

Bacterial Wall Attachment in a Flow Reactor: mixed culture

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Abstract

A mathematical model of a mixed culture of bacteria in a fully three dimensional flow reactor which accounts for the colonization of the reactor wall surface by the microbes is studied both analytically and by simulation. It can be viewed as a model of the large intestine or of the fouling of a commercial bio-reactor or pipe flow. The primary focus is on coexistence of microbial populations in the reactor.

1 Introduction

In [13] we studied a fully three dimensional model of a bacterial population colonizing the fluid environment and the lateral surface of a cylindrical flow reactor. The model was inspired by work of Freter et al [10, 11] whose primary motivation was to understand the phenomena of colonization resistance in the mammalian gut: the resistance of the natural gut micro-flora to colonization by ingested organisms. However, we feel that it may also be useful as a relatively simple model of biofilm formation in both natural environments and in man-made ones such as pipe flow and bio-reactors. Our work in [13] builds on earlier work [1, 2, 3, 4, 12] on a one-space dimensional model.

Our main focus in [13] was to identify conditions under which a bacterial population can colonize both the fluid and the wall environment of the cylindrical reactor under substrate limitation. In the present work we ask whether the flow reactor can support several populations of bacteria competing for a growth-limiting

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substrate and limited wall-attachment space on the lateral surface of the cylinder wall. It is natural to seek conditions under which coexistence is possible.

The Freter model considered here as a model of a biofilm is far from being a state of the art biofilm model. See [5] for an up-to-date review. The focus of most recent modeling has been directed toward replicating the remarkable spatial structure of biofilms as seen using the latest imaging techniques ([6, 7, 5]). The Freter model, by contrast, ignores completely the spatial structure of the biofilm. However, there seems to be a lack of a relatively simple, conceptual biofilm model which is amenable to mathematical analysis. The Freter model, though far from being simple, is at least mathematically tractable essentially due to the assumption that the biofilm growing on the cylindrical surface is infinitesimally thin and consequently that it does not affect the fluid velocity field, which we take to be a steady Poiseau flow. While this assumption is clearly unrealistic (see e.g.[7, 5]), we believe that the results obtained here can serve as a reference point from which to examine more realistic scenarios. State of the art biofilm models which account for the spatial structure of the biofilm are, with few exceptions [9], too complicated for mathematical analysis [8, 5]; numerical simulations then provide the only window through which to study these models.

Several of the mathematical results derived in this paper improve on ones obtained in [13]. Our principal new mathematical result is directed towards resolving the stability of a mono-culture steady state to invasion by a rival organism. Essentially, it amounts to a spectral analysis of a non-standard elliptic eigenvalue system. However, we are unable at this time to provide a mathematical existence proof for a coexistence steady state. It is conjectured that a coexistence steady state involving two competing populations occurs when both single-population steady states are stable (unstable) to invasion by its rival.

Numerical simulations establish that coexistence is possible and allow an exploration of its robustness. From a biological viewpoint, these simulations are the main result of the paper. Our simulations show that three populations can coexist in the flow reactor; these three populations compete for two limited resources, namely substrate and wall-attachment space (a refuge from washout). Coexistence is facilitated by a spatially inhomogeneous substrate profile in the bio-reactor and the choice of substrate uptake functions which give each competitor an advantage over its rivals in a region of the bio-reactor. Equilibrium distributions of the three populations on the reactor wall form a pattern of segregation: roughly, one organism dominates the upstream end, a second dominates an adjacent downstream segment and a third appears to share with the second organism the far downstream end. Interesting, and somewhat unusual in competition models, are transient oscillations in total population levels prior to reaching steady state.

2 The Model

We follow [13], which treated a single bacterial strain, by adding additional strains. A flow reactor amounts to a section of a cylindrical tube $\Omega \equiv \{0 < x < L, 0 \leq r^2 = y^2 + z^2 < R^2\}$ in which a steady flow $v(r) = V_{max}[1 - \epsilon(r/R)^2]$ of fluid in the direction of increasing x is imposed. Here, $\epsilon = 0, 1$ are of primary interest; $\epsilon = 1$ corresponds to Poiseau flow of fluid medium through the reactor. The flow carries fresh nutrient at concentration S^0 into the reactor across the $x = 0$ interface and carries unused nutrient and bacteria out of the reactor across the $x = L$ interface. The equations describing nutrient density $S = S(x, y, z, t)$ and biomass density $u^i = u^i(x, y, z, t)$ of bacteria of strain i in the fluid (i.e., in Ω) are given by:

$$S_t = d_x^S S_{xx} + d_r^S [S_{yy} + S_{zz}] - v(r)S_x - \sum_i \gamma_i^{-1} u^i f_{ui}(S) \quad (2.1)$$

$$u_t^i = d_x^i u_{xx}^i + d_r^i [u_{yy}^i + u_{zz}^i] - v(r)u_x^i + u^i (f_{ui}(S) - k_i) \quad (2.2)$$

for $(x, y, z) \in \Omega$. The areal density of wall-attached cells of strain i on the radial boundary $r = R$ of Ω , denoted by $w^i = w^i(x, y, z, t)$, satisfy the equations by

$$w_t^i = w^i [f_{wi}(S)G_i(W) - k_{wi} - \beta_i] + \alpha_i u^i (1 - W). \quad (2.3)$$

The specific growth rate of strain i in the fluid $f_{ui}(S)$ and on the wall $f_{wi}(S)$ are further described below. Constants k_i and k_{wi} represent cell death rates in fluid and wall environments, respectively, β_i is the rate of sloughing of wall-attached bacteria into the fluid, and α_i is the rate coefficient of adhesion to the wall surface for strain i . Axial and radial nutrient diffusion coefficients are given by d_x^S, d_r^S , respectively; axial and radial

bacterial motility coefficients for the i th strain are d_x^i, d_r^i , respectively. A model assumption is that there is a maximum attainable areal density of wall-attached bacteria w_∞ and

$$W = \sum_i \frac{w^i}{w_\infty}$$

represents the occupation fraction. Danckwerts' boundary conditions describe the interface conditions between the up-stream and down-stream flow and the reactor. They are as follows :
at $x = 0$:

$$\begin{aligned} v(r)S^0 &= -d_x^S S_x + v(r)S \\ 0 &= -d_x^i u_x^i + v(r)u^i, \end{aligned} \quad (2.4)$$

at $x = L$:

$$S_x = u_x^i = 0. \quad (2.5)$$

These conditions reflect the assumption that the diffusive component of the total flux of nutrient and of biomass crossing $x = 0$ and $x = L$ should be neglected so that bacteria do not contaminate the fresh nutrient in the upstream flow and advection alone is responsible for flushing out planktonic cells (those not attached to the wall) and unused nutrient at $x = L$. The radial boundary conditions at $r = R$ reflect important biological considerations:

$$\begin{aligned} 0 &= d_r^S S_r + \sum_i \gamma_i^{-1} w^i f_{wi}(S) \\ 0 &= d_r^i u_r^i + \alpha_i u^i (1 - W) - w^i [f_{wi}(S)(1 - G_i(W)) + \beta_i]. \end{aligned} \quad (2.6)$$

These boundary conditions describe the fluxes of nutrient and biomass between the fluid and wall environment. The first describes the flux of nutrient from the fluid to the wall environment due to consumption by wall-attached bacteria. The first term in the second equation represents the flux of biomass from the fluid to the wall due to passive attraction of planktonic cells to the wall; the second term represents flux in the opposite direction caused by a fraction of the progeny of wall-attached cells being forced into the fluid. These are further described below. In addition, S, u, w satisfy (non-negative) initial conditions at $t = 0$:

$$\begin{aligned} S(x, y, z, 0) &= S_0(x, y, z) \\ u^i(x, y, z, 0) &= u_0^i(x, y, z) \\ w^i(x, y, z, 0) &= w_0^i(x, y, z). \end{aligned} \quad (2.7)$$

We assume that S_0, u_0^i, w_0^i are continuous. For further details of the modeling, see [13].

It will also be of interest to allow the initial "charging" of the reactor with microbes to take place via the boundary condition at $x = 0$ by replacing zero on the left side of (2.4) by $v(r)u^{0i}(t)$, where $u^{0i}(t) \equiv u^{0i}$, a constant, on $0 \leq t \leq t_0$ and $u^{0i}(t) = 0, t \geq t_0$.

