + \frac{\bar{s}}{2}$ for $0 < t < \bar{t}$ and $s(\bar{t}) = \bar{s}$.

It is clear that h is continuous. That g is continuous follows from continuous dependence on initial data for ordinary differential equations (see Lemma 5.1).

The map f has two equilibrium points, corresponding to the periodic orbits on the sx plane and sy plane. Let $P_1 = (Y_1(s^i - \bar{s}), 0)$ denote the equilibrium on the x axis and $P_2 = (0, Y_2(s^i - \bar{s}))$ denote the equilibrium on the y axis. Clearly P_1 is the maximal invariant set in some neighbourhood of itself, so it is an isolated invariant set. Similarly P_2 is an isolated invariant set.

Suppose $(x(t_1), y(t_1))$ is any point that satisfies $x(t_1) > 0$ and $y(t_1) > 0$. Consider the positive orbit $\{x(t_n), y(t_n)\}_{n \in \mathbb{Z}_+}$ generated by the map f. Suppose

$$\liminf_{n\to\infty} x(t_n) = 0 \quad \text{or} \quad \liminf_{n\to\infty} y(t_n) = 0.$$

Then either

a) there is a subsequence such that

$$\lim_{k\to\infty} x(t_{n_k}) = 0 \quad \text{and} \quad \lim_{k\to\infty} y(t_{n_k}) = 0, \qquad \text{or}$$

b) there is a subsequence such that

$$\lim_{k\to\infty} x(t_{n_k}) = 0 \quad \text{and} \quad \lim_{k\to\infty} y(t_{n_k}) > 0, \qquad \text{or}$$

c) there is a subsequence such that

$$\lim_{k\to\infty} x(t_{n_k}) > 0 \quad \text{and} \quad \lim_{k\to\infty} y(t_{n_k}) = 0.$$

Case a) is impossible since by Proposition 5.1

$$s^i = \lim_{k\to\infty} \left(s(t_{n_k}) + \frac{x(t_{n_k})}{Y_1} + \frac{y(t_{n_k})}{Y_2} \right) = \bar{s} + 0 + 0 = \bar{s} \neq s^i.$$

In case b), again by Proposition 5.1,

$$s^i = \lim_{k\to\infty} \left(s(t_{n_k}) + \frac{x(t_{n_k})}{Y_1} + \frac{y(t_{n_k})}{Y_2} \right) = \bar{s} + 0 + \lim_{k\to\infty} \frac{y(t_{n_k})}{Y_2}$$

and hence $\lim_{k\to\infty} y(t_{n_k}) = Y_2(s^i - \bar{s})$. Therefore,

$$P_2 \in \omega\left(\{x(t_n), y(t_n)\}_{n\in\mathbb{Z}_+}\right).$$

However, since $\mu_{2y} > 1$, the stable manifold of P_2 is the set

$$W^+(P_2) = \{(x,y) : x = 0, y > 0\}.$$

Since $x(t_{n_k}) > 0$ for all k,

$$\{x(t_n), y(t_n)\}_{n\in\mathbb{Z}_+} \in W^+_{\mathrm{W}}(P_2)\backslash W^+(P_2).$$

Hence by Theorem 5.1, there exists a positive orbit $\{a(t_n), b(t_n)\}_{n\in\mathbb{Z}_+}$ in

$$\omega\left(\{x(t_n), y(t_n)\}_{n\in\mathbb{Z}_+}\right)$$

such that $(a(t_1), b(t_1)) \neq P_2$ and

$$\{a(t_n), b(t_n)\}_{n\in\mathbb{Z}_+} \in W^+(P_2).$$

By Proposition 5.1, $\frac{a(t_n)}{Y_1} + \frac{b(t_n)}{Y_2} = s^i - \bar{s}$, and

$$\{a(t_n), b(t_n)\}_{n\in\mathbb{Z}_+} \in W^+(P_2).$$

implies that $a(t_n) = 0$ for all n. Therefore $(a(t_n), b(t_n)) = P_2$ for all n, contradicting $(a(t_1), b(t_1^*)) \neq P_2$. Thus case (b) is impossible.

Case (c) can be ruled out in a similar fashion.

Thus, for any point $(x(t_1), y(t_1))$ with $x(t_1) > 0$, $y(t_1) > 0$, we have

$$\liminf_{n\to\infty} x(t_n) > 0 \qquad \text{and} \liminf_{n\to\infty} y(t_n) > 0.$$

Furthermore if

$$Y = \{(x,y) : x = 0, y > 0\} \cup \{(x,y) : y = 0, x > 0\}$$

then $f(Y) \subset Y$ and $f(X\backslash Y) \subset X\backslash Y$. Thus f is persistent with respect to Y. Hence solutions of (5.2.1) with initial conditions

$$s(0) > \bar{s}, \quad x(0) > 0, \quad y(0) > 0$$

satisfy

$$\liminf_{t\to\infty} x(t) > 0, \quad \liminf_{t\to\infty} y(t) > 0.$$

□

Remark. Applications of the Butler-McGehee Theorem do not usually eliminate a single point from the boundary as we have done. To extend X to the entire first quadrant would require defining f at the origin. Since the s axis is a line of equilibria for system (5.2.1), we cannot use the definition given. We could define $f(0,0) = (0,0)$ for completeness, but due to the nature of the impulsive effect f would not be continuous at the origin and we could not apply Theorem 5.1. This explains our choice of X.

5.5 Three-species competition in the SCF process

The possibility of survival for two competing species in the self-cycling fermentation process raises the question of whether more species can coexist on a single nonreproducing limiting nutrient. Application of the results in the previous sections to competition of n species (where $n \geq 3$) is significantly more difficult, since the impulsive Floquet theory only applies to systems that can be reduced to two dimensional systems.

However, numerical simulations were run to determine whether three species could coexist. These simulations built on the ideas for two species competition, using the same parameters for coexistence of x and y from the previous section, and then varying the parameters of z.

The model for three-species competition in the self-cycling fermentation process is

$$
\begin{aligned}
\frac{ds}{dt} &= -\frac{xf_1(s)}{Y_1} - \frac{yf_2(s)}{Y_2} - \frac{zf_3(s)}{Y_3} && s \neq \bar{s} \\
\frac{dx}{dt} &= xf_1(s) && s \neq \bar{s} \\
\frac{dy}{dt} &= yf_2(s) && s \neq \bar{s} \\
\frac{dz}{dt} &= zf_3(s) && s \neq \bar{s} \\
\Delta s &= -\frac{s}{2} + \frac{s^i}{2} && s = \bar{s} \\
\Delta x &= -\frac{x}{2} && s = \bar{s} \\
\Delta y &= -\frac{y}{2} && s = \bar{s} \\
\Delta z &= -\frac{z}{2} && s = \bar{s},
\end{aligned}
\tag{5.5.7}
$$

where

$$
f_i(s) = \frac{\mu_i s}{K_i + s}, \qquad i = 1, 2, 3,
$$

μ_i is the maximum specific growth rate and K_i is the half saturation constant for each species.

We have the condition $\left(s + \frac{x}{Y_1} + \frac{y}{Y_2} + \frac{z}{Y_3}\right)'(t) = 0$ within each cycle and so

$$
s(t) + \tfrac{x(t)}{Y_1} + \tfrac{y(t)}{Y_2} + \tfrac{z(t)}{Y_3} = c_n \qquad t_{n-1} < t \leq t_n.
$$

We have the recurrence relation

$$
c_{n+1} = \frac{c_n}{2} + \frac{s^i}{2},
$$

which has general solution

$$
c_n = \frac{c_1}{2^{n-1}} + s^i \sum_{i=1}^{n-1} \frac{1}{2^i}.
$$

Thus

$$\lim_{n\to\infty} c_n = s^i.$$

System (5.5.7) was modelled in MATLAB with $Y_1 = Y_2 = Y_3 = 1$, $\mu_1 = 2$, $K_1 = 6.33$, $\mu_2 = 1$, $K_2 = 1$, $\mu_3 = 7$, $K_3 = 32.5$, $s^i = 20$ and $\bar{s} = 0.1$. The initial conditions used were $s(0) = 10$, $x(0) = 7$, $y(0) = 6$, $z(0) = 4$. Solutions converged to a periodic orbit. See Figure 5.4. The first part of Figure 5.4 shows the first 30 iterations. The second part shows iterations 200 through 230. The third part shows iterations 500 through 530. Note that we used parametes from the central region of coexistence for f_1 and f_2. The parameters for f_3 were then varied until three species coexistence was found.

