Computational Study of the Drag and Oscillatory Movement of Biofilm Streamers in Fast Flows

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Received 19 June 2009; revision received 5 September 2009; accepted 14 September 2009

ABSTRACT: Hydrodynamic conditions have a significant impact on the biofilm lifecycle. Not well understood is the fact that biofilms, in return, also affect the flow pattern. A decade ago, it was already shown experimentally that under fast flows, biofilm streamers form and oscillate with large amplitudes. This work is a first attempt to answer the questions on the mechanisms behind the oscillatory movement of the streamers, and whether this movement together with the special streamlined form of the streamers, have both a physical and biological benefit for biofilms. In this study, a state of the art two-dimensional fluid–structure interaction model of biofilm streamers is developed, which implements a transient coupling between the fluid and biofilm mechanics. Hereby, it is clearly shown that formation of a Karman vortex street behind the streamer body is the main source of the periodic oscillation of the streamers. Additionally, it is shown that the formation of streamers reduces the fluid forces which biofilm surface experiences.


KEYWORDS: biofilm; drag; mathematical model; fluid–structure interaction; biofilm streamers; biomechanics

Introduction

In fast flows, biofilm clusters tend to become elongated in the flow direction to form filamentous streamers. Streamers are structures consisting of a base attached to a substratum and a tail in the downstream fluid flow free to oscillate laterally in the flow. Stoodley et al. (1998) grew mixed population biofilms consisting of Pseudomonas aeruginosa, Pseudomonas fluorescens, and Klebsiella pneumoniae in a flow cell under turbulent flow conditions. The formed streamers oscillated rapidly, with frequencies proportional to the flow velocity, suggesting that the vortex shedding from the cell clusters was the cause of the oscillations.

The forces on a living object in a flow depend on its shape, and its shape also depends on the forces it experiences (Vogel, 1996). The formation of streamers is generally linked to two factors: the fluid shear and the viscoelastic nature of the biofilm clusters (Shaw et al., 2004). However, up to now the interaction of local flow with biofilm could hardly be investigated due to, for example, difficulties in micro-scale in situ flow and force measurements. Hence, in search for alternatives, modeling studies could be of a great assistance. A literature survey shows that the interaction of fluid with deformable biological structures (such as biofilms) is becoming an increasingly active field of research both in biology and numerical methods (Alpkvist and Klapper, 2007; Böll et al., 2009; Duddu et al., 2008; Zhang et al., 2000; Zhu and Peskin, 2007).

Why do biofilms exhibit a streamlined shape in fast flows? Drag is the component of the fluid force in the direction of the flow, acting on any obstacle along the way. Streamlining, the modification of shape to reduce drag, is commonly seen in birds, fish, insects, and aquatic mammals. Streamlining in high Reynolds number (Re) flow acts to reduce the costs of fluid forces on the structure by delaying separation of the flow from the surface of the object in fast flows. In contrast, streamlining at low Reynolds numbers is not effective, as
streamline separation only occurs when inertia becomes the dominant force at high Reynolds numbers. The Fineness Ratio \((FR)\) defined as the ratio of maximum length to the maximum thickness is an indicator of streamlining. Bodies of revolution, symmetrical about their long axis, demonstrate minimum drag in the range of \(FR\) of 3–7 (Fish, 1998). In airship design an optimal \(FR\) is 4.5, which provides the minimum drag for the maximum volume (von Mises, 1959). The streamer Stoodley et al. (1998) studied had a \(FR\) of 4.48.

Therefore, based on this preliminary evidence, formation of biofilm streamers may be one possibility for the aggregated microorganisms, amongst others, to reduce the fluid forces acting on the biofilm structure. This work investigates the local environment of flexible biofilm streamers in fast flows and presents results that support the above hypothesis.