Although it is usual to non-dimensionalize variables, we avoid it in order that the biological meaning of key quantities will be transparent. Keeping in mind that $0 \leq w^i \leq w_\infty$, the initial data and solutions S, u^i, w^i must satisfying:

$$S, u^i, w^i \geq 0, \quad \sum_i w^i \leq w_\infty. \quad (2.8)$$

Hereafter, we refer to these restrictions as the range conditions.

For brevity, we let L^S and L^i denote the differential operators for the S and u^i equations so they become:

$$\begin{aligned} S_t &= L^S S - \sum_i \gamma_i^{-1} u^i f_{wi}(S) \\ u_t^i &= L^i u^i + u^i (f_{ui}(S) - k_i) \end{aligned}$$

We make several biologically reasonable assumptions concerning the functions G_i, f_{ui}, f_{wi} . We assume that $G_i : [0, 1] \rightarrow [0, 1]$ is C^1 with $G'_i < 0$. Indeed, it is assumed that $G_i(W) = (1 - W)g_i(W)$ where $g_i \geq 0$ and $g'_i > 0$. For example, Freter [10, 11] employs:

$$G_i(W) = \frac{1 - W}{1.1 - W}.$$

As usual, f_{ui}, f_{wi} are C^1 functions, vanishing at zero and $f'_{ui}, f'_{wi} \geq 0$. We further assume that these functions are dominated by linear functions: there exists $p > 0$ such that for $f = f_{wi}, f_{ui}$ we have $f'(S) \leq p$. The prototypical f is the Monod form:

$$f(S) = \frac{mS}{a + S}.$$

3 Eigenvalue Problems

A family of non-standard eigenvalue problems plays a central role in our analysis so we introduce them here. The adjoint operator to $L^S (L^i)$ with homogeneous boundary conditions (2.4) with $S^0 = 0, (2.5)$, and radial boundary condition $S_r = 0$ is denoted by $L_S (L_i)$. L_S is given by:

$$L_S \phi = d_x^S \phi_{xx} + d_r^S [\phi_{yy} + \phi_{zz}] + v(r) \phi_x$$

with homogeneous boundary conditions

$$\begin{aligned} 0 &= d_x^S \phi_x + v(r) \phi, & x = L \\ 0 &= \phi_x, & x = 0 \\ 0 &= \phi_r, & r = R \end{aligned}$$

and similarly for L_i . It's as if the the flow through the reactor changes from left to right to right to left. Denote by $-\lambda^S$ the principal eigenvalue of the eigenvalue problem:

$$L_S \phi = \lambda \phi,$$

together with the above boundary conditions. Then $-\lambda^S < 0$ and the corresponding eigenfunction ϕ satisfies $\phi > 0$ on $\bar{\Omega}$ and can be normalized by assuming that it attains a maximum of unity (see Appendix 6 in [13]). Let $-\lambda^i < 0$ be the principal eigenvalue of L_i subject to analogous homogeneous boundary conditions. It is well-known that $-\lambda^i < 0$ is also the principal eigenvalue of L^i corresponding to boundary conditions (2.4),(2.5), and $u_r = 0$ on $r = R$.

Another important pair of eigenvalue problems is the following.

$$\begin{aligned} \lambda u &= L^i u + au, & \Omega \\ \lambda w &= bw + \alpha u, & r = R \\ 0 &= d_r u_r + \alpha u - cw, & r = R \\ 0 &= -d_x u_x + v(r)u, & x = 0 \\ 0 &= u_x, & x = L \end{aligned} \tag{3.1}$$

The corresponding adjoint problem is given by:

$$\begin{aligned} \lambda u &= L_i u + au, & \Omega \\ \lambda w &= bw + cu, & r = R \\ 0 &= d_r u_r + \alpha u - \alpha w, & r = R \\ 0 &= d_x u_x + v(r)u, & x = L \\ 0 &= u_x, & x = 0 \end{aligned} \tag{3.2}$$

In order to see in what sense (3.2) is adjoint to (3.1) we make the following observation.

Proposition 3.1 Let $u \in C^2(\Omega) \cap C^1(\bar{\Omega})$ satisfy the Danckwerts' boundary conditions at $x = 0, L$, $\hat{u} \in C^2(\Omega) \cap C^1(\bar{\Omega})$ satisfy the adjoint Danckwerts' boundary conditions at $x = 0, L$, u, w satisfy the inhomogeneous radial boundary condition

$$h = d_r u_r + \alpha u - cw, \quad r = R$$

and \hat{u}, \hat{w} satisfy the homogeneous adjoint radial boundary condition in (3.2). Then we have

$$\int_{\Omega} (L^i u) \hat{u} dV + \int_{r=R} (bw + \alpha u) \hat{w} dA = \int_{\Omega} (L_i \hat{u}) u dV + \int_{r=R} h \hat{u} + w(b\hat{w} + c\hat{u}) dA \quad (3.3)$$

If $h \equiv 0$, then we obtain the adjoint relation of (3.2) and (3.1).

Proof: Use of Green's identities leads to

$$\int_{\Omega} (L^i u) \hat{u} dV = \int_{\Omega} (L_i \hat{u}) u dV + \int_{r=R} \hat{u} d_r u_r - u d_r \hat{u}_r dA$$

if u, \hat{u} satisfy the above-mentioned Danckwerts' boundary conditions. Multiplying the radial boundary condition satisfied by u by \hat{u} and the radial boundary condition satisfied by \hat{u} by u and subtracting leads to $\hat{u} d_r u_r - u d_r \hat{u}_r = h \hat{u} + cw \hat{u} - \alpha u \hat{w}$. The equation (3.3) results from inserting this equality into the last integral above and adding $\int_{r=R} \hat{w} [bw + \alpha u] dA$ to both sides. ■

One of our main tools is the following result, Theorem 3.3 in [13]. It will be generalized to non-constant coefficients later in Theorem 4.4.

Proposition 3.2 Principal Eigenvalue Let $\alpha, c > 0$. Then there exists a real simple eigenvalue $\lambda^* > b$ of (3.1) satisfying:

$$\begin{aligned} b + c < \lambda^* \leq a - \lambda_i, & \quad \text{if } b + c < a - \lambda_i \\ b + c = \lambda^*, & \quad \text{if } b + c = a - \lambda_i \\ a - \lambda_i < \lambda^* < b + c, & \quad \text{if } b + c > a - \lambda_i \end{aligned}$$

Corresponding to eigenvalue λ^* is an eigenvector (\bar{u}, \bar{w}) satisfying $\bar{u} > 0$ in $\bar{\Omega}$ and $\bar{w} > 0$ in $r = R$. If λ is any other eigenvalue of (3.1) corresponding to an eigenvector $(u, w) \geq 0$, then $\lambda = \lambda^*$ and $(u, w) = c(\bar{u}, \bar{w})$ for some $c > 0$. \bar{u}, \bar{w} are axially symmetric, i.e., in cylindrical coordinates (r, θ, x) , $\bar{u} = \bar{u}(r, x)$, $\bar{w} = \bar{w}(x)$. λ^* is also an eigenvalue of (3.2) corresponding to an eigenvector $(u, w) = (\psi, \chi)$. Moreover, (ψ, χ) has the same uniqueness up to scalar multiple, positivity and symmetry properties as does (\bar{u}, \bar{w}) .

4 Main Results

We begin by establishing that bacterial growth is limited by the supplied substrate. Let (ψ^i, χ^i) be the principal eigenvector corresponding to the eigenvalue $\bar{\lambda}_i$ of (3.2) in the case that $a = 0, b = -\beta_i, \alpha = \alpha_i, c = \beta_i, d_r = d_r^i, d_x = d_x^i$. Normalize (ψ^i, χ^i) by requiring $\psi^i, \chi^i \leq \phi \leq 1$ with equality holding at some point for each inequality. By Proposition 3.2 and the fact that $b + c = 0$, we have $\bar{\lambda}_i < 0$ and, by the second of equations (3.2), $\psi^i < \chi^i$ on $r = R$.

Our first result represents a significant improvement over Theorem 3.1 in [13] in the case of a single species since we obtain useful bounds even when $k_{wi} = 0$.

Theorem 4.1 We have the estimates

$$\limsup_{t \rightarrow \infty} S(t, x, y, z) \leq S^0,$$

uniformly in $(x, y, z) \in \Omega$ and

$$\limsup_{t \rightarrow \infty} \left(\int_{\Omega} S \phi dV + \sum_i \gamma_i^{-1} \left[\int_{\Omega} u^i \psi^i dV + \int_{r=R} w^i \chi^i dA \right] \right) \leq \frac{2\pi S^0 \int_0^R r v(r) dr}{\min_j \{ \lambda^S, -\bar{\lambda}_j + k_j, -\bar{\lambda}_j + k_{wj} \}} \quad (4.1)$$

where the minimum, taken over all indices j , is positive.