5.6 Discussion

Coexistence of more than one species is possible in the self-cycling fermentation process. Numerical simulations suggest that both two and three species can coexist on a single nonreproducing nutrient.

In the case of two-species competition, Floquet theory allowed us to predict in advance when the parameters of the system would be such that two species could coexist. By reducing the problem to one of maps on the impulse points, we could use the convergence of the constants and the Butler-McGehee Theorem for maps to prove that any solution with initial conditions satisfying

$$s(0) > \bar{s}, \quad x(0) > 0, \quad y(0) > 0$$

was persistent. This proves that two competitors can coexist on a single nonreproducing nutrient in the self-cycling fermentation process.

It is interesting to note that we could reduce the problem to a lower dimensional problem due to the nature of the impulsive effect. In general, for impulsive systems, such a lower dimensional set would be possible, but difficult to work with.

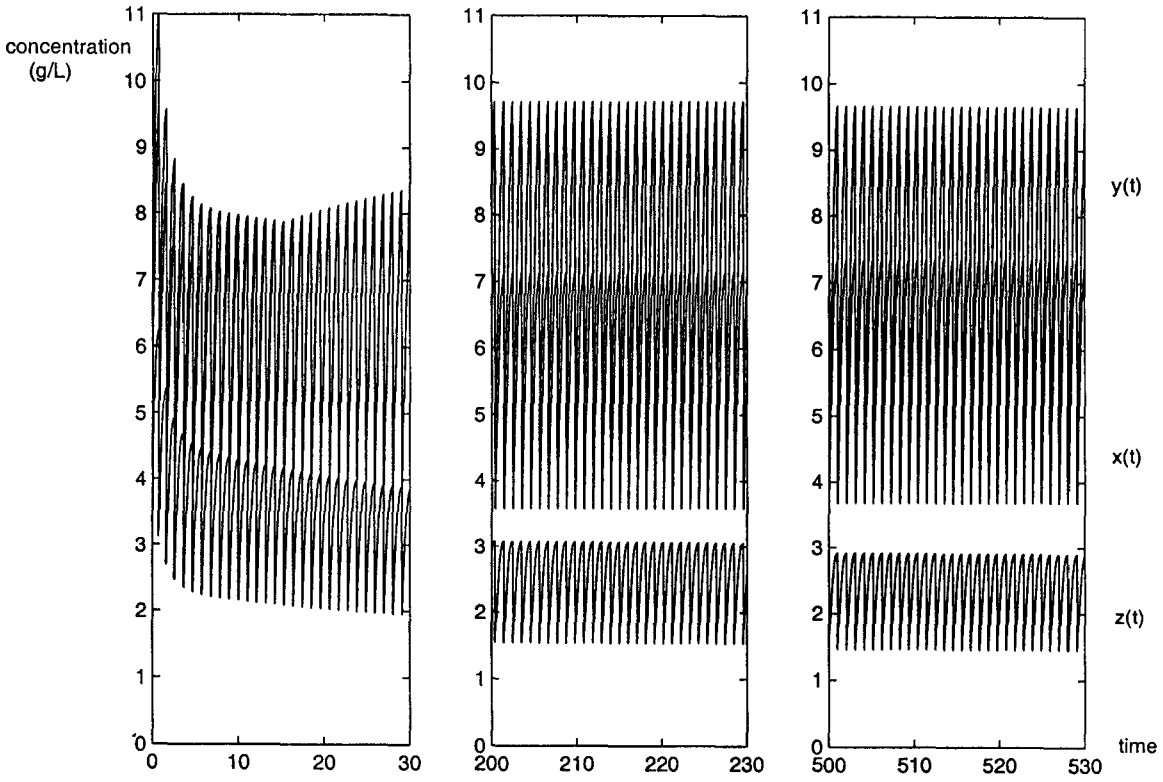

Figure 5.4: Coexistence of three microorganisms in the SCF process. The data used for the x and y parameters is taken from the central region of coexistence in Figure 5.1. The graph on the left shows three species converging to what appears to be a stable periodic orbit. The graphs in the middle and on the right show the dynamics after the system has run for a long period of time and appears to have settled at the periodic orbit. The species are not diminishing over time, suggesting coexistence.

The results can be generalized to any fraction r. We do not include the death rate in this chapter, assuming that it is negligible, as in the original hypothesis for the oxygen-driven model. We could also show that two species could not coexist in the SCF process if the uptake function of one species dominated the other during each cycle.

In the analogous model of the chemostat, where the nutrient is pumped in continuously at a constant rate, aside from a few knife-edge cases involving the equality of certain parameters, coexistence of two species competing for a single nonreproducing nutrient is not possible (see Smith and Waltman [32]). The results here are analogous to competition on three trophic levels in the chemostat, where two predators can survive on a common prey, but only in an oscillatory manner (see Smith and Waltman [32] or Butler, Hsu and Waltman [10]). The impulsive effect makes such oscillatory phenomena more likely.

We have also not ruled out periodic orbits of higher order. However, simulations in the region where coexistence is possible have not revealed any periodic orbits of order greater than one.

There was no similar theory for three-species competition to determine in advance when all three species would survive, but we could use the results in the two-species case to determine parameters for x and y and then vary the parameters for z.

The SCF process requires at least one competitor to run, but more than one competitor provides a stronger system. If one species suddenly becomes extinct, then we have a backup in the form of the second or third species so that the system will continue to run.

On the other hand, we may wish to ensure that only one particular species survives. In the case of two-species competition, we can determine in advance which parameters will lead to coexistence and which will lead to one species or the other being washed out of then system. The process may come with one species intrinsic to the system, which would allow introduction of a superior species to ensure that the required competitor wins the competition.

One species might be scarce, or expensive, but the SCF process can lead to growth of this species. We could introduce small numbers of the desired species along with large numbers of a compatible second species. If both species coexist, the system will run smoothly and the desirable species will be able to exist in small numbers while the second species keeps the system running by consuming relatively larger amounts of nutrient. Over time, the system will (presumably) approach a positive periodic orbit, with larger numbers of the desired species. Furthermore, since the output of the SCF process is half the tank, at each stage we will be collecting relatively high numbers of the desired species. This exploits the multi-faceted use of the SCF process, as outlined in Chapter 1.

It follows that coexistence of more than one species in the self-cycling fermentation process is both interesting and useful in practical applications. With advance knowledge of the dynamics of the system, we can ensure maximum productivity of the self-cycling fermentation process and thus improve cleanup of the environment.

Conclusions

The model describing self-cycling fermentation in Wincure, Rey and Cooper [38] had a serious problem, in that the dissolved oxygen could theoretically become negative, which is meaningless in a practical experiment. We reformulated the oxygen equation to include an oxygen transfer function g that satisfied

i. $g : \mathbb{R}^3 \to \mathbb{R}$ is continuously differentiable,

ii. $g(0, x, [O_2]) = g(s, 0, [O_2]) = g(s, x, 0) = 0$,

iii. g is increasing in s, x and $[O_2]$,

iv. $g(s, \alpha x, [O_2]) = \alpha g(s, x, [O_2])$ for any $\alpha \in \mathbb{R}$,

v. g is bounded.

An analysis of the oxygen-driven model for self-cycling fermentation revealed potential problems guaranteeing indefinite cycling and the nonnegativity of dissolved oxygen. We could solve these problems by requiring that the initial conditions and constants satisfy

$$\begin{aligned} s(0) + \frac{x(0)}{Y} &< s^i, \\ [O_2](0) &= [O_2]^*, \end{aligned}$$

and

$$[O_2]^i = [O_2]^*.$$

However, while the last two assumptions are plausible, the first is quite restrictive.

In order to address the problems in the oxygen-driven model more fully and to tailor the process more specifically to problems such as sewage treatment or toxic waste cleanup, we reformulated the model. The impulsive effect was triggered by a tolerance choice $\bar{s}$ and we included the death rate $\bar{d}$ and a generalized monotone uptake function $f(s)$. The natural choice for the tolerance was the maximum allowable concentration of pollutant in the output, as set by the Ontario Ministry of the Environment. The nutrient-driven model had several advantages over the oxygen-driven model, especially for nutrient minimizing problems such as environmental cleanup. Comparison with the oxygen-driven model when $\bar{d} = 0$ shows that we are guaranteed to cycle indefinitely for any initial conditions with $s(0) > \bar{s}$ and $x(0) > 0$.

There is a value

$$s_{\text{int}} \equiv Y \int_{(1-r)\bar{s}+rs^i}^{\bar{s}} \left(\frac{\bar{d}}{f(s)} - 1 \right) ds,$$

such that if $s_{\text{int}} > 0$ and $\bar{s} < s^i$ then, using the Floquet theory for impulsive differential equations, we could prove the existence of a unique periodic orbit with one impulse per period having the property of asymptotic phase.