**Materials and Methods**

Modeling the oscillation of biofilm streamers is a fluid–structure interaction (FSI) problem, where two tightly coupled phenomena must be taken into account: the biofilm structural motion and the fluid flow. The structural motion can be safely described by large deformation elastodynamics, neglecting visco-elastic contributions to the streamer deformation due to very short motion time-scales compared to visco-elastic deformation time-scales (Shaw et al., 2004). The fluid flow is modeled by the incompressible Navier–Stokes equations. In this study, the arbitrary Lagrangian–Eulerian (ALE) formulation for fluid domain is employed to account for the common deformation of fluid and solid at their interface. From a solid mechanics point of view, the deformed shape of the streamer is determined by pressure load and shear stresses exerted by the fluid on the streamer boundaries. From a fluid dynamics perspective, the motion of the streamer is imposed on the fluid as a moving boundary condition.

**Model Domain**

To model the oscillation of the biofilm streamers, a two-dimensional streamer, shown in Figure 1, is subjected to a range of flow conditions similar to those considered in the experimental settings of Stoodley et al. (1998) and with the same dimensions as the streamer studied therein. The domain is a rectangular channel, with length \(L_x\) in the main stream direction, \(x\), and width \(L_y\) in the side stream direction, \(y\).

Besides avoiding extreme computational difficulties, there are also physical reasons to start with a 2D approximation. Stoodley et al. (1998) found out that the streamer had no significant vertical motion \((z\text{-direction})\). This finding ensures the assumption that the flow has an \(x\text{-}y\)
plane transient variation, which can be captured by a 2D model.

To replicate the formation of the streamer and study the various transient streamer lengths, several streamers of different tail lengths from the limit case \( L/D = 0 \) (only the circular base) to \( L/D = 7 \) were simulated—\( D \) is the diameter of the circular biofilm base and \( L \) is the streamer tail length. The streamer studied by Stoodley et al. (1998) is represented by \( L/D = 4.5 \).

The problem domain is divided into two nonoverlapping computational sub-domains \( \Omega_F \) and \( \Omega_S \). \( \Omega_F \) is the deforming fluid sub-domain, where the Navier–Stokes equations are solved to obtain both pressure and velocity field; \( \Omega_S \) is the biofilm streamer tail sub-domain, where the structural elastodynamic equation is solved for the displacement field. Both sub-domains share a common interface \( \Gamma \).

Three different systems of reference are used within this work. Structural deformations are described in the Lagrangian or material formulation. The corresponding Lagrangian coordinate system denoted by \( \mathbf{X} \) is associated with the particular material points. The Eulerian or spatial system of reference denoted by \( \mathbf{x} \), in which the observer is fixed in space and looks at the fluid passing. In the ALE description of the motion, a third reference system, denoted by \( \mathbf{x} \), is required to identify the grid points. The derivation of the ALE formulation of the flow equations can be found in the book by Donea and Huerta (1989).

### Fluid Mechanics

The laminar fluid flow in the deforming sub-domain \( \Omega_F \) is described by ALE version of the incompressible Navier–Stokes equations, consisting of momentum equation

\[
\frac{\partial \mathbf{u}}{\partial t} + (\mathbf{u} - \mathbf{u}_G) \nabla \mathbf{u} - 2\nu \nabla \varepsilon(\mathbf{u}) + \nabla p = \mathbf{b}_F \tag{1}
\]

and continuity condition

\[
\nabla \cdot \mathbf{u} = 0 \tag{2}
\]

These time-dependent equations are solved for the velocity field \( \mathbf{u} \) and the kinematic pressure \( \mathbf{p} \) in the fluid sub-domain \( \Omega_F \). In these equations, \( \varepsilon(\mathbf{u}) \) denotes the strain rate tensor, \( \mathbf{b}_F \) represents vector of body forces, \( \nu = \mu/\rho_F \), is the kinematic viscosity with dynamic viscosity \( \mu \) and fluid density \( \rho_F \), and \( \nabla \) denotes the gradient with respect to the spatial coordinates \( \mathbf{x} \). Here we assume that no gravitation or other volume forces affect the fluid, so that \( \mathbf{b}_F = 0 \). The term \( (\mathbf{u} - \mathbf{u}_G) \) in Equation (1) defines the ALE-convective velocity, that is, the relative velocity of the fluid flow inside a moving mesh.