Proof: It is easy to establish that $S \leq \tilde{S}$, where \tilde{S} satisfies $S_t = L^S S$ with homogeneous radial boundary condition $S_r = 0$ and (2.4),(2.5), by a simple comparison argument. Furthermore, noting that $S = S^0$ is a steady state of this comparison equation, the linearization of which having a dominant negative eigenvalue, we conclude that $\tilde{S} \rightarrow S^0$ as $t \rightarrow \infty$ uniformly in $(x, y, z) \in \Omega$.

Now, corresponding to the normalized eigenfunctions ϕ, ψ^i, χ^i , define

$$X = \int_{\Omega} \phi S dV, \quad Y^i = \int_{\Omega} \psi^i u^i dV, \quad Z = \int_{r=R} \chi^i w^i dA$$

We note the following, which follow by integration by parts and Green's third identity applied to the two dimensional Laplacian in y, z and using the boundary conditions satisfied by S :

$$\begin{aligned} \int_{\Omega} \phi L^S S dV &= \int_{\Omega} S L_S \phi dV - \sum_i \gamma_i^{-1} \int_{r=R} \phi w^i f_{wi}(S) dA + S^0 \int_{r \leq R} v(r) \phi(0, y, z) dy dz \\ &= -\lambda^S X - \sum_i \gamma_i^{-1} \int_{r=R} \phi w^i f_{wi}(S) dA + S^0 \int_{r \leq R} v(r) \phi(0, y, z) dy dz \end{aligned}$$

Differentiation of X, Y^i, Z^i and using these relations leads to the following:

$$X_t = -\lambda^S X - \sum_i \gamma_i^{-1} \int_{\Omega} u^i \phi f_{ui}(S) dV - \sum_i \gamma_i^{-1} \int_{r=R} \phi w^i f_{wi}(S) dA + S^0 \int_{r \leq R} v(r) \phi(0, y, z) dy dz$$

$$Y_t^i = \int_{\Omega} \psi^i L^i u^i dV + \int_{\Omega} u^i \psi^i [f_{ui}(S) - k_i] dV \quad (4.2)$$

$$Z_t^i = \int_{r=R} \chi^i [-\beta_i w^i + \alpha_i u^i] dA + \int_{r=R} \chi^i w^i [f_{wi}(S) G_i(W) - k_{wi}] - \chi^i \alpha_i u^i W dA \quad (4.3)$$

Now, using the adjoint relation (3.3), the eigenvalue problem satisfied by (ψ^i, χ^i) , and $\psi^i < \chi^i$ on $r = R$, we find that

$$\begin{aligned} (Y^i + Z^i)_t &= \int_{\Omega} \psi^i L^i u^i dV + \int_{r=R} \chi^i [-\beta_i w^i + \alpha_i u^i] dA + \int_{\Omega} (f_{ui}(S) - k_i) \psi^i u^i dV \\ &+ \int_{r=R} \chi^i w^i [f_{wi}(S) G_i(W) - k_{wi}] - \alpha_i \chi^i u^i W dA \\ &= \int_{\Omega} (L_i \psi^i) u^i dV + \int_{r=R} \psi^i [\alpha_i u^i W + w^i f_{wi}(S) (1 - G_i(W))] + w^i [-\beta_i \chi^i + \beta_i \psi^i] dA \\ &+ \int_{\Omega} f_{ui}(S) \psi^i u^i dV + \int_{r=R} \chi^i w^i f_{wi}(S) G_i(W) dA - k_i Y^i - k_{wi} Z^i - \int_{r=R} \alpha_i \chi^i u^i W dA \\ &= \bar{\lambda}_i (Y^i + Z^i) - k_i Y^i - k_{wi} Z^i + \int_{\Omega} f_{ui}(S) \psi^i u^i dV \\ &+ \int_{r=R} w^i f_{wi}(S) [G_i(W) \chi^i + (1 - G_i(W)) \psi^i] dA + \int_{r=R} \alpha_i u^i W (\psi^i - \chi^i) dA \\ &\leq \bar{\lambda}_i (Y^i + Z^i) - k_i Y^i - k_{wi} Z^i + \int_{\Omega} f_{ui}(S) \psi^i u^i dV + \int_{r=R} w^i f_{wi}(S) \chi^i dA \end{aligned} \quad (4.4)$$

Let $Q = X + \sum_i \gamma_i^{-1}(Y^i + Z^i)$. Using $\chi^i, \psi^i \leq \phi \leq 1$, we find that

$$\begin{aligned}
Q_t &\leq -\lambda^S X + \sum_i \gamma_i^{-1}(\bar{\lambda}_i - k_i)Y^i + \sum_i \gamma_i^{-1}(\bar{\lambda}_i - k_{wi})Z^i \\
&+ \sum_i \int_{\Omega} \gamma_i^{-1} u^i f_{ui}(S) [\psi^i - \phi] dV + \sum_i \int_{r=R} \gamma_i^{-1} w^i f_{wi}(S) [\chi^i - \phi] dA \\
&+ S^0 \int_{r \leq R} v(r) \phi(0, y, z) dy dz \\
&\leq -\lambda^S X + \sum_i \gamma_i^{-1}(\bar{\lambda}_i - k_i)Y^i + \sum_i \gamma_i^{-1}(\bar{\lambda}_i - k_{wi})Z^i + S^0 \int_{r \leq R} v(r) \phi(0, y, z) dy dz \\
&\leq -\min_j \{\lambda^S, -\bar{\lambda}_j + k_j, -\bar{\lambda}_j + k_{wj}\} Q + 2\pi S^0 \int_0^R r v(r) dr.
\end{aligned}$$

Therefore,

$$\limsup_{t \rightarrow \infty} Q(t) \leq \frac{2\pi S^0 \int_0^R r v(r) dr}{\min_j \{\lambda^S, -\bar{\lambda}_j + k_j, -\bar{\lambda}_j + k_{wj}\}} \quad (4.5)$$

This completes our proof. \blacksquare

As the numerator of the fraction on the right side of (4.1) is precisely the net flux of nutrient into the reactor across $x = 0$, (4.1) says precisely that the output of organisms is limited by the input of substrate. Since $\psi^i > 0$ is continuous on $\bar{\Omega}$, (4.1) implies the existence of an a priori asymptotic estimate for $\int_{\Omega} u^i dV$ for each i .

In [13] we showed for the single strain system ($n = 1$), consisting of only the i th strain, that the washout steady state $S = S^0$, $u^i = w^i = 0$ is unstable in the linear approximation if the principal eigenvalue, λ_i^* , of the eigenvalue problem (3.1) with $a = a_i \equiv f_{ui}(S^0) - k_i$, $b = b_i \equiv f_{wi}(S^0)G_i(0) - k_{wi} - \beta_i$, $c = c_i \equiv f_{wi}(S^0)(1 - G_i(0)) + \beta_i$, $d_r = d_r^i$, $d_x = d_x^i$ is positive and is stable in the linear approximation if it is negative. Below, improving on Proposition 3.2 in [13], we provide a number of sufficient conditions for the extinction of the i th strain.