If $s_{\text{int}} > 0$ and $\bar{s} \geq \lambda$, where λ is the value of s such that $f(\lambda) = \bar{d}$ (or $\lambda = \infty$ if $f(s) < \bar{d}$ for all s) then the nontrivial periodic orbit attracts all solutions with initial conditions satisfying $s(0) > \bar{s}$ and $x(0) > 0$. If $s_{\text{int}} > 0$ and $\bar{s} < \lambda$ then the nontrivial periodic orbit attracts all solutions with initial conditions satisfying $s(0) \geq (1-r)\bar{s} + rs^i$ and $x(0) > 0$, or $s(0) > \bar{s}$ but $x(0)$ sufficiently large. The endpoints of each cycle in x will approach the endpoint of the periodic orbit monotonically. Furthermore, the cycle times will monotonically approach the period of the periodic orbit.

If $s_{\text{int}} > 0$ and $s(0) < \bar{s}$ or $s(0)$ satisfies $Y \int_{s(0)}^{(1-r)\bar{s}+rs^i} \left(1 - \frac{\bar{d}}{f(s)}\right) ds > s_{\text{int}}$ and $x(0) > 0$ is sufficiently small, then there are no moments of impulse and $x(t) \to 0$, $s(t) \to s^*$, where $\bar{s} \leq s^* < \lambda$.

If $s_{\text{int}} = 0$, then there is no nontrivial periodic solution and $\liminf_{t\to\infty} x(t) = 0$. If $s_{\text{int}} < 0$, then there is no nontrivial periodic orbit and solutions undergo at most a

finite number of impulses and eventually $s(t) \to s^*$ and $x(t) \to 0$, where $\bar{s} \leq s^* < \lambda$.

Looking at the nutrient-driven model of self-cycling fermentation with cell size as a factor, we could refine our value of s_{int} so that

$$s_{\text{intsize}} = \int_{(1-r)\bar{s}+rs^i}^{\bar{s}} \left(\frac{\bar{d}}{f(s)l_b^2 w_1} - \frac{\bar{\mu}}{l_b^3 w_1} \right) ds.$$

where l_b is the size at birth and $\bar{\mu}$ is the physiological efficiency coefficient.

The system could be reduced so that the earlier results applied. Thus, if $s_{\text{intsize}} > 0$, then there exists a unique periodic orbit with one impulse per period having the property of asymptotic phase.

Despite the possibility that some cells could grow to unnaturally large sizes, the average surface areas and lengths approached constant values, so the percentage of unnaturally large microorganisms is negligible in the self-cycling fermentation process.

We considered the nature of reproduction by cell division as a stochastic process, and adapted the existing chemostat model to an impulsive one. We reduced the system of partial differential equations with impulsive effect to the same system of ordinary differential equations with impulsive effect as in Chapter 3. Consequently, the same results applied, leading to a value $s_{\text{intfission}}$ such that there was a unique periodic orbit with one impulse per period having the property of asymptotic phase if and only if $s_{\text{intfission}} > 0$.

We then investigated two species competition in the self-cycling fermentation process, under some simplifying assumptions. We showed that the constants $\{c_n\}$ converged, meaning that solutions with $s(0) > \bar{s}$, $x(0) \geq 0$, $y(0) \geq 0$ approached the plane defined by $s + \frac{x}{Y_1} + \frac{y}{Y_2} = s^i$. If the uptake function of one species dominates the other in the interval $[\bar{s}, s^i - \bar{s})$ then the species with the dominant uptake function wins the competition. An application of the impulsive Floquet theory gave conditions for the periodic orbits on the boundaries to be unstable, suggesting coexistence when the Floquet multipliers μ_{2x} and μ_{2y} were greater than one. Letting μ_1 and K_1 vary over all possible positive values, we found a central region where coexistence was possible. Numerical simulations in this region showed that coexistence was in the form of an asymptotically stable positive periodic orbit.

We then considered a lower dimensional set, defined by $s = \bar{s}$ so that we could reduce the problem to one of considering the impulse points only. Using the convergence of the constants and the analogue of the Butler-McGehee theorem for maps, we were able to prove that solutions with $s(0) > \bar{s}$, $x(0) > 0$, $y(0) > 0$ are persistent when we are in the region where μ_{2x} and μ_{2y} are both greater than one. We were thus able to prove that two species could coexist when competing for a single nutrient in the self-cycling fermentation process, a result that does not hold in the cases where the nutrient washout is continuous, such as the chemostat.

Numerical simulations demonstrated that coexistence was also possible with three competitors. There was no similar theory to predict the appropriate parameters, but the two-species case suggested appropriate parameters for two of the species.

Further work might involve an approach using impulsive delay-differential equations. There is a natural delay, especially in the oxygen-driven model, that might lend itself to such an application. There are also other possible models to consider, such as a food web. It is possible that non-monotone uptake functions could be considered as well. There is some concern in the literature about cell synchronization in the SCF process (see Wentworth and Cooper [36], for example). A comparison of cell synchrony between the oxygen-driven process and the nutrient-driven process, or for coexisting competitors might be interesting. It would also be nice to find a general result for three or more species competing, analagous to the result for two-species competition.

More work is needed in the analysis of cycle times and how they change as the parameters of the model change. There is also a control problem in choosing r so that we clean up the most amount of nutrient in a given time. Finally, the original model might be greatly improved if we could predict in advance which choices of initial conditions or input constants would lead to the system halting.

For applications to problems involving the reduction of nutrient, such as sewage treatment, or toxic waste cleanup, the results in this thesis favour the implementation of the nutrient-driven self-cycling fermentation process.

Appendix A

Systems With Impulsive Effect

A.1 Introduction

This appendix describes background material on systems with impulsive effect. The material on impulsive semidynamical systems and stability is developed in Lakshmikantham, Bainov and Simeonov [20], while the material on existence, uniqueness, continuability of solutions and autonomous impulsive differential equations is developed in Lakshmikantham, Bainov and Simeonov [20] and Bainov and Simeonov [2], [3]. The material in section A.3 is included only for completeness.

A.2 Impulsive semidynamical systems

Definition A.1. *A triple* $(X, \pi, \mathbb{R}_+)$ *is a* semidynamical system *if* X *is a metric space,* $\mathbb{R}_+$ *the set of all nonnegative reals and* $\pi : X \times \mathbb{R}_+ \to X$ *is a continuous function such that*

i) $\pi(x, 0) = x$ *for all* $x \in X$, *and*

ii) $\pi(\pi(x, t), s) = \pi(x, t + s)$ *for all* $x \in X$ *and* $t, s \in \mathbb{R}_+$.

Notation. $(X, \pi, \mathbb{R}_+)$ is sometimes denoted (X, π). The triple $(X, \pi, \mathbb{R})$ is said to be a *dynamical system.*

For all $x \in X$, define $\pi_x : \mathbb{R}_+ \to X$ by $\pi_x(t) = \pi(x, t)$. π_x is continuous for all x. We call π_x the *trajectory* of x. The set

$$C^+(x) = \{\pi(x,t) : t \in \mathbb{R}_+\}$$

is called the *positive orbit* of x. Note that $x \in C^+(x)$. We also have

$$C^+(x,r) = \{\pi(x,t) : 0 \leq t \leq r\}.$$

For any $M \subseteq X$, we define the following sets: for $t \in \mathbb{R}_+$,

$$G(x,t) = \{y \in X : \pi(y,t) = x\},$$

is the attainable set of x at $t \in \mathbb{R}_+$,

$$\begin{aligned} G(x) &= \bigcup_{t \in \mathbb{R}_+} G(x,t), \\ M^-(x) &= G(x) \cap M \backslash \{x\}, \end{aligned}$$

and

$$M^+(x) = C^+(x) \cap M \backslash \{x\}.$$

We then set $M(x) = M^+(x) \cup M^-(x)$. Note that $x \notin M(x)$.

Definition A.2. *An* impulsive semidynamical system $(X, \pi; M, A)$ *consists of a semidynamical system* (X, π)*, a nonempty closed subset* M *of* X *and a continuous function* $A : M \to X$ *such that*

i) No point $x \in X$ *is a limit point of* $M(x)$*, and*

ii) $\{t \in \mathbb{R}_+ : G(x,t) \cap M \neq \emptyset\}$ *is a closed subset of* $\mathbb{R}_+$.

Notation. We denote the image of M under the operator A by $N = A(M)$ and, for all $x \in M$, $A(x) = x^+$.