The constitutive equation for a Newtonian fluid reads

\[
\mathbf{\sigma}_F = -p \mathbf{I} + 2\mu \varepsilon(\mathbf{u}) \tag{3}
\]

whereby \( p = \rho_F p_F \) denotes the physical pressure within the fluid field. The strain rate tensor \( \varepsilon(\mathbf{u}) \) can be written as:

\[
\varepsilon(\mathbf{u}) = \frac{1}{2}(\nabla \mathbf{u} + (\nabla \mathbf{u})^T) \tag{4}
\]

### Structural Mechanics

The structural deformations of the biofilm streamer (sub-domain \( \Omega_S \)) are obtained using an elastic material model together with a geometrically nonlinear formulation to allow for large structural deformations. The equations for the structure are formulated in a Lagrangian frame of reference. The coordinates in the current and reference configurations are denoted by \( \mathbf{x} \) and \( \mathbf{X} \), respectively. Initially, the current coordinates are taken to equal the reference coordinates (i.e., \( \mathbf{x} = \mathbf{X} \) at \( t = 0 \)).

The displacement \( \mathbf{d} \) is the difference between the initial position of a material point and its current position:

\[
\mathbf{d} = \mathbf{x} - \mathbf{X} \tag{5}
\]

The structural field \( \Omega_S \) is governed by the nonlinear elastodynamics equation

\[
\rho_S \frac{d^2 \mathbf{d}}{dt^2} = \nabla (\mathbf{F}_S \mathbf{S}) + \rho_S \mathbf{b}_S \tag{6}
\]

that determines the structural displacements \( \mathbf{d} \) by prescribing equilibrium between the body forces \( \mathbf{b}_S \), the internal forces determined from the second Piola–Kirchhoff stress tensor \( \mathbf{S}_S \), the deformation gradient \( \mathbf{F}_S \), the deformation gradient \( \mathbf{F}_S \), and forces of inertia.

For the employed St. Venant–Kirchhoff type of material used in this work, the second Piola–Kirchhoff stress tensor \( \mathbf{S}_S \) is related to the Green–Lagrangian strains \( \mathbf{E} \) via:

\[
\mathbf{S}_S = l_S tr \mathbf{E} \mathbf{I} + 2\mu_S \mathbf{E} \tag{7}
\]

with

\[
\mathbf{E} = \frac{1}{2} (\mathbf{F}_S^T \mathbf{F}_S - \mathbf{I}) \tag{8}
\]

The Lame' constants \( l_S \) and \( \mu_S \) are related to the Young’s modulus \( E_S \) and Poisson’s ratio \( \nu_S \) via:

\[
l_S = \frac{E_S \nu_S}{(1 + \nu_S)(1 - 2\nu_S)}; \quad \mu_S = \frac{E_S}{2(1 + \nu_S)} \tag{9}
\]

The biofilm density \( \rho_S \), Young’s modulus \( E_S \), and Poisson’s ratio \( \nu_S \) are reported in Table I.
Table 1. Table of model parameters.

<table>
<thead>
<tr>
<th>Name</th>
<th>Description</th>
<th>Value</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>μ</td>
<td>Water dynamic viscosity</td>
<td>$1 \times 10^{-3}$</td>
<td>kg/(m s)</td>
</tr>
<tr>
<td>ρf</td>
<td>Water density</td>
<td>1,000</td>
<td>kg/m³</td>
</tr>
<tr>
<td>Umean</td>
<td>Water inlet velocity</td>
<td>0.1–0.5</td>
<td>m/s</td>
</tr>
<tr>
<td>ρs</td>
<td>Biofilm density</td>
<td>1,000</td>
<td>kg/m³</td>
</tr>
<tr>
<td>Es</td>
<td>Young’s modulus</td>
<td>5,000</td>
<td>kg/(m s²)</td>
</tr>
<tr>
<td>νs</td>
<td>Poisson’s ratio</td>
<td>0.4</td>
<td>—</td>
</tr>
</tbody>
</table>