Proposition 4.2 Washout of strain i : *If for some i , one of the following holds*

- (a) $\lambda_i^* < 0$ and $f_{ui}(S^0) - k_i - \lambda_i \leq f_{wi}(S^0) - k_{wi}$.
- (b) $f_{ui}(S^0) - k_i - \lambda_i < 0$ and $f_{wi}(S^0) - k_{wi} < 0$.
- (c) $f_{ui}(S^0) - k_i + \bar{\lambda}_i < 0$ and $f_{wi}(S^0) - k_{wi} + \bar{\lambda}_i < 0$.

then

$$\lim_{t \rightarrow \infty} \left(\int_{\Omega} u^i dV + \int_{r=R} w^i dA \right) = 0. \quad (4.6)$$

Proof: Assume that (a) holds. We reuse the notation (ψ^i, χ^i) for the positive eigenvector of (3.2) with parameters described in the paragraph above corresponding to eigenvalue λ_i^* . Note that λ_i^* is the principal eigenvalue of both (3.1) and (3.2) because of their adjoint relationship. We also use the notation Y^i and Z^i for the integrals of $u^i \psi^i$ and $w^i \chi^i$ respectively. As $S \leq \tilde{S} \rightarrow S^0$ as $t \rightarrow \infty$, uniformly in $x \in \Omega$, there exists $\epsilon > 0$ so small that $\lambda_i^* + \epsilon < 0$ and $T > 0$ such that

$$f_{ui}(S) - f_{ui}(S^0), f_{wi}(S) - f_{wi}(S^0) < \epsilon$$

for all $x \in \bar{\Omega}$ and $t > T$. Now, proceeding as in (4.2) and (4.4) using (3.3), we have for $t > T$.

$$\begin{aligned}
(Y^i + Z^i)_t &= \int_{\Omega} \psi^i L^i u^i dV + \int_{\Omega} u^i \psi^i [f_{wi}(S) - k_i] dV + \int_{r=R} \chi^i [b_i w^i + \alpha_i u^i] dA \\
&\quad + \int_{r=R} \chi^i w^i [f_{wi}(S) G_i(W) - f_{wi}(S^0) G_i(0)] - \chi^i \alpha_i u^i W dA \\
&= \int_{\Omega} u^i L_i \psi^i dV + \int_{\Omega} u^i \psi^i [f_{wi}(S) - k_i] dV \\
&\quad + \int_{r=R} \psi^i [\alpha_i u^i W + w^i (f_{wi}(S)(1 - G_i(W)) - f_{wi}(S^0)(1 - G_i(0)))] + w^i [b_i \chi^i + c_i \psi^i] dA \\
&\quad + \int_{r=R} \chi^i w^i [f_{wi}(S) G_i(W) - f_{wi}(S^0) G_i(0)] - \chi^i \alpha_i u^i W dA \\
&\leq (\lambda_i^* - a_i) Y^i + (a_i + \epsilon) Y^i + \lambda_i^* Z^i + \int_{r=R} w^i \psi^i [f_{wi}(S) - f_{wi}(S^0)] dA \\
&\quad + \int_{r=R} \alpha_i u^i W (\psi^i - \chi^i) dA + \int_{r=R} w^i (\chi^i - \psi^i) [f_{wi}(S) G_i(W) - f_{wi}(S^0) G_i(0)] dA \\
&\leq (\lambda_i^* + \epsilon) Y^i + \lambda_i^* Z^i + \int_{r=R} w^i \psi^i [f_{wi}(S) - f_{wi}(S^0)] dA \\
&\quad + \int_{r=R} w^i (\chi^i - \psi^i) G_i(0) [f_{wi}(S) - f_{wi}(S^0)] dA \\
&\leq (\lambda_i^* + \epsilon) Y^i + \lambda_i^* Z^i + (1 - G_i(0)) \epsilon Z^i + G_i(0) \epsilon Z^i \\
&\leq (\lambda_i^* + \epsilon) (Y^i + Z^i)
\end{aligned}$$

where we have used that $c_i(\psi^i - \chi^i) = [\lambda_i^* - (b_i + c_i)]\chi^i \leq 0$, since $b_i + c_i \geq \lambda_i^*$ by Proposition 3.2 and our assumption that $a_i + \lambda_i \leq b_i + c_i$, so $\psi^i \leq \chi^i$ on $r = R$. Since $\lambda_i^* + \epsilon < 0$, the result follows in this case.

The proof in case (b) is exactly as in Proposition 3.2 of Jones et al. The proof in case (c) is simpler than case (a), using (4.4), and we leave it to the reader. \blacksquare

We now turn to the problem of finding non-trivial steady states. The equations for a steady state are

$$\begin{aligned}
0 &= L^S S - \sum_i \gamma_i^{-1} u^i f_{wi}(S) \\
0 &= L^i u^i + u^i [f_{wi}(S) - k_i], \quad \text{in } \Omega \\
0 &= w^i [f_{wi}(S) G_i(W) - k_{wi} - \beta_i] + \alpha_i u^i (1 - W), \quad \text{in } \partial_r \Omega.
\end{aligned} \tag{4.7}$$

with boundary conditions (2.4, 2.5, 2.6). We are unable to address the general problem at this time; however, we have shown the existence of single-population steady states where $w^j, w^j \equiv 0$ for $j \neq i$ and $u^i, w^i > 0$ in Theorem 3.5 in [13].

Theorem 4.3 *Let $\lambda_i^* > 0$ for some i and*

$$b_i = f_{wi}(S^0) G_i(0) - k_{wi} - \beta_i \neq 0. \tag{4.8}$$

Then there exists a radially symmetric, single-population steady state solution of (4.7) with $w^j, w^j \equiv 0$ for $j \neq i$ satisfying (in cylindrical coordinates)

$$0 < \bar{S}(x, r) \leq S^0, \bar{u}^i(x, r) > 0, \text{ and } 0 < \bar{w}^i(x) \leq w_{\infty}.$$

The stability of this single-population steady state can be determined, at least formally, by linearization. In order to simplify the calculations, suppose there are only two populations and that we are considering the stability of the single population steady state where only the first population is present:

$$S = \bar{S}, \quad u^1 = \bar{u}^1, \quad w^1 = \bar{w}^1, \quad u^2 \equiv 0, \quad w^2 \equiv 0. \tag{4.9}$$

We obtain the variational equations about this steady state by putting

$$S = \bar{S} + \epsilon \hat{S}, \quad u^1 = \bar{u}^1 + \epsilon \hat{u}^1, \quad w^1 = \bar{w}^1 + \epsilon \hat{w}^1, \quad u^2 \equiv \epsilon \hat{u}^2, \quad w^2 \equiv \epsilon \hat{w}^2$$

into (2.1)-(2.6), letting $\epsilon \rightarrow 0$, and keeping only first order terms in ϵ . It is given by (we drop “hats” on variables so they are distinguishable from the “bars” on steady state variables)

$$\begin{aligned}
S_t &= L^S S - \gamma_1^{-1} \bar{u}^1 f'_{u1}(\bar{S}) S - \sum_i \gamma_i^{-1} u^i f_{ui}(\bar{S}) \\
u_t^1 &= L^1 u^1 + \bar{u}^1 f'_{u1}(\bar{S}) S + u^1 (f_{u1}(\bar{S}) - k_1) \\
w_t^1 &= \bar{w}^1 (f'_{w1}(\bar{S}) G_1(\bar{W}) S + f_{w1}(\bar{S}) G'_1(\bar{W}) W) \\
&\quad + w^1 [f_{w1}(\bar{S}) G_1(\bar{W}) - k_{w1} - \beta_1] - \alpha_1 \bar{u}^1 W + \alpha_1 u^1 (1 - \bar{W}) \\
u_t^2 &= L^2 u^2 + u^2 [f_{u2}(\bar{S}) - k_2] \\
w_t^2 &= w^2 [f_{w2}(\bar{S}) G_2(\bar{W}) - k_{w2} - \beta_2] + \alpha_2 u^2 (1 - \bar{W})
\end{aligned}$$

with radial boundary conditions

$$\begin{aligned}
0 &= d_r^S S_r + \gamma_1^{-1} \bar{w}^1 f'_{w1}(\bar{S}) S + \gamma_2^{-1} w^2 f_{w1}(\bar{S}) \\
0 &= d_r^1 u_r^1 - \alpha_1 \bar{u}^1 W + \alpha_1 u^1 (1 - \bar{W}) \\
&\quad - \bar{w}^1 [f'_{w1}(\bar{S}) S - f'_{w1}(\bar{S}) G_1(\bar{W}) S - f_{w1}(\bar{S}) G'_1(\bar{W}) W] \\
0 &= d_r^2 u_r^2 + \alpha_2 u^2 (1 - \bar{W}) - w^2 [f_{w2}(\bar{S}) (1 - G_2(\bar{W})) + \beta_2]
\end{aligned}$$

together with homogeneous Danckwerts' boundary conditions at $x = 0, L$ for S, u^i . We used notation $\bar{W}(x) = \frac{\bar{w}^1(x)}{w_\infty}$ and $W = \sum_{i=1}^2 \frac{w^i}{w_\infty}$.

Amidst the messy equations one can discern that the variational system is reducible in the sense that the u^2, w^2 subsystem decouples from the remainder of the system. The equations for S, u^1, w^1 have u^2, w^2 as inputs. If the latter terms are set to zero, the resulting subsystem is the variational equation for determining the “internal stability” of the single population steady state where the only perturbations allowed are in variables S, u^1, w^1 . Our simulations suggest that this subsystem should be stable. Therefore, we expect that the most important part of the variational system is the u^2, w^2 subsystem because it determines whether the second strain can invade.