Lemma A.1. *Let $(X, \pi; M, A)$ be an impulsive semidynamical system. Then for any $x \in X$, there exists $r, s \in \mathbb{R}_+ \cup \{\infty\}$ such that $0 < r$, $s \leq \infty$ and, for $0 < t < s$ and $0 < t < r$,*

a) $\pi(x,t) \notin M$ and if $M^+(x) \neq \emptyset$, then $\pi(x,s) \in M$

b) $G(x,t) \cap M = \emptyset$ and if $M^-(x) \neq \emptyset$, then $G(x,r) \cap M \neq \emptyset$.

Proof. a) If $M^+(x) = \emptyset$ then the lemma is satisfied for all $t \in \mathbb{R}_+$. Suppose $M^+(x) \neq \emptyset$. Then there exists $t_2 \in \mathbb{R}_+$ such that $\pi(x,t_2) \in M$. By property (i) of Definition A.2, there exists $t_1 \in \mathbb{R}_+$ such that $\pi(x,t) \notin M$ for $t \leq t_1$. M is closed, so the nonempty, compact subset $[t_1, t_2] \cap \pi_x^{-1}(M)$ of $\mathbb{R}_+$ has a least element s. This s satisfies (a) since $\pi(x,s) \in M$.

b) First, define $G_x(t) \equiv G(x,t)$ for each x. If $M^-(x) = \emptyset$, the lemma is satisfied for all $t \in \mathbb{R}_+$. Suppose $M^-(x) \neq \emptyset$. Then there exists $t_4 \in \mathbb{R}_+$ such that $G(x,t_4) \cap M \neq \emptyset$. By property (i) of Definition A.2, there exists t_3 such that $G(x,t) \cap M = \emptyset$ for $t \leq t_3$. Then $[t_3, t_4] \cap G_x^{-1}(M)$ is nonempty and closed, by property (ii) of Definition A.2 and hence has a least element r that satisfies (b).

□

Notation. We call s the *time without impulse of x*. We define $\Phi : X \to \mathbb{R}_+ \backslash \{0\}$ such that $\Phi(x)$ is the time without impulse of x. If $\{x_n\}$ is the set of impulse points, then $\{s_n\}$ are the corresponding times without impulse. We can think of a given s_n as the time taken from the trajectory starting at x_n until x_{n+1} (the next impulse point). Naturally, if there is no further impulse point, then $s_{n+1} = \infty$.

Definition A.3. Let $(X, \pi; M, A)$ be an impulsive semidynamical system and $x \in X$. The *(impulsive) trajectory* of x is a function $\tilde{\pi}_x$ defined on a subset $[0, s)$, $s \in (0, \infty]$ as follows:

Let $x = x_0$. If $M^+(x_0) = \emptyset$, then $\tilde{\pi}_x(t) = \pi_x(t)$ for all $t \in \mathbb{R}_+$. If $M^+(x_0) \neq \emptyset$, then by Lemma A.1, there exists $s_0 \in \mathbb{R}_+\backslash\{0\}$ such that $\pi(x_0, s_0) = x_1 \in M$ and $\pi(x_0, t) \notin M$ for all $0 < t < s_0$. We define $\tilde{\pi}_x$ on $[0, s_0]$ by

$$\tilde{\pi}_x(t) \;=\; \pi(x_0, t) \qquad\qquad 0 \leq t \leq s_0$$

We then continue this process, starting at x_1^+ (which is not equal to x_1 in general). That is, if $M^+(x_1^+) = \emptyset$ then we define $\tilde{\pi}_x(t) = \pi(x_1^+, t - s_0)$ for all $t > s_0$ and $s = \infty$. If $M^+(x_1^+) \neq \emptyset$, then by Lemma A.1 there exists $s_1 \in \mathbb{R}_+\backslash\{0\}$ such that $\pi(x_1^+, s_1) = x_2 \in M$ and $\pi(x_1^+, t) \notin M$ for all $0 < t < s_1$. We define $\tilde{\pi}_x$ on $(s_0, s_0 + s_1]$ by

$$\tilde{\pi}_x(t) \;=\; \pi(x_1^+, t - s_0) \qquad\qquad s_0 < t \leq s_0 + s_1.$$

If $M^+(x_2^+) \neq \emptyset$, then by Lemma A.1 there exists $s_2 \in \mathbb{R}_+\backslash\{0\}$ such that $\pi(x_2^+, s_2) = x_3 \in M$ and $\pi(x_2^+, t) \notin M$ for all $0 < t < s_2$. We define $\tilde{\pi}_x$ on $(s_0 + s_1, s_0 + s_1 + s_2]$ by

$$\tilde{\pi}_x(t) \;=\; \pi(x_2^+, t - s_0 - s_1) \qquad\qquad s_0 + s_1 < t \leq s_0 + s_1 + s_2.$$

If $M^+(x_n^+) = \emptyset$ for some n, then the process halts. On the other hand, if $M^+(x_n^+) \neq \emptyset$ for all $n = 1, 2, \ldots$ then the process continues indefinitely, with

$$\tilde{\pi}_x(t) \;=\; \pi(x_n^+, t - \sum_{i=0}^{n-1} s_i), \qquad\qquad \sum_{i=0}^{n-1} s_i < t \leq \sum_{i=0}^{n} s_i$$

for each $n \geq 1$.

Thus the process gives rise to either a finite or infinite sequence $\{x_n\}$ of points of X such that with each x_n there is associated a positive real number s_n (or ∞) and, for $s_n < \infty$, an impulse x_{n+1}, where $\pi(x_n^+, s_n) = x_{n+1}$.

The interval of definition of $\tilde{\pi}_x$ is $[0, s] = [0, \sum_{i=0}^{\infty} s_i]$.

This completes the definition of the trajectory of $\tilde{\pi}_x$.

Notation. We call $\{x_n\}$ the sequence of impulse points of x.

Definition A.4. *A trajectory $\tilde{\pi}_x$ is* periodic *of period r and order k if there exists $m \in \mathbb{Z}^+$ and $k \in \mathbb{Z}^+$ such that k is the smallest integer satisfying $x_m^+ = x_{m+k}^+$ and*

$$r = \sum_{i=m}^{m+k-1} s_i.$$

Remark. A periodic trajectory with no impulse points can be considered to be an impulsive trajectory with one moment of impulse, such that the trajectory is continuous at the impulse point. Thus a periodic trajectory with no impulse points is a first order periodic orbit and the period is the time taken to travel from the impulse point back to itself; hence the period in this case corresponds to the definition of period in the non-impulsive case.

Note that the trajectory $\tilde{\pi}_x$ is continuous if either $M^+(x) = \emptyset$ or for each n, $x_n = x_n^+$. Otherwise, the trajectory has discontinuities at a finite or infinite number of impulse points x_n. However, at any such point $\tilde{\pi}_x$ is continuous from the left.

Trajectories of interest for impulsive semidynamical systems are those with an infinite number of discontinuities and an interval of definition of $\mathbb{R}_+$. We call these *infinite trajectories.*

Theorem A.1. *Let $\tilde{\pi}_x$ be an infinite trajectory and denote $s_n = \Phi(x_n^+)$. Suppose*

$$\lim_{n\to\infty} x_n^+ = y \qquad \text{and} \qquad \lim_{n\to\infty} s_n = \Phi(y) = s.$$

Then

i) if $s = \infty$, then $\tilde{\pi}_y = \pi_y$,

ii) if $s = 0$, $y = y^+$, and

iii) if $0 < s < \infty$, $\tilde{\pi}_y$ is periodic of period s and order 1.

Proof. If $s = \infty$, then $M^+(y) = \emptyset$, so clearly $\tilde{\pi}_y = \pi_y$, the trajectory without impulse.

If $s = 0$, then the time taken from x_n^+ to x_{n+1} approaches zero in the limit, so y is a fixed point of the impulsive effect.

For $0 < s < \infty$, we have $\pi(x_n^+, s_n) \to \pi(y, s) \equiv z$ by continuity. Since each s_n is a time without impulse, it follows that $z \in M$. However, $\pi(x_n^+, s_n) = x_{n+1}$, since s_n is the time taken to travel from x_n^+ to the next impulse point. That is, $x_{n+1} \to z$. By continuity of A, $x_{n+1}^+ \to z^+$. Hence $z^+ = y$, so $\tilde{\pi}_y$ is periodic and of order 1. By assumption, $s = \Phi(y)$, so the period is s.