Boundary Conditions

Because the streamer position changes continuously in time, the finite element mesh will be continuously deformed. The boundary conditions control the displacement of the moving fluid mesh with respect to the initial geometry. The boundary connecting the tail to the streamer base is fixed and the rest of tail boundaries are free to move. At the moving boundaries of the streamer, the interface $\Gamma$, the mesh velocities, representing the fluid, equal the deformation rate, representing the biofilm:

$$u_I = \frac{dd_I}{dt} = u_{G\Gamma} \tag{10}$$

where $d_I$ is the interface structural displacement, $u_I$ the interface fluid velocity, and $u_{G\Gamma}$ the interface mesh velocity. At all other boundaries of the domain the mesh movement is set to zero in all directions.

At the interface $\Gamma$ the dynamic continuity states:

$$\sigma_S n = \sigma_F n \tag{11}$$

where $n$ is the unit vector normal to the boundary, and $\sigma_F$ and $\sigma_S$ are the Cauchy stresses of fluid and structure, respectively. Equations (10) and (11) form the coupling conditions on the FSI interface $\Gamma$.

The inlet flow boundary condition (at $x = 0$) is defined as a uniform velocity profile with horizontal velocity component $u = U_{mean}$ and transverse velocity component $v = 0$. The velocity $U_{mean}$ is set from 0.1 to 0.5 m/s, corresponding to Reynolds numbers of up to 167 with respect to the diameter $D$ of the base of the streamer. To improve the convergence of the numerical procedure at the beginning of the simulations, the inlet flow velocity is smoothly increased from zero to the target velocity during the initial 0.1 s. The slip condition is applied to the upper and lower domain walls, at $y = 0$ and $y = L_y$. This condition assumes that there are no tangential forces on the boundary and that $v = 0$; this implies that no boundary layer develops. Due to this boundary condition, both the inlet flow velocity and the average channel velocity before the streamer are identical and equal to $U_{mean}$. The slip boundary condition is selected to reduce the domain size, which is necessary to avoid the adjacent wall interferences in calculating the forces. At the outflow ($x = L_x$), the zero pressure and no viscous forces boundary condition is applied. In addition, the no-slip condition is imposed on the circular base of the streamer: $u = 0$, $v = 0$.

Drag Force and Drag Coefficients

When a fluid flows past a body, forces that occur at the body–fluid interface are (i) tangential (shear) stresses and (ii) normal stresses, which are a function of position. If we integrate the forces over the surface of the body, the resultant in the direction of the upstream flow is called drag. The force exerted depends on the object shape (and its possible deformations), fluid velocity and fluid properties. In water, drag can be decomposed into two different forms: skin friction (viscous drag) and pressure drag. Skin friction exists due to the interaction of the surface of an object with fluid; pressure drag is due to the difference in pressure between the front and the rear side of a body. The dimensionless drag coefficient is used to compare the drag of objects with different sizes and is defined as:

$$C_D = \frac{2FD}{\rho_f U_{mean}^2 A_F} \tag{12}$$

where $F_D$ is the drag force, $\rho_f$ the fluid density, $U_{mean}$ the mean flow velocity, and $A_F$ the frontal area facing the flow, in this case the diameter $D$ of the streamer base. In our simulations, the drag force is calculated as follows:

$$F_D = \int_{A_w} (-F_{V,x} + pn_x) dA \tag{13}$$

where, $F_{V,x}$ is the $x$-component of the viscous force, $p$ the pressure, $n_x$ the $x$-component of the outer normal vector, and $A_w$ the outer area of the streamer.