On setting $z = e^{\lambda t} \hat{z}$ for each variable $z = S, u^i, w^i$ we obtain the eigenvalue problem. Below, we give only the u^2, w^2 part of the eigenvalue system. It may be written as

$$\begin{aligned}
\lambda \hat{u} &= L^2 \hat{u} + a(x, r) \hat{u}, & \Omega \\
\lambda \hat{w} &= b(x) \hat{w} + \alpha(x) \hat{u}, & r = R \\
0 &= d_r \hat{u}_r + \alpha(x) \hat{u} - c(x) \hat{w}, & r = R \\
0 &= -d_x \hat{u}_x + v(r) \hat{u}, & x = 0 \\
0 &= \hat{u}_x, & x = L,
\end{aligned} \tag{4.10}$$

where

$$\begin{aligned}
a(x, r) &= f_{u2}(\bar{S}(x, r)) - k_2 \\
\alpha(x) &= \alpha_2 (1 - \bar{W}(x)) \geq 0 \\
b(x) &= f_{w2}(\bar{S}(x, R)) G_2(\bar{W}(x)) - k_{w2} - \beta_2 \\
c(x) &= f_{w2}(\bar{S}(x, R)) (1 - G_2(\bar{W}(x))) + \beta_2 \geq 0 \\
d_x &= d_x^2, \quad d_r = d_r^2
\end{aligned}$$

This is just (3.1) with variable coefficients.

Denote by $\partial_r \Omega$ the radial portion of the boundary of Ω : $r = R, 0 \leq x \leq L$. Consider the operator \tilde{A} defined on $D(\tilde{A}) \subset Y \equiv C(\bar{\Omega}) \times C(\partial_r \Omega)$, by

$$\tilde{A}(u, w) = (L^2 u + au, bw + \alpha u)$$

for $(u, w) \in D(\tilde{A})$, given by

$$D(\tilde{A}) = \{(u, w) \in (C^2(\Omega) \cap C^{1+\mu}(\bar{\Omega})) \times C^\mu(\partial_r \Omega) : 0 = d_r^\mu u_r + \alpha u - cw \text{ and Danckwert's b.c. for } u \text{ at } x = 0, L\}.$$

Define $A : D(A) \rightarrow Y$ as the closure of \tilde{A} . Recall that the essential spectrum of A is the closed subset of the spectrum of A consisting of those λ which satisfy (1) λ is a limit point of the spectrum, or (2) $R(\lambda - A)$ is not closed, or (3) the generalized null space $\cup_{n \geq 1} N[(\lambda - A)^n]$ is infinite dimensional. Here, $R(B)$ denotes the range of B and $N(B)$ the null space. The following result concerning the spectrum of A generalizes Theorem 3.3 [13] (Proposition 3.2) to the case of non-constant coefficients.

Theorem 4.4 *Assume that $\alpha(x), c(x) \geq 0$ and let $B = \sup_x b$. If b is nonconstant, then the image of b belongs to the essential spectrum of A . Exactly one of the following holds:*

- (1) *there exists an eigenvalue $\lambda^* > B$ of A with corresponding eigenvector $(\hat{u}, \hat{w}) > 0$. $\Re(\lambda) \leq \lambda^*$ for all other spectral values λ of A .*
- (2) *$\Re(\lambda) \leq B$ for all other spectral values λ of A .*

Alternative (1) holds if and only if there exists $v \in C^2(\bar{\Omega})$, $v > 0$ and $\lambda > B$ such that

$$\begin{aligned} -L^2 v + (\lambda - a)v &\leq 0 \\ (\lambda - b)(d_r v_r + \alpha v) &\leq \alpha c v \end{aligned} \tag{4.11}$$

and the usual boundary conditions hold at $x = 0, L$, in which case, $\lambda \leq \lambda^*$. In particular, (1) holds if either

- (a) $\sup_x b - \inf_x b$ is sufficiently small.
- (b) $B \leq p \equiv \min\{\inf_x (b + c), \inf_{\Omega} a - \lambda^2\}$.
- (c) $B \leq \mu$, the principal eigenvalue of (4.12).

λ^2 is defined above (3.1). μ is the principal eigenvalue of

$$\begin{aligned} -L^2 u + (\lambda - a)u &= 0 \\ d_r u_r + \alpha u &= 0. \end{aligned} \tag{4.12}$$

In case (b) $p \leq \lambda^*$; in case (c) $\mu \leq \lambda^*$. If (1) holds then

$$B < \lambda^* \leq \max\left\{B + \frac{\sup_x \alpha c}{\inf_x \alpha}, \sup a - \lambda^2\right\}. \tag{4.13}$$

Remark 4.1 *In case (1) it can be shown that the ‘‘principal eigenvector’’ (\hat{u}, \hat{w}) is radially symmetric: $\hat{u} = \hat{u}(x, r)$, $\hat{w} = \hat{w}(x)$. The argument is given in [13].*

Remark 4.2 *As noted earlier, A is not the full linearization about the single-population steady state (4.9) because it does not account for its ‘‘internal stability’’. The full linearization has the form*

$$\begin{pmatrix} D & C \\ 0 & A \end{pmatrix}$$

relative to the partition of variables $((S, u^1, w^1), (u^2, w^2))$, where D determines ‘‘internal stability’’ in the linear approximation. However, if we make the plausible assumption that the single population steady state is unique and locally attracting (relative to the single-population model), so that the spectrum of D lies in the open left half plane, then the full linearization will have the property that $\Re(\lambda) > 0$ for some spectral value if and only if $\Re(\lambda) > 0$ for A for some spectral value of A . In that case, we could say that steady state (4.9) is unstable to invasion by the second strain u_2 , in the linear approximation, if $\lambda^* > 0$. However, at this time we do not have a proof of the validity of the linear approximation to local stability.

In summary, assuming linearized stability to be valid and assuming internal stability of steady state (4.9), then it is unstable to invasion by the second strain if

$$\max\{B, p, \mu\} > 0.$$

However, it would appear to be difficult to compute this number. In [14] we showed that in the absence of wall growth, when each single-population steady state was stable (unstable) in the linear approximation to invasion by its rival, then a coexistence steady state where both populations are present exists. We hope to establish such a result for the wall-growth model in the future.

5 Simulations

For PFR, the governing PDE, (2.1)-(2.3), is discretized using a standard second-order finite difference scheme with an explicit temporal discretization. We assume the solution is radially symmetric making the physical domain equivalent to the rectangle $\{(x, r) : 0 \leq x \leq L, 0 \leq r \leq R\}$. The symmetry assumption implies the artificial boundary condition $\nabla S \cdot \hat{\mathbf{r}} = \nabla u \cdot \hat{\mathbf{r}} = 0$ at $r = 0$. To determine S and u on the boundary, the boundary conditions are employed. The condition (2.6) at $r = R$, $0 = d_r^S \partial S / \partial r + \sum_i \gamma_i^{-1} w^i f_{wi}(S)$, is nonlinear in S since $f_{wi}(\cdot)$ is nonlinear. To solve for S on the boundary, the derivative is approximated using a second-order, one-sided differencing, and a nonlinear system is formed for S on the boundary. The system is solved using a Newton-Raphson scheme. The value for u^i on the $x = L$ boundary as well as S and u^i on the other boundaries are then found by approximating the derivatives in the boundary conditions by second-order, one-sided differences.

Parameters for the simulations have been chosen following Freter et al [10], modified for the different units used here (biomass density as opposed to cell density used by Freter) following Ballyk et al [4]. The initial conditions for wall-attached bacteria and planktonic bacteria are $S^0 = S_0$, $w_0^i = 0$, and $u_0^i = 10^{-6} g/ml$, respectively. In order to provide a steady-state profile, the equations were integrated to time $T = 35,000$ hours at which point no further change could be detected.

The other parameters are as follows. We set $d_x^S = d_r^S = 0.2 cm^2/hr$, $d_x^{u_i} = d_r^{u_i} = 0.002 cm^2/hr$ for $i = 1, 2, 3$. The concentration of the substrate feed, $S_0 = 2.09 \times 10^{-6} g/ml$. The fluid in the center of the tube is $V_{max} = 5 cm/hr$. The velocity is higher than suggested by the biology. However, coexistence does not seem possible at lower velocities (holding all other parameters fixed except for uptake functions, m_i, a_i). The larger velocity apparently provides a more uniform nutrient field near the tube wall allowing the microbes to persist. We use Monod uptake functions, $f_{wi}(S) = f_{ui}(S) = m_i S / (a_i + S)$ with $m_1 = 1.66/hr$, $a_1 = 9 \times 10^{-7} g/ml$, $m_2 = .277/hr$, $a_2 = 1 \times 10^{-8} g/ml$, and $m_3 = .45/hr$, $a_3 = 1.05 \times 10^{-7} g/ml$.

