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# Emergence of coexistence and limit cycles in the chemostat model with flocculation for a general class of functional responses

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ABSTRACT

We consider a model of two microbial species in a chemostat competing for a single-resource, involving the flocculation of the most competitive species which is present in two forms: isolated and attached. We first show that the model with one species and a non-monotonic growth rate of isolated bacteria may exhibit bi-stability and allows the appearance of unstable limit cycles through a sub-critical Hopf bifurcations due to the joined effect of inhibition and flocculation. We then show that the model with two species presents an even richer set of possible behaviors: coexistence, bi-stability and occurrence of stable limit cycles through a super-critical Hopf bifurcations. All these features cannot occur in the classical chemostat model, where generically at most one competitor can survive on a single resource.



## 1. Introduction

In the mathematical model of competition of $n$ species for a single growth-limiting nutrient in a chemostat, a classical result, well-known as the *Competitive Exclusion Principle* (CEP), asserts that generically at most one species can survive to the competition [1–6]. The dynamical equations of the model are

$$\begin{cases} \dot{S} = D(S_{in} - S) - \sum_{i=1}^{n} \frac{1}{y_i} f_i(S) x_i, \\ \dot{x}_i = [f_i(S) - D] x_i, \qquad i = 1, \ldots, n \end{cases} \tag{1}$$

where $S(t)$ denotes the concentration of the substrate at time $t$, $x_i(t)$ denotes the concentration of the species $i$ at time $t$ and $n$ represents the number of species. The operating parameters $S_{in}$ and $D$ denote, respectively, the concentration of the substrate in the feed device and the dilution rate of the chemostat. For $i = 1, \ldots, n$, the function $f_i(\cdot)$ represents the per-capita growth rate of the species $i$ (or its functional response) and $y_i$ is the yield constant which can be chosen equal to

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one, without loss of generality. A crucial assumption in this classical chemostat model (1) is that the specific growth rates only depend upon the substrate concentration and that are independent of the concentration of microbial species.

Model (1) has been extensively studied in the literature, see for example Smith and Waltman [6]. In [7], Butler and Wolkowicz have studied model (1) for a general class of growth rates including monotonic and non-monotonic growth functions such as the Monod and Haldane laws. This last law takes into account the growth-limiting for low concentrations of substrate and the growth-inhibiting for high concentrations. For distinct break-even concentrations, they have demonstrated that the competitive exclusion holds where at most one competitor avoids extinction. In some cases, the species that wins the competition depends on the initial condition. Extension with inhibition by reaction product has been also considered in [8].

Essajee and Tanner [9] have introduced in their study variable yields that depend linearly on the substrate concentration and they have showed the occurrence of limit cycles. See also [10,11] for a numerical solutions and other growth models. Recently, Sari and Mazenc, in [5], were able to construct a Lyapunov function to study the global dynamics of model (1) with a general class of growth rates, distinct removal rates for each species and variable yields, depending on the concentration of substrate. They showed that at most one competitor can survive, the one with the lowest break-even concentration, that is the species that consumes less substrate at steady state. Sari, in [4,12], proposed a new Lyapunov function for the study of global asymptotic behavior of model (1), which is an extension of the Lyapunov functions used by Hsu [13] and by Wolkowicz and Lu [14].

However, the CEP contradicts the biodiversity that is observed, for instance in aquatic ecosystems where phytoplankton species competing for same resources can coexist (see [15,16]). Such a biodiversity is also observed in laboratory, with mixed cultures including at least two competitors for a single resource (see [17,18]).

To construct mathematical models that are more consistent with real-world observations, several improvements of the idealized model of competition have been proposed. Typically, adding terms of inter-specific competition between populations of microorganisms and/or intra-specific competition between individuals of the same species in the classical chemostat model leads to dynamics where species can coexist at the equilibrium [19–21]. Many papers in the literature have proposed extensions of the classical chemostat model that present periodic solutions or limit cycles due to impulsive effect [22,23]. The predator–prey models show the existence of periodic solutions due to Hopf bifurcations [6]. Research on such models dates back to Drake et al. [24]. Recently, a predator–prey model with three different simultaneous time delays and diffusion shows the existence of a periodic solution and Hopf bifurcation [25]. Fowler [26] studied a competition model of several species on a single resource which exhibits oscillations when the competition is not entirely antagonistic but is partly syntrophic. In a starvation situation, these oscillations are extreme and the deterministic model becomes inappropriate and must be replaced by the stochastic model that permits the extinction of species in finite time.

Flocculation is a physical and chemical process in which the isolated or planktonic bacteria naturally aggregate, reversibly, to one another to form macroscopic flocs. This mechanism of attachment could be to a wall like biofilms [27,28] or simply a formation of flocs or aggregates [29]. Jones et al. [30] studied the Freter model of biofilm formation (that represents the functioning of intestine, cf. [52]) where the parameter values used for the simulations have been chosen from the experimental data of Freter et al. [31].

In this paper, we consider a flocculation mechanism and show how it can lead also to oscillations and non-intuitive phenomena of the dynamics. This mechanism is different than the ones previously considered in the literature for explaining the oscillations that are observed experimentally. Indeed, understanding and exploiting the flocculation process appears to be a major challenge to tackle contemporary issues in the fields of wastewater treatments and development of renewable energy, and to improve next future bioprocesses. In [32], the effect of flocculation on the growth dynamics was analyzed with an arbitrary number of bacteria in flocs. Haegeman and Rapaport [33] proposed a competition model of two microbial species on a single nutrient with monotonic increasing uptake functions, where attached bacteria or flocs of bacteria do not grow and are subject to the same dilution rate than isolated biomass. Assuming that the most competitive species inhibits its growth by the formation of flocs, they could explain the coexistence between two species. An extension of this model was studied in [34] without neglecting the substrate consumption of attached bacteria, but assuming that they consume less substrate than the isolated bacteria, since the bacteria at the surface of flocs have easier access to the substrate than the bacteria inside the flocs. More recently, Fekih-Salem et al. [35] proposed a model of flocculation of $n$ species that generalizes several models [30,36,37] that have been considered in the literature. Assuming that the flocculation and deflocculation dynamics are fast compared to the growth dynamics, Haegeman and Rapaport [33] could build a density-dependent model with the same dilution rate that is studied in [38,39]. More precisely, the specific growth rate of each species $i$ does not depend only upon the substrate concentration but depends also on the concentration of the same species. In [39], the authors determines a sufficient conditions for coexistence of several species in competition for a single resource by introducing the concept of *steady-state characteristic*. When the dilution rates are identical, Lobry et al. [38,39] were able to show the existence and the global stability of the coexistence equilibrium. From experimental data, Harmand and Godon [40] have shown that the bioprocesses with attached biomass is better described using ratio-dependent kinetics. Moreover, the study of a flocculation model [35] with different dilution rates leads also to density-dependent dilution rates for the overall biomass [35], which is a new feature. In the present work, we revisit the flocculation model proposed in [33], but considering that the attached bacteria consumes also the substrate. Moreover, we consider a general class of growth rates to study the effects on coexistence of two competitors, to be compared with the results obtained by Butler and Wolkowicz [7], where at most one competitor can survive on a single resource in absence of flocculation.