□

Example. Consider the autonomous system

$$x' = x \qquad y' = \alpha y, \qquad \alpha > 0,$$

the sets $M = \{(x, y) \in \mathbb{R}_+^2 : y = \frac{1}{x+1}\}$, $N = \{(x, y) \in \mathbb{R}_+^2 : x + y = 1\}$, and an operator $A : M \to N$ that associates with each point P on M the point P^+ on N which is on the ray OP. A is a continuous, bijective mapping.

We shall consider only those trajectories with initial points in the first quadrant. Note that this quadrant in invariant. We assume initial points are not on M, by convention.

Trajectories with initial points in the region $y > \frac{1}{1+x}$ do not undergo any impulsive effect. Trajectories with initial points on the x-axis also do not undergo impulsive effect, since M does not intersect the x-axis. Trajectories with initial points on the y-axis undergo impulsive effect once, at (0,1), but motion is continuous, since this is a fixed point of the operator A. Both axes are invariant.

For $0 < \alpha < 1$, trajectories with initial points in the region $y < \frac{1}{1+x}$ undergo impulsive effect an infinite number of times. $(x_n^+, y_n^+) \to (1, 0)$, $s = \infty$ and $\tilde{\pi}_{(1,0)} = \pi_{(1,0)}$. This demonstrates (i).

Let $\alpha > 1$. Trajectories with initial points in the region $y < \frac{1}{1+x}$ are subject to impulsive effect an infinite number of times and tend towards the point (0,1), which is a fixed point of the impulsive effect. This demonstrates (ii).

When $\alpha = 1$, all trajectories with initial points in the region $y < \frac{1}{1+x}$ eventually become periodic, with order 1. Motion between N and M is performed along rays $y = cx$. This case demonstrates (iii).

A.3 Existence, uniqueness and continuability of solutions

Let $\Omega \subset \mathbb{R}^n$ be an open set. Suppose that for each $k \in \mathbb{Z}$ the functions $\tau_k : \Omega \to \mathbb{R}$ are continuous in Ω and satisfy

$$\tau_k(x) < \tau_{k+1}(x), \text{ with } \lim_{k \to \pm\infty} \tau_k(x) = \infty$$

for $x \in \Omega$. Let $f : \mathbb{R} \times \Omega \to \mathbb{R}^n$, $I_k : \Omega \to \mathbb{R}^n$, $(t_0, x_0) \in \mathbb{R} \times \Omega$ and $\alpha < \beta$.

Consider the impulsive differential system

$$\begin{aligned} \frac{dx}{dt} &= f(t,x), & t &\neq \tau_k(x), \\ \Delta x &= I_k(x), & t &= \tau_k(x), \end{aligned} \tag{A.3.1}$$

with initial condition

$$x(t_0^+) = x_0. \tag{A.3.2}$$

By definition, $\Delta x \equiv x^+ - x$, so $I_k(x) = x + A_k(x)$.

Definition A.5. *The function $\varphi : \langle \alpha, \beta \rangle \to \mathbb{R}^n$ is a* solution *of (A.3.1) if*

1. $(t, \varphi(t)) \in \mathbb{R} \times \Omega$ *for* $t \in \langle \alpha, \beta \rangle$,

2. $\varphi(t)$ *is differentiable, with*

$$\frac{d\varphi}{dt}(t) = f(t, \varphi(t))$$

for $t \in (\alpha, \beta)$, $t \neq \tau_k(\varphi(t))$, *and*

3. $\varphi(t)$ *is continuous from the left in* $\langle \alpha, \beta \rangle$ *and if* $t \in \langle \alpha, \beta \rangle$, $t = \tau_k(\varphi(t))$ *and* $t \neq \beta$, *then* $\varphi(t^+) = \varphi(t) + I_k(\varphi(t))$ *and, for each* $j \in \mathbb{Z}$ *and some* $\delta > 0$, $s \neq \tau_j(\varphi(s))$ *for* $t < s < t + \delta$.

Definition A.6. *A* solution of the initial value problem (A.3.1)-(A.3.2) *is a function* φ *which is defined in an interval of the form* (t_0, β), *is a solution of (A.3.1) and satisfies (A.3.2).*

If $t_0 \neq \tau_k(x_0)$ for $k \in \mathbb{Z}$, then the existence and uniqueness conditions of the solution of the initial value problem (A.3.1)-(A.3.2) match the standard definitions. Thus if f is continuous in a neighbourhood of (t_0, x_0) then there exists a solution of the initial value problem and this solution is unique if f is Lipschitz continuous in this neighbourhood. If $t_0 = \tau_k(x_0)$ for some k then we need to impose additional conditions on f and τ_k to guarantee the existence of a solution. The following theorem, from Bainov and Simeonov [3], provides such conditions.

Theorem A.2. *Suppose*

1. *The function* $f : \mathbb{R} \times \Omega \to \mathbb{R}^n$ *is continuous in* $t \neq \tau_k(x)$, $k \in \mathbb{Z}$,

2. *For any* $(t, x) \in \mathbb{R} \times \Omega$, *there exists a locally integrable function* l *such that*

$$|f(s, y)| \ < \ l(s)$$

   in a small neighbourhood of (t, x), *and*

3. *For each* $k \in \mathbb{Z}$ *the condition* $t_1 = \tau_k(x_1)$ *implies the existence of a* $\delta > 0$ *such that*

$$t \ \neq \ \tau_k(x)$$

   for all $0 < t - t_1 < \delta$ *and* $|x - x_1| < \delta$.

Then for each $(t_0, x_0) \in \mathbb{R} \times \Omega$ *there exists a solution* $\varphi : (t_0, \beta) \to \mathbb{R}^n$ *of the initial value problem (A.3.1)-(A.3.2).*

Remark. The solution $x(t)$ of the initial value problem (A.3.1)-(A.3.2) is unique if the function f is such that the solution of the initial value problem

$$x' = f(t,x), \qquad x(t_0) = x_0$$

is unique. Thus the solution is unique if f is (locally) Lipschitz continuous with respect to x in a neighbourhood of (t_0, x_0), for example.

If the initial value problem (A.3.1)-(A.3.2) has a unique solution, we shall denote it by $x(t; t_0, x_0)$.

The following theorem is from Lakshmikantham, Bainov and Simeonov [20].

Theorem A.3. *Let $\Omega = \mathbb{R}^n$. Suppose $f : \Omega \to \mathbb{R}^n$ is continuous and $I_k : \Omega \to \mathbb{R}^n$ and $\tau_k : \Omega \to (0, \infty)$ are continuous for all $k \geq 1$. Then, for any solution $x(t)$ of (A.3.1)-(A.3.2) with a maximal interval of existence $[t_0, b)$, where $t_0 < b < \infty$, we have*

$$\lim_{t \to b^-} |x(t)| = \infty,$$

provided that one of the following three conditions in satisfied:

1. *for any $k \geq 1$, $t_1 = \tau_k(x_1)$ implies the existence of a $\delta > 0$ such that $t \neq \tau_k(x)$ for all $0 < t - t_1 < \delta$ and $|x - x_1| < \delta$,*

2. *for all $k \geq 1$, $t_1 = \tau_k(x_1)$ implies that $t_1 \neq \tau_j(x_1 + I_k(x_1))$ for all $j \geq 1$,*

3. *τ_k is differentiable for all $k \geq 1$ and $t_1 = \tau_k(x_1)$ implies $t_1 = \tau_j(x_1 + I_k(x_1))$ for some $j \geq 1$ and*

$$\frac{\partial \tau_j(x_1^+)}{\partial x} \cdot f(t_1, x_1^+) \neq 1,$$

where $x_1^+ = x_1 + I_k(x_1)$.

If the impulses occur at fixed times, then the system is significantly simpler and a great deal more can be said about continuation of solutions (see, for example, Bainov

and Simeonov [2], [3], Ballanger [4], and Lakshmikantham, Bainov and Simeonov [20]). With variable impulse times, different solutions will generally undergo impulsive effect at different times, so we cannot ordinarily expect solutions to depend continuously on initial data.

A.4 Definitions of stability

The discontinuous nature of solutions of systems with impulsive effect means that we must adjust our definitions of stability. In particular, stability of a given solution $x_0(t)$ cannot be determined from the trivial solutions by a change of variables.