Finally, the rate of adhesion is $\alpha_i = 500 cm/hr$; the maximum areal biomass density of adherent bacteria is $w_\infty = 2.78 \times 10^{-6} g/cm^2$; the yield constant $\gamma = 0.75$. The planktonic cell and adherent cell death rates are $k_i = k_{w_i} = .01 hr^{-1}$.

Our simulations show that three populations can coexist in the flow reactor; these three populations compete for two limited resources, namely substrate and wall-attachment space (a refuge from washout). The three organisms differ only in their uptake functions (m_i, a_i); death rates, wall-affinities, sloughing rates, and yield constants are identical for the three populations. Figure 1 (top) and Figure 3 (top) show transient oscillations in the total planktonic and wall-attached populations, respectively, of each of the three organisms prior to reaching steady state. Coexistence is facilitated by a spatially inhomogeneous substrate steady state profile as depicted in Figure 1 (bottom); the choice of substrate uptake functions gives each competitor an advantage over its rivals in a region of the bio-reactor. Equilibrium distributions of the three planktonic populations are shown in Figure 2; their distributions on the reactor wall are shown in Figure 3 (bottom). The latter form a pattern of segregation: roughly, one organism dominates the nutrient-rich upstream end, a second dominates an adjacent downstream segment and a third appears to share with the second organism the far downstream end. A similar segregation profile was shown in [4] for the analogous one-space dimensional system with three populations and in [12] for an approximate hyperbolic system with two populations. Although not shown here, populations one and two coexist in the absence of population three using the same parameters and initial data as above for the first two populations.

6 Appendix

Proof of Theorem 4.4: For simplicity, we drop the superscript on L^2 and write simply L . It will be convenient to write $A = \tilde{A} + \hat{A}$ where $\tilde{A}(u, w) = (Lu + au, bw)$ and $\hat{A}(u, w) = (0, \alpha t(u))$ where $t(u)$ is the restriction of u to $r = R$ and the domains of \tilde{A}, \hat{A} are taken to be $D(A)$. We will relate certain portions of the essential spectrum of \tilde{A} and that of A .

The equation $(\lambda - \tilde{A})(u, w) = (f, g)$ is equivalent to

$$\begin{aligned} -Lu + (\lambda - a)u &= f \\ d_r u_r + \alpha u &= cw \\ (\lambda - b)w &= g \end{aligned} \tag{6.1}$$

where the latter two equations hold on $r = R$. Let $T : C(\partial_r\Omega) \rightarrow C(\partial_r\Omega)$ be the multiplication operator $Tw = bw$. It is easy to see that if λ belongs to image of b and $b^{-1}(\lambda)$ is nowhere dense in $\partial_r\Omega$ then $R(\lambda - T)$ is not closed. If also λ is not an eigenvalue of (4.12) then $R(\lambda - \tilde{A}) = C(\bar{\Omega}) \times R(\lambda - T)$ is not closed in Y . Thus λ belongs to the essential spectrum of A if it belongs to the set Q consisting of those λ belonging to the image of b for which $b^{-1}(\lambda)$ is nowhere dense and it is not an eigenvalue of (4.12).

Kato [16] has a more restrictive definition of essential spectrum, we call it the Kato essential spectrum, which requires that $\lambda - \tilde{A}$ is not semi-Fredholm, i.e., either $R(\lambda - \tilde{A})$ is not closed or both the nullity and the deficiency of $\lambda - \tilde{A}$ is infinite. Thus the Kato essential spectrum is a subset of the (Browder) essential spectrum. From the above, we have that the Kato essential spectrum of \tilde{A} contains Q .

We now show that \hat{A} is \tilde{A} -compact (see [16] p. 244). Suppose that $(u_n, w_n) \in D(A)$ and that $\{(u_n, w_n)\}$ and $\{\tilde{A}(u_n, w_n)\}$ are bounded. We must show that $\{(u_n, w_n)\}$ contains a convergent subsequence. $\tilde{A}(u_n, w_n) = (Lu_n + au_n, bw_n) \equiv (f_n, bw_n)$ and the boundedness of f_n implies that u_n is bounded in $C^\mu(\bar{\Omega})$ and therefore $\{t(u_n)\}$ contains a convergent subsequence. By Theorem IV 5.35 of [16], we conclude that the Kato essential spectrum of A equals that of \tilde{A} . This implies that the essential spectrum of A contains Q .

It is easy to see that the set of all λ for which $b^{-1}(\lambda)$ contains a nontrivial open set (and thus has positive Lebesgue measure) is at most countable. From this we conclude that the set of all λ for which $b^{-1}(\lambda)$ contains a nontrivial open set or is an eigenvalue of (4.12) is at most countable. Consequently, if the image of b is a nontrivial interval (uncountable) then it follows that every point of the image of b is a limit point of the set Q . Therefore, if b is nonconstant, the image of b belongs to the essential spectrum of A since the latter is closed.

The equation $(\lambda - A)(u, w) = (f, g)$ is equivalent to

$$\begin{aligned} -Lu + (\lambda - a)u &= f \\ d_r u_r + \alpha u - cw &= 0 \\ (\lambda - b)w - \alpha u &= g \end{aligned} \tag{6.2}$$

and usual boundary conditions at $x = 0, L$. For $\lambda \notin \text{Im} b$, this becomes

$$\begin{aligned} -Lu + (\omega - a)u &= (\omega - \lambda)u + f \\ d_r u_r + \alpha u &= \frac{\alpha c}{\lambda - b}u + \frac{cg}{\lambda - b} \\ w &= \frac{\alpha u + g}{\lambda - b} \end{aligned} \tag{6.3}$$

and usual boundary conditions at $x = 0, L$. We assume that $\omega > B, \sup a$ and will adjust it further later on. This in turn is equivalent

$$u = K_\omega((\omega - \lambda)u, \frac{\alpha c}{\lambda - b} t(u)) + K_\omega(f, \frac{cg}{\lambda - b}) \tag{6.4}$$

where $u = K_\omega(f, g)$ is the solution operator for the elliptic problem

$$\begin{aligned} -Lu + (\omega - a)u &= f \\ d_r u_r + \alpha u &= g. \end{aligned}$$

By Theorem 6.1 [13], $K_\omega : C(\bar{\Omega}) \times C(\partial_r\Omega) \rightarrow C(\bar{\Omega})$ is compact and strongly positive: $u > 0$ if $u = K_\omega(f, g)$, $(f, g) \geq 0$, and $(f, g) \neq (0, 0)$.

Define

$$T(u, \lambda) = K_\omega((\omega - \lambda)u, \frac{\alpha c}{\lambda - b} t(u))$$

for λ not belonging to the image of b . Then, (6.4) becomes

$$(I - T(\cdot, \lambda))u = K_\omega(f, \frac{cg}{\lambda - b}).$$

For such fixed λ , $T(\cdot, \lambda)$ is a compact operator and so $I - T(\cdot, \lambda)$ has a bounded inverse if and only if its nullspace is trivial. But if its nullspace is nontrivial then so is that of $\lambda - A$. We conclude that

$$\sigma(A) \subset \text{Im } b \cup P\sigma(A) \tag{6.5}$$

where $P\sigma(A)$ denotes the eigenvalues of A and $\sigma(A)$ denotes the spectrum of A .

The injectivity question is just for what λ

$$u = T(u, \lambda) \tag{6.6}$$

has nontrivial solutions. If we regard λ as a parameter, then we may interpret (6.6) as that one is an eigenvalue of the operator $T(\cdot, \lambda)$ with eigenvector $u \neq 0$, in which case $r(\lambda) \geq 1$ where $r(\lambda) = \rho(T(\cdot, \lambda))$ is the spectral radius of $T(\cdot, \lambda)$.

