Transient oscillations induced by delayed growth response in the chemostat

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Abstract. In this paper, in order to try to account for the transient oscillations observed in chemostat experiments, we consider a model of single species growth in a chemostat that involves delayed growth response. The time delay models the lag involved in the nutrient conversion process. Both monotone response functions and nonmonotone response functions are considered. The nonmonotone response function models the inhibitory effects of growth response of certain nutrients when concentrations are too high. By applying local and global Hopf bifurcation theorems, we prove that the model has unstable periodic solutions that bifurcate from unstable nonnegative equilibria as the parameter measuring the delay passes through certain critical values and that these local periodic solutions can persist, even if the delay parameter moves far from the critical (local) bifurcation values. When there are two positive equilibria, then positive periodic solutions can exist. When there is a unique positive equilibrium, the model does not have positive periodic oscillations and the unique positive equilibrium is globally asymptotically stable. However, the model can have periodic solutions that change sign. Although these solutions are not biologically meaningful, provided the initial data starts close enough to the unstable manifold of one of these periodic solutions they may still help to account for the transient oscillations that have been frequently observed in chemostat experiments. Numerical simulations are provided to illustrate that the model has varying degrees of transient oscillatory behaviour that can be controlled by the choice of the initial data.

1. Introduction

In this paper, we study the following single-species chemostat model with delay:

\[
\begin{align*}
S'(t) &= (S^0 - S(t)) D - p(S(t))x(t), \\
x'(t) &= -Dx(t) + \alpha p(S(t-\tau))x(t-\tau).
\end{align*}
\] (1.1)

In this model, \(S(t)\) denotes the concentration of the unconsumed nutrient in the growth vessel at time \(t\) and \(x(t)\) denotes the biomass of the population of microorganisms at time \(t\). The function \(p(S)\) represents the species specific per-capita
nutrient uptake rate. It also models the rate of conversion of nutrient to viable biomass. The growth yield constant has been scaled out for mathematical convenience. The constant \( \tau \geq 0 \) denotes the time delay involved in the conversion of nutrient to viable biomass. \( S_0 \) and \( D \) are positive constants and denote, respectively, the concentration of the growth-limiting nutrient and the flow rate of the chemostat (see more details in [19], [51] and [52]). The constant positive constant, \( \alpha = e^{-D\tau} \), is required, because it is assumed that the current change in biomass depends on the amount of nutrient consumed \( \tau \) units of time in the past by the microorganisms that were in the growth vessel at that time and managed to remain in the growth vessel the \( \tau \) units of time required to process the nutrient.

We show that (1.1) has unstable periodic solutions for certain ranges of the time delay \( \tau \). We provide numerical solutions of (1.1) as well, which illustrate how transient oscillatory solutions can be obtained numerically by choosing the initial data appropriately.

The main purpose of this paper is to study the transient behaviour of (1.1) and to give an analytic approach to explain the existence of transient oscillatory solutions. We consider both monotone response functions and nonmonotone response functions. Nonmonotone response functions are important in order to model the inhibitory effects of growth response of certain nutrients when their concentrations are too high. By applying the local Hopf bifurcation theorem, we prove that (1.1) has unstable periodic solutions that bifurcate from unstable nonnegative equilibria as the time delay \( \tau \) passes through certain critical values. Global Hopf bifurcation is also considered, and it is shown that these local periodic solutions can persist, even if the delay parameter moves far from the critical (local) bifurcation values. The unstable periodic solutions of the model may help to account for the transient oscillations observed in chemostat experiments, provided that the initial data starts close enough to the unstable manifold of one of these periodic solutions. Numerical simulations indicate that the model has varying degrees of transient oscillatory behaviour that can be controlled by the choice of the initial data.

We remark that transient dynamics are usually more difficult to study than the asymptotic behaviour of solutions. As a result, fewer analytic tools are available for studying transient dynamics and most authors have used a numerical approach, despite the fact that transient behaviour is of great importance in understanding microbial growth in the chemostat. One tool to study asymptotic behaviour is to study equations linearized about the equilibrium solution and show that the characteristic equation has complex eigenvalues with negative real parts (see [30], [32], [39] and [41]). This results in solutions that approach the steady state via damped sinusoidal oscillations, provided that the solution starts close enough to the steady state. Results in this paper indicate that unstable periodic solutions can be viewed as sources of transient oscillations, and even though they are unstable, their detection might be useful in understanding transient dynamics.

This paper is organized as follows. In Section 2, we give a brief literature review on transient dynamics for chemostat models. In Section 3, we establish some preliminary results on (1.1) that are used in later sections. In Section 4, we first consider the case where the model has a unique positive equilibrium and explore its global asymptotic behaviour as well as the transient dynamics. The case where