Definition A.7. *Let $x_0(t) = x(t; t_0, x_0)$ be a given solution of the initial value problem (A.3.1)-(A.3.2), existing for $t \geq t_0$. Suppose $x_0(t)$ hits the surfaces $S_k : t = t_k(x)$ at the moments t_k such that $t_k < t_{k+1}$ and $t_k \to \infty$ as $k \to \infty$. Then the solution $x_0(t)$ of (A.3.1)-(A.3.2) is*

- stable *if for each $\epsilon > 0$, $\eta > 0$ and $t_0 \in \mathbb{R}_+$, there exists $\delta = \delta(t_0, \epsilon, \eta) > 0$ such that $|y_0 - x_0| < \delta$ implies $|y_0(t) - x_0(t)| < \epsilon$ for $t \geq t_0$ and $|t - t_k| > \eta$, where $y_0(t) = x(t; t_0, y_0)$ is any solution of (A.3.1)-(A.3.2) existing for $t \geq t_0$;*
- uniformly stable *if it is stable and δ is independent of t_0;*
- attractive *if for each $\epsilon > 0$, $\eta > 0$ and $t_0 \in \mathbb{R}_+$, there exists $\delta_0 = \delta_0(t_0) > 0$ and a $T = T(t_0, \epsilon, \eta) > 0$ such that $|y_0 - x_0| < \delta_0$ implies $|y_0(t) - x_0(t)| < \epsilon$ for $t \geq t_0 + T$ and $|t - t_k| > \eta$;*
- uniformly attractive *if it is attractive and δ_0 and T are independent of t_0;*
- asymptotically stable *if it is stable and attractive; and*
- uniformly asymptotically stable *if it is uniformly stable and uniformly attractive*

Remarks. The standard definitions are modified so that we can choose initial points suitably close together so that trajectories remain arbitrarily close for all time, except in any neighbourhood of the impulse points, no matter how small.

If $\tau_k(x)$ is independent of x then for every solution the impulse effect occurs at the same time, so the notions of stability coincide with the standard definition.

The system (A.3.1)-(A.3.2) only possesses the trivial solution if $f(t,0) \equiv 0$ and $I_k(0) = 0$ for all k.

If there are only a finite number of impulse points, then the usual definitions of stability can be applied to the trajectories after the last impulse point.

If there are an infinite number of impulse points then we do not want the points to accumulate at some finite value, such that $t_k \to r < \infty$. This accounts for our requiring that $t_k \to \infty$ as $k \to \infty$.

A.5 Autonomous systems with impulsive effect

Autonomous systems with impulsive effect are written in the form

$$\begin{aligned} \frac{dx}{dt} &= g(x) \qquad x \notin M \\ \Delta x &= I(x) \qquad x \in M. \end{aligned} \tag{A.5.3}$$

At an instant $t = t_k$ when $x(t)$ encounters the set M, it is instantaneously transferred to the point $x(t_k) + I(x(t_k))$ of the set N.

The set M is sometimes given in the form $\phi(x) = 0$.

The system (A.5.3) has the property of autonomy, so that $x(t; t_0, x_0) = x(t - t_0; 0, x_0)$. Note that systems of the form (A.3.1) do not possess this property, even if $f(t,x) = g(x)$ and $I_k(x) = I(x)$.

Example. Consider the system

$$\begin{aligned} \frac{dx}{dt} &= x & t_k &\neq k \\ \Delta x &= -\frac{x}{2}+1 & t_k &= k \\ x(0.5) &= 2. \end{aligned}$$

Solutions are given by

$$x(t) = \begin{cases} 2e^{t-0.5} & 0.5 \leq t \leq 1 \\ x_k^+ e^{t-k} & k < t \leq k+1, \qquad k \geq 1. \end{cases}$$

Thus $x(1) = 2e^{0.5}$, so

$$\begin{aligned} x(2) &= x(1)^+ e \\ &= (e^{0.5}+1)e. \end{aligned}$$

Hence $x(2; 0.5, 2) = e^{1.5} + e$.

Conversely, consider the initial condition

$$x(0) = 2.$$

Then $x(1) = 2e$, so

$$\begin{aligned} x(1.5) &= x(1)^+ e^{0.5} \\ &= (e+1)e^{0.5}. \end{aligned}$$

Thus $x(1.5; 0, 2) = e^{1.5} + e^{0.5}$, so $x(2; 0.5, 2) \neq x(1.5; 0, 2)$. Hence the system does not have the property of autonomy.

Distinct solutions of (A.5.3) have different points of discontinuity, making the analysis difficult. Most of the work in Lakshmikantham, Bainov and Simeonov [20] and Bainov and Simeonov [2], [3] is carried out with non-autonomous impulsive differential equations where the moments of impulse are fixed.

Appendix B

Floquet Theory for Impulsive Differential Equations

B.1 Introduction

The Floquet theory for ordinary differential equations has analogues in impulsive differential equations. We outline the basic theory for stability of periodic solutions. We also provide the proofs of some of the basic theorems. These proofs are straightforward, but were not included in the literature, so we have included them here for completeness.

For two-dimensional systems there is a detailed, but relatively straightforward formula for calculation of the second multiplier for a periodic orbit. The theory here is developed in Bainov and Simeonov [2], [3]. This allows the theory of Floquet multipliers to be applied to two dimensional systems, or systems that can be reduced to two dimensional systems, with ease.

B.2 Floquet theory

Consider the linear T-periodic system with fixed moments of impulsive effect

$$\begin{aligned} \frac{dx}{dt} &= P(t)x \qquad t \neq t_k \\ \Delta x &= B_k x \qquad t = t_k, \end{aligned} \tag{B.2.1}$$

subject to the following assumptions:

H1 The matrix $P(\cdot) : \mathbb{R} \to \mathbb{C}^{n\times n}$ is piecewise continuous and $P(t+T) = P(t)$ for $t \in \mathbb{R}$.

H2 $t_k < t_{k+1}$ for $k \in \mathbb{Z}$, $B_k \in \mathbb{C}^{n\times n}$ and $\det(I + B_k) \neq 0$, where I is the $n \times n$ identity matrix.

H3 There exists an integer $q > 0$ such that $B_{k+q} = B_k$, $t_{k+q} = t_k + T$ for $k \in \mathbb{Z}$.

Definition B.1. *Let $x_1(t), ..., x_n(t)$ be solutions to (B.2.1) defined on the interval $(0, \infty)$. Let $X(t) = \{x_1(t), ..., x_n(t)\}$ be a matrix valued function whose columns are these solutions. $x_1(t), ..., x_n(t)$ are linearly independent if and only if* $\det X(0^+) \neq 0$. *In this case, we say that $X(t)$ is a* fundamental matrix *of solutions of (B.2.1).*

Lemma B.1. *Suppose H1-H3 hold and $\lim_{k\to\infty} t_k = \infty$. Let $X(t)$ be a fundamental matrix of solutions of (B.2.1) in $\mathbb{R}_+$. Then*

1. *For any constant matrix $\bar{M} \in \mathbb{C}^{n\times n}$, $X(t)\bar{M}$ is also a solution of (B.2.1).*
2. *If $Y : \mathbb{R} \to \mathbb{C}^{n\times n}$ is a solution of (B.2.1), there exists a unique matrix $\bar{M}$ such that $Y(t) = X(t)\bar{M}$. Furthermore, if $Y(t)$ is also a fundamental matrix of solutions, then* $\det \bar{M} \neq 0$.

Proof. 1. $X(t)\bar{M}$ satisfies

$$\begin{aligned} \frac{d}{dt}\left(X(t)\bar{M}\right) &= \frac{dX(t)}{dt}\bar{M} \\ &= P(t)X(t)\bar{M} \end{aligned}$$

for $t \neq t_k$, and

$$\begin{aligned}\Delta\left(X(t_k)\bar{M}\right) &= X(t_k^+)\bar{M} - X(t_k)\bar{M} \\ &= \left[X(t_k^+) - X(t_k)\right]\bar{M} \\ &= \left[\Delta X(t_k)\right]\bar{M} \\ &= B_k X(t_k)\bar{M}.\end{aligned}$$

2. Since $X(t)$ is a fundamental matrix, it is invertible for each t. Let $\bar{M} = X(0^+)^{-1}Y(0^+)$ and let $Z(t) \equiv Y(t) - X(t)\bar{M}$. Then $Z(0^+) = 0$ and

$$\begin{aligned}\frac{dZ(t)}{dt} &= \frac{dY(t)}{dt} - \frac{dX(t)}{dt}\bar{M} \\ &= P(t)Y(t) - P(t)X(t)\bar{M} \\ &= P(t)Z(t) \\ \Delta Z &= Y(t_k)^+ - X(t_k)^+\bar{M} - \left[Y(t_k) - X(t_k)\bar{M}\right] \\ &= \Delta Y(t_k) - \Delta X(t_k)\bar{M} \\ &= B_k Y(t_k) - B_k X(t_k)\bar{M} \\ &= B_k Z(t_k),\end{aligned}$$

so $Z(t) \equiv 0$ is the unique solution satisfying $Z(0^+) = 0$. Hence $Y(t) = X(t)\bar{M}$

If Y is fundamental, then

$$\begin{aligned}\det \bar{M} &= \frac{1}{\det X(0^+)} \det Y(0^+) \\ &\neq 0.\end{aligned}$$

□

Theorem B.1. *Suppose conditions H1-H3 hold. Then each fundamental matrix of (B.2.1) can be represented in the form*

$$X(t) = \varphi(t)e^{\Lambda t} \qquad t \in \mathbb{R}$$

for a non-singular, T-periodic matrix $\varphi(\cdot) \in PC^1(\mathbb{R}, \mathbb{C}^{n\times n})$ and a constant matrix $\Lambda \in \mathbb{C}^{n\times n}$.