Because K_ω is strongly positive, if we require λ to satisfy $B < \lambda < \omega$, then $T(\cdot, \lambda)$ is strongly positive and compact. By the Krein-Rutman Theorem, there is an eigenvalue $B < \lambda < \omega$ corresponding to a positive eigenvector u if and only if $r(\lambda) = 1$. As $\lambda \rightarrow \omega - \lambda$ and $\lambda \rightarrow \frac{\alpha c}{\lambda - b}$ are strictly decreasing, it follows that $r : (B, \omega) \rightarrow [0, \infty)$ is strictly decreasing and it is well-known that it is a continuous function of λ . (See [13] for citations.) Now, we show that by choosing ω large enough, we can ensure that $r(\omega) < 1$. Indeed,

$$\|T(u, \omega)\| = \|K_\omega(0, \frac{\alpha c}{\omega - b} t(u))\| \leq \|K_\omega(0, \cdot)\| \|\frac{\alpha c}{\omega - b}\|_\infty \|u\|_\infty$$

so, as $\|\frac{\alpha c}{\omega - b}\|_\infty \rightarrow 0$ as $\omega \rightarrow \infty$, it suffices to show that $\|K_\omega(0, \cdot)\|$ is bounded for large ω . But this is established exactly as in [13] (where the notation is $K_n(0, f)$, see page 26 [13]) by the maximum principle. Hence, by the intermediate value theorem, the two cases (1) and (2) amount to whether $r(B+) > 1$ or $r(B+) \leq 1$.

Suppose there exists $\lambda > B$ and $v > 0$ such that (4.11) holds. It follows that there exists $f \geq 0$ and $g \geq 0$ such that

$$\begin{aligned} -Lv + (\omega - a)v &= (\omega - \lambda)v - f \\ d_r v_r + \alpha v &= \frac{\alpha c}{\lambda - b} v - g \end{aligned}$$

or, equivalently

$$v = K_\omega((\omega - \lambda)v, \frac{\alpha c}{\lambda - b} t(v)) - K_\omega(f, g) = T(v, \lambda) - K_\omega(f, g).$$

As $K_\omega(f, g) \geq 0$ we conclude that $T(v, \lambda) \geq v$ which implies that $r(\lambda) \geq 1$ (see Theorem 2.5 [15]). Since $r(\omega -) < 1$, the continuity of r implies the existence of a unique root λ^* of $r(\lambda^*) = 1$ satisfying $\lambda \leq \lambda^* < \omega$.

Conversely, if $r(\lambda^*) = 1$ for some $\lambda^* > B$ then the Krein-Rutman Theorem implies the existence of $u > 0$ such that $T(u, \lambda^*) = u$, so u satisfies

$$\begin{aligned} -Lu + (\omega - a)u &= (\omega - \lambda^*)u \\ d_r u_r + \alpha u &= \frac{\alpha c}{\lambda^* - b} u \end{aligned}$$

and with $v = u$ we get equality in (4.11).

For $u \geq 0$ and $B < \lambda < \omega$ we have

$$T(u, \lambda) \geq K_\omega(0, \frac{\alpha c}{\lambda - \inf_x b} t(u)) = \frac{1}{\lambda - \inf_x b} K_\omega(0, \alpha c t(u)).$$

If $B = K_\omega(0, \alpha c t(\cdot))$ then $B : C(\bar{\Omega}) \rightarrow C(\bar{\Omega})$ is positive and compact. Moreover, because K_ω is strongly positive, $B(1) > 0$ (1 stands for the function identically equal to one) so there exists $\delta > 0$ such that $B(1) \geq \delta 1$. By Theorem 2.5 [15], there exists $\rho \geq \delta$ and $\hat{u} > 0$ such that $B\hat{u} = \rho\hat{u}$. Consequently, $T(\hat{u}, \lambda) \geq \frac{\rho}{\lambda - \inf_x b} \hat{u}$, which implies that $r(\lambda) \geq \frac{\rho}{\lambda - \inf_x b}$. This leads to

$$r(B+) \geq \frac{\rho}{\sup_x b - \inf_x b}$$

and $r(B+) > 1$ if $\sup_x b - \inf_x b < \rho$.

Now recall that there exists $v > 0$ such that $L^2 v = -\lambda^2 v$ and $v_r = 0$ and the usual boundary conditions at $x = 0, L$ hold. We will show that condition (b) implies that there exists λ such that v and λ satisfy (4.11). Obviously, $-Lv + (\lambda - a)v = v(\lambda + \lambda^2 - a) \leq 0$ if $\lambda \leq \inf a - \lambda^2$. Also,

$$(\lambda - b)(d_r v_r + \alpha v) - \alpha c v = \alpha[\lambda - b - c]v \leq 0$$

if $\lambda \leq \inf_x(b + c)$. Thus, if we can choose $\lambda > B$ satisfying the above two inequalities, then v and λ satisfy (4.11). This will be the case precisely when (b) holds.

If (c) holds, i.e., $B < \mu$ where μ is the principal eigenvalue of (4.12), then there exists a positive principal eigenvector $v > 0$. It follows that $\lambda = \mu$ and v satisfy (4.11). Indeed, $(\lambda - b)(d_r v_r + \alpha v) = 0 \leq \alpha cv$.

The argument that $\Re(\lambda) \leq \lambda^*$ in (1) is proved exactly as in the proof of Theorem 3.3 in [13] by appealing to Theorem 1.1 [17]. In case (2), the result of Nussbaum shows that $\mu_0 = \inf\{\mu \in R : (\mu - A)^{-1} \in L(Y), (\mu - A)^{-1} \geq 0\}$ belongs to the spectrum of A if it exceeds $-\infty$ and if $\beta > \mu_0$, then β belongs to the resolvent set of A and $(\beta - A)^{-1}$ is a positive operator. This implies that $\mu_0 = B$. For if $\mu_0 < B$, then B would belong to the resolvent set of A contradicting that it belongs to the essential spectrum. If $B < \mu_0$, then, because μ_0 belongs to spectrum of A , it must be an eigenvalue by (6.5). But then we are in case (1) since $r(\mu_0) \geq 1$, a contradiction. Therefore, $\mu_0 = B$ and by Theorem 1.1 of [17], $\Re(\lambda) \leq B$ for all λ in the spectrum of A . ■

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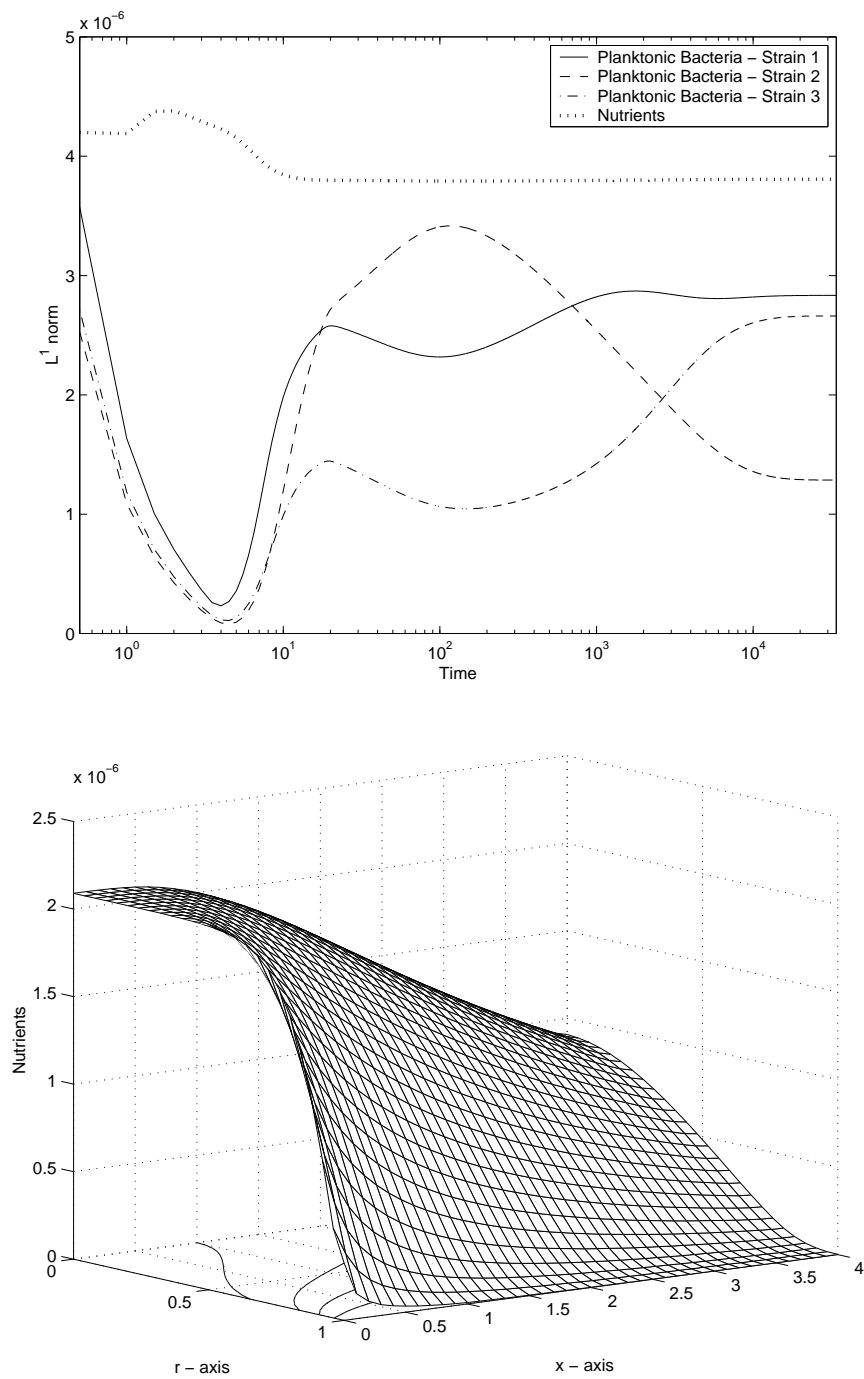