Speed-Specific Drag

In contrast with rigid bodies, flexible bodies may deform or reconfigure to reduce (or increase) the forces of the fluid acting on them (i.e., bending of pine trees at high winds). Besides, the flexible and rigid bodies may have different shapes and sizes, which make it difficult to compare them by drag coefficients only. Hence, a new parameter is needed to emphasize the importance of flexibility (vs. stiffness) regardless of the shape and size, and have a measure for reconfiguration. We call this factor $G$ factor (refer to Vogel, 1996, pp. 116–120; therein termed $E$).

By definition, the drag coefficient is proportional to drag divided by the square of velocity. For the cases, where the drag coefficient is independent from $Re$, the plot of $C_D$ versus $Re$ will be a horizontal line; that is, the exponent $G$ in (14) is zero.

$$C_D \propto \frac{F_D}{U_{mean}^2} \propto U_{mean}^G \propto Re^G \tag{14}$$

If the line in this plot ascends, that is, if $G$ is greater than zero, it means that the structure is deforming (reconfiguring) in a way that makes the drag become relatively higher.
compared to typical bluff bodies. For example, a $G$ value of $+1.0$ means that the drag is proportional to the cube of velocity, rather than to the square. However, a line with negative slope (a negative $G$ value) indicates that the drag will be less for the structure at faster flows, compared to bluff bodies. Hence, by plotting $F_D/U_{\text{mean}}^3$, termed “speed-specific drag,” versus the flow velocity $U_{\text{mean}}$ and measuring the slope of the curve, we can predict the drag performance of the body in fast flows (Vogel, 1996, pp. 116–120).

Model Solution

The equations governing the flow and the displacement of the biofilm structure are solved with a monolithic FSI approach, where the equations governing the fluid flow and the displacement of the structure are solved simultaneously using a single solver. BACI, a finite element code developed by Institute for Computational Mechanics at Technische Universität München (Küttler et al., 2009) is used to simulate the FSI aspects of biofilm mechanics.

The computations are done on an ALE mesh using 9,560 triangular mesh elements, yielding 83,702 degrees of freedom. The maximum time step used by the solvers was $10^{-4}$ s. For details regarding the FSI implementation and solution procedure refer to Küttler and Wall (2008) and Küttler et al. (2009).

The simulations were performed on Amazon EC2 cloud servers (High-CPU Extra Large Instance, eight virtual cores, 3 GHz each). The simulation times were up to 15 hours per second of simulations for high frequency oscillations.

Results and Discussion

Table I summarizes the parameters used in the simulations together with the characteristics of the streamer studied. The Young modulus, the measure for streamer elasticity, is taken between the values reported by (Aravas and Laspidou, 2008; Stoodley et al., 1999) and (Körstgens et al., 2001). The model simulation results are analyzed from two perspectives: the effect of the streamer on the flow characteristics and, vice versa, as well as the influence of the flow-induced vibrations on the stress inside the streamer.

Oscillation of Biofilm Streamers

When flow past the streamer generates a pattern of swirling vortices in the wake region (the well-known Kármán vortex street), periodic shedding of these vortices from the surface of the streamer body induces periodic pressure variations on the structure (Fig. 2). Despite using a laminar flow model, our simulations show that the streamers begin to oscillate due to formation of these vortices in a specific range of Reynolds numbers between 60 and 80 (see Lewandowski and Stoodley, 1995 for a discussion on the validity of laminar flow assumption).

A series of snapshots showing the transient movement of the ALE mesh is shown in Figure 3A. Starting from the rest configuration, the flow develops and finally reaches a periodic stage with regular oscillations in the flow pattern. Vortex shedding makes the streamer vibrate, as it can be seen from Figure 3B. Figure 4A shows the amplitude and frequency of the oscillations in the streamer tip position, starting after a certain time and reaching a steady oscillatory pattern. Vortex shedding causes the drag force $F_D$ to oscillate as well (Fig. 4B). The streamer reaches a quasi steady-state oscillation pattern, in which the amplitudes, frequencies, and average drag remain periodically unchanged.

Oscillation Characteristics of Biofilm Streamers