Proof. Let $X(t)$ be a fundamental matrix for (B.2.1) and define $Y(t) = X(t+T)$. Then using H1, we have

$$\begin{aligned}\frac{dy_j(t)}{dt} &= \frac{dx_j(t+T)}{dt} \\ &= P(t+T)x_j(t+T) \\ &= P(t)y_j(t)\end{aligned}$$

for $t \neq t_k$, and using H3,

$$\begin{aligned}\Delta y_j(t_k) &= \Delta x_j(t_k+T) \\ &= \Delta x_j(t_{k+q}) \\ &= B_{k+q}x_j(t_{k+q}) \\ &= B_k x_j(t_k+T) \\ &= B_k y_j(t_k)\end{aligned}$$

for each j. $\det Y(0^+) = \det X(T^+) \neq 0$, since $x_1(t), ..., x_n(t)$ are linearly independent in the interval $(0, \infty)$ and are hence independent in the interval (T, ∞). Thus $Y(t)$ is also a fundamental matrix.

By the lemma, there exists a unique matrix $\bar{M} \in \mathbb{C}^{n\times n}$ such that

$$X(t+T) = X(t)\bar{M}$$

for all $t \in \mathbb{R}$. Set

$$\begin{aligned}\Lambda &= \frac{1}{T}\ln \bar{M} \\ \varphi(t) &= X(t)e^{-\Lambda t}.\end{aligned}$$

Hence $\varphi(t)$ is non-singular and belongs to the class $PC^1(\mathbb{R}, \mathbb{C}^{n\times n})$. Furthermore,

$$\begin{aligned}\varphi(t+T) &= X(t+T)e^{-\Lambda T}e^{-\Lambda t} \\ &= X(t)\bar{M}e^{-\Lambda T}e^{-\Lambda t} \\ &= X(t)e^{-\Lambda t} \\ &= \varphi(t)\end{aligned}$$

since $\bar{M} = e^{\Lambda T}$, by definition of Λ. Hence φ is T-periodic.

□

To the fundamental matrix $X(t)$ there corresponds a unique matrix $\bar{M}$ such that $X(t+T) = \bar{M}X(t)$ for all $t \in \mathbb{R}$. The eigenvalues $\mu_1, \ldots, \mu_n$ of $\bar{M}$ are called *Floquet multipliers* of (B.2.1). The eigenvalues $\lambda_1, \ldots, \lambda_n$ of Λ are called the *characteristic exponents* of (B.2.1).

Corollary B.1. *Let conditions H1-H3 hold. Then $\mu \in \mathbb{C}$ is a Floquet multiplier of (B.2.1) if and only if there exists a non-trivial solution $\gamma(t)$ such that $\gamma(t+T) = \mu\gamma(t)$ for all $t \in \mathbb{R}$.*

The following theorem is from Bainov and Simeonov [3].

Theorem B.2. *Suppose conditions H1-H3 hold. Then (B.2.1) is*

1. *stable if and only if all multipliers μ_j satisfy $|\mu_j| \leq 1$; and for those multipliers for which $|\mu_j| = 1$, the corresponding characteristic exponent (which has zero real part) is a simple zero of the characteristic polynomial of Λ,*
2. *asymptotically stable if and only if all multipliers satisfy $|\mu_j| < 1$, and*
3. *unstable if $|\mu_j| > 1$ for some j.*

B.3 Orbital stability in $\mathbb{R}^2$

Consider the two dimensional autonomous system

$$\begin{aligned} \frac{dx}{dt} &= P(x,y), \quad \frac{dy}{dt} = Q(x,y) && (x,y) \notin M \\ \Delta x &= a(x,y), \quad \Delta y = b(x,y) && (x,y) \in M \end{aligned} \tag{B.3.2}$$

where $t \in \mathbb{R}$, and $M \subset \mathbb{R}^2$ is the set defined by the equation $\phi(x,y) = 0$.

Let $\gamma(t)$, $t \in \mathbb{R}$ be a solution of (B.3.2), with instants of impulsive effect t_k, such that

$$0 < t_1 < t_2 < ...; \qquad \lim_{k\to\infty} t_k = \infty$$

and let $L_+ = \{u \in \mathbb{R}^2 : u = \gamma(t), t \in \mathbb{R}_+\}$. Denote by $J^+(t_0, z_0)$ the maximal interval of the form (t_0, ω) in which the solution $z(t; t_0, z_0)$ of (B.3.2) is defined.

For $y \in \mathbb{R}^2$, let $d(y, L^+) = \min_{u\in L^+} |y - u|$ and $B_\eta(\gamma(t_1))$ be the ball of radius η centred at $\gamma(t_1)$.

Definition B.2. *The solution $z = \gamma(t)$ of (B.3.2) is called*

1. orbitally stable *if for all $\epsilon > 0$, $\eta > 0$ and $t_0 \in \mathbb{R}_+$, there exists $\delta > 0$ such that $d(z_0, L^+) < \delta$ and $z_0 \notin \bar{B}_\eta(\gamma(t_k)) \cup \bar{B}_\eta(\gamma(t_k^+))$ implies $d(z(t), L^+) < \epsilon$ for $t \in J^+(t_0, z_0)$ and $|t_0 - t_k| > \eta$, where $z(t) = z(t; t_0, z_0)$ is any solution of (B.3.2) for which $z(t_0^+; t_0, z_0) = z_0$.*

2. orbitally attractive *if for all $\epsilon > 0$, $\eta > 0$ and $t_0 \in \mathbb{R}_+$, there exists $\delta > 0$ and $T > 0$ such that $t_0 + T \in J^+(t_0, z_0)$ and $d(z_0, L^+) < \delta$ and $z_0 \notin \bar{B}_\eta(\gamma(t_k)) \cup \bar{B}_\eta(\gamma(t_k^+))$ implies $d(z(t), L^+) < \epsilon$ for $t \geq t_0 + T$, $t \in J^+(t_0, z_0)$ and $|t_0 - t_k| > \eta$, where $z(t) = z(t; t_0, z_0)$ is any solution of (B.3.2) for which $z(t_0^+; t_0, z_0) = z_0$.*

3. orbitally asymptotically stable *if it is orbitally stable and orbitally attractive.*

Definition B.3. *The solution $z = \gamma(t)$ of (B.3.2) has the property of* asymptotic phase *if for all $\epsilon > 0$, $\eta > 0$ and $t_0 \in \mathbb{R}_+$, there exists $\delta > 0$, $c > 0$ and $T > |c|$ such that $t_0 + T \in J^+(t_0, z_0)$ and $|z_0 - \gamma(t_0)| < \delta$ implies $|z(t + c) - \gamma(t)| < \epsilon$ for $t \geq t_0 + T$, $t \in J^+(t_0, z_0)$ and $|t_0 - t_k| > \eta$, where $z(t + c) = z(t; t_0 - c, z_0)$ is any solution of (B.3.2) for which $z(t_0^+; t_0, z_0) = z_0$.*

Suppose (B.3.2) has a T-periodic solution

$$\vec{p}(t) = \begin{bmatrix} \xi(t) \\ \eta(t) \end{bmatrix},$$

with

$$\left|\frac{d\xi}{dt}\right| + \left|\frac{d\eta}{dt}\right| \neq 0.$$

Assume further that the periodic solution $\vec{p}(t)$ has q instants of impulsive effect in the interval $(0, T)$. Since we have a periodic orbit, one multiplier is equal to 1. The other is calculated according to the formula

$$\mu_2 = \prod_{k=1}^{q} \Delta_k \exp\left[\int_0^T \left(\frac{\partial P}{\partial x}(\xi(t), \eta(t)) + \frac{\partial Q}{\partial y}(\xi(t), \eta(t))\right) dt\right], \qquad \text{(B.3.3)}$$

where

$$\Delta_k = \frac{P_+\left(\frac{\partial b}{\partial y}\frac{\partial \phi}{\partial x} - \frac{\partial b}{\partial x}\frac{\partial \phi}{\partial y} + \frac{\partial \phi}{\partial x}\right) + Q_+\left(\frac{\partial a}{\partial x}\frac{\partial \phi}{\partial y} - \frac{\partial a}{\partial y}\frac{\partial \phi}{\partial x} + \frac{\partial \phi}{\partial y}\right)}{P\frac{\partial \phi}{\partial x} + Q\frac{\partial \phi}{\partial y}}.$$

P, Q, $\frac{\partial a}{\partial x}$, $\frac{\partial b}{\partial x}$, $\frac{\partial a}{\partial y}$, $\frac{\partial b}{\partial y}$, $\frac{\partial \phi}{\partial x}$ and $\frac{\partial \phi}{\partial y}$ are computed at the point $(\xi(t_k), \eta(t_k))$ and $P_+ = P(\xi(t_k^+), \eta(t_k^+))$, $Q_+ = Q(\xi(t_k^+), \eta(t_k^+))$.