Figure 1: L^1 norm versus time of the nutrients and free bacteria (top) and a surface plot of the nutrient density S (bottom).

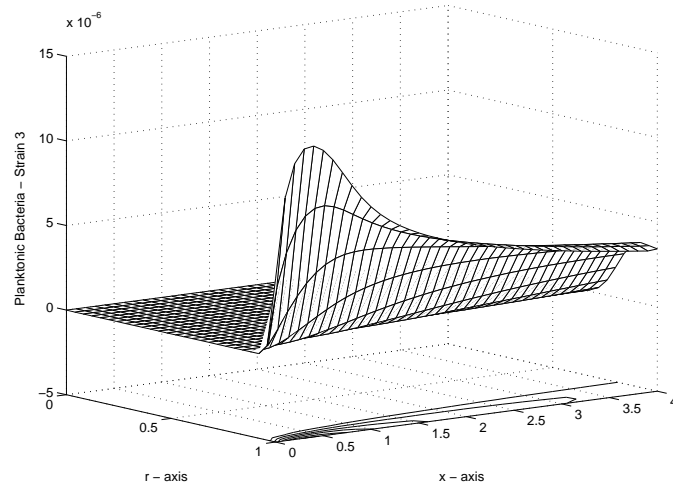
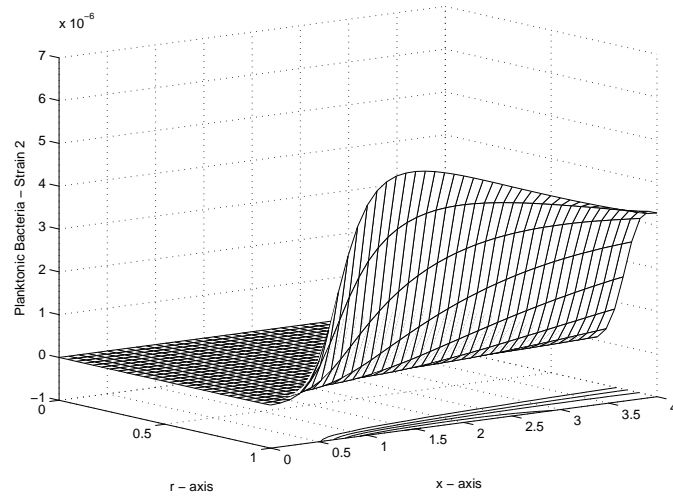
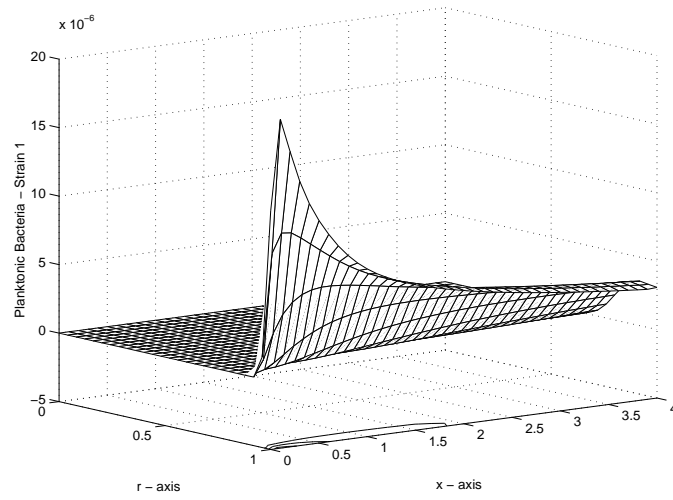


Figure 2: Surface plots of the planktonic biomass density u^i - strain 1 (top), strain 2 (center), strain 3 (bottom).

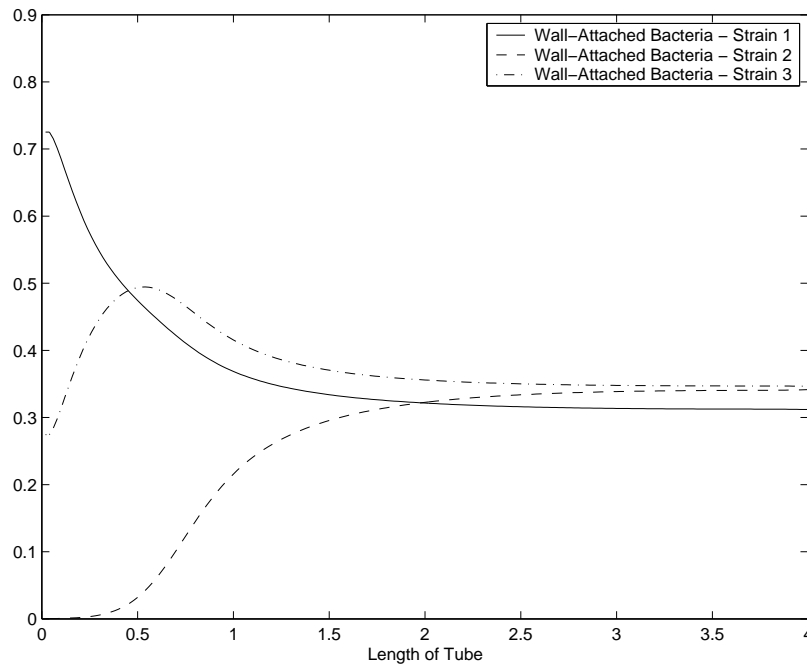
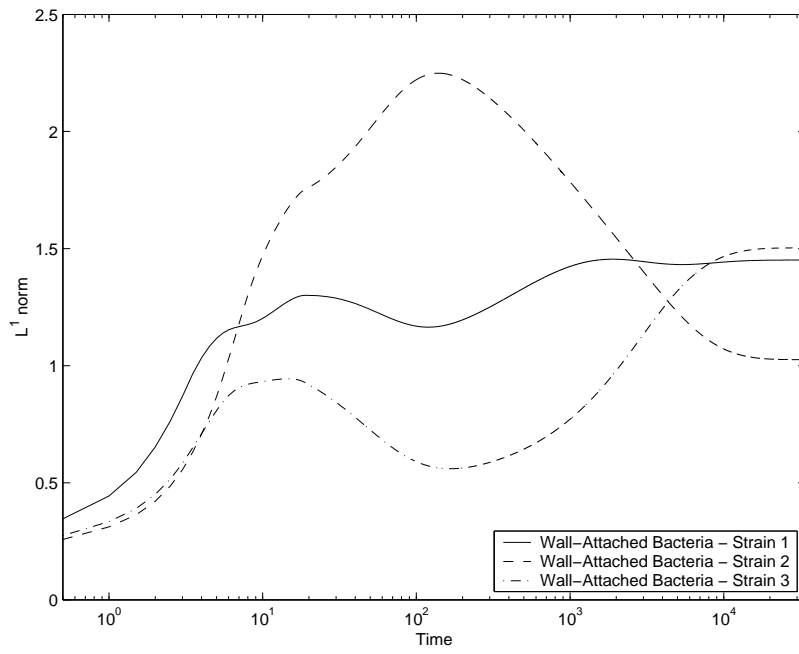


Figure 3: L^1 norm versus time of the wall-attached bacteria (top) and a plot of the areal density of wall-attached bacteria w^i at a steady-state (bottom).