We then have the following theorem, from Bainov and Simeonov [3] which is an analogue of the Poincaré criterion.

Theorem B.3. *The solution $\vec{p}(t)$ of (B.3.2) is orbitally asymptotically stable and has the property of asymptotic phase if the multiplier μ_2 calculated by (B.3.3) satisfies the condition $|\mu_2| < 1$.*

The Floquet theory for impulsive dynamical systems in $\mathbb{R}^n$, $n \geq 3$ is also developed in Bainov and Simeonov [2], [3], but calculation of the multipliers is much more difficult.

In practice, the theory is only useful in low dimensional systems. If we are in $\mathbb{R}^2$ or the system can be reduced to a two dimensional system, then we can apply the results in this section.

Notation index

Symbol	Description	Page
SCF	Self Cycling Fermentation	5
Δy	$= y(t_k^+) - y(t_k)$	8
t_k	time at which the dissolved oxygen minimum occurs for the kth cycle	8
s	limiting substrate concentration	12
x	biomass concentration	12
$[O_2]$	dissolved oxygen concentration	12
t	time	12
μ	maximum specific growth rate	12
K_s	half saturation constant	12
$[O_2]_{min}$	dissolved oxygen concentration at dissolved oxygen minimum	12
Y	cell yield	12
$g(s, x, [O_2])$	oxygen transfer function	12
k	liquid-side dissolved oxygen mass transfer coefficient	13
$[O_2]^*$	dissolved oxygen concentration at saturation	13
r	emptying/refilling fraction	13
s^i	nutrient input concentration at the beginning of each cycle	13
$[O_2]^i$	dissolved oxygen input concentration at the beginning of each cycle	13
c	$= s(0) + x(0)$ in the dimensionless system, without impulse	15

x_n	the value of the biomass at the end of the nth cycle	16
x_n^+	the value of the biomass at the beginning of the $n+1$st cycle	16
c_n	$= x_n + s_n$	17
MAC	Maximal Acceptable Concetration	32
IMAC	Interim Maximal Acceptable Concetration	32
$\bar{d}$	the death rate	32
$\bar{s}$	the nutrient tolerance which signifies the impulsive effect in the nutrient-driven model	33
$f(s)$	the monotone, increasing uptake function	34
s_{int}	$= -\int_{\bar{s}}^{(1-r)\bar{s}+rs^i} \left(\frac{\bar{d}}{f(s)} - 1\right) ds$	37
λ	the value of nutrient such that $f(\lambda) = \bar{d}$	34
l_b	the size of all individuals at birth	62
κ	the fraction of energy used for growth	62
ϖ	the conversion factor relating nutrient to biomass	62
ω	the conversion factor relating nutrient to weight of offspring	62
$\rho(t,l)$	the density of individuals of size l at time t	63
$a(t)$	the minimum size range of individuals at time t who had minimum size range a at time t_0	63
$b(t)$	the maximum size range of individuals at time t who had maximum size range b at time t_0	63
$A(t)$	the total surface area of the population at time t	68
$L(t)$	the total length of the population at time t	68
$P(t)$	the total number of individuals at time t	68
α	$= \frac{1-\kappa}{\omega}$	68
β	$= \frac{\kappa}{\varpi}$	68
$\vec{p}$	$= (A, L, P)^t$	71
H	$= \begin{pmatrix} \alpha & \alpha & \alpha \\ \frac{2}{3}\beta & 0 & 0 \\ 0 & \frac{1}{3}\beta & 0 \end{pmatrix}$	71

$\bar{\mu}$	the physiological efficiency coefficient, a positive eigenvalue of H	72
$\vec{v}$	the eigenvector corresponding to $\bar{\mu}$	72
$\gamma \pm i\nu$	the remaining eigenvalues of H, with $\gamma > 0$, $\nu < 0$	72
u	$= y + iz$	73
$\bar{A}$	the average surface area	76
$\bar{L}$	the average length	76
χ	the ratio between the birth size of a daughter and mother at division	79
$\rho(\chi)$	a smooth probability density function	79
$n(t,x)$	the size distribution per unit volume	80
$b(x)$	the division rate	80
$x_{\min}$	the minimum size of the cells	80
a	the minimum size for division	81
$W[\phi]$	the biomass of a population with size distribution ϕ	82
$W(t)$	$= W[n(t,x;s^0,n^0)]$	82
s^*	the point at which the uptake functions of competing species cross	89
μ_{2x}	the non-trivial Floquet multiplier on the x-axis	93
μ_{2y}	the non-trivial Floquet multiplier on the y-axis	93
$\omega(\{x_n\}_{n\in\mathbb{Z}_+})$	the omega limit set of a sequence $\{x_n\}_{n\in\mathbb{Z}_+}$	99
$\alpha(\{x_{-n}\}_{n\in\mathbb{Z}_+})$	the alpha limit set of a sequence $\{x_{-n}\}_{n\in\mathbb{Z}_+}$	99
$W^+(M)$	the stable set of M	99
$W^-(M)$	the unstable set of M	99
$W^+_{\mathrm{W}}(M)$	the weakly stable set of M	100
$W^-_{\mathrm{W}}(M)$	the weakly unstable set of M	100
P_0	the equilibrium at the origin	103
P_1	the equilibrium on the x-axis	103

P_2	the equilibrium on the y-axis	103
$(X, \pi, \mathbb{R}_+)$	a semidynamical system	115
π_x	the trajectory of x	116
$C^+(x)$	the positive orbit of x	116
$C^+(x, r)$	$= \{\pi(x,t) : 0 \leq t \leq r\}$	116
$G(x,t)$	the attainable set of x at t	116
$G(x)$	$= \cup_{t \in \mathbb{R}_+} G(x,t)$	116
$M^-(x)$	$= G(x) \cap M \backslash \{x\}$	116
$M^+(x)$	$= C^+(x) \cap M \backslash \{x\}$	116
$M(x)$	$= M^+(x) \cap M^-(x)$	116
$(X, \pi; M, A)$	an impulsive semidynamical system	116
$\Phi(x)$	the time without impulse of x	117
$\tilde{\pi}_x$	the impulsive trajectory of x	117
$P(t)$	a piecewise continuous T-periodic matrix	128
B_k	a T-periodic matrix of impulsive effect	128
$X(t)$	a fundamental matrix of solutions	128
$\bar{M}$	the unique matrix such that $X(t+T) = X(t)\bar{M}$	128
μ_j	the Floquet multipliers	131
λ_j	the characteristic exponents	131
$\phi(x,y)$	the surface defining impulsive effect	131
$\dot{\gamma}(t)$	a solution with infinite points of impulse	132
L_+	$= \{z \in \mathbb{R}^2 : z = \gamma(t)\}$	132
$J^+(t_0, z_0)$	the maximal interval in which solutions are defined	132
$(\xi(t), \eta(t))$	a T periodic solution of the two dimensional system	132
μ_2	the nontrivial Floquet multiplier of the two dimensional periodic orbit	133
Δ_k	$= \frac{P_+\left(\frac{\partial b}{\partial y}\frac{\partial \phi}{\partial x} - \frac{\partial b}{\partial x}\frac{\partial \phi}{\partial y} + \frac{\partial \phi}{\partial x}\right) + Q_+\left(\frac{\partial a}{\partial x}\frac{\partial \phi}{\partial y} - \frac{\partial a}{\partial y}\frac{\partial \phi}{\partial x} + \frac{\partial \phi}{\partial y}\right)}{P\frac{\partial \phi}{\partial x} + Q\frac{\partial \phi}{\partial y}}$	133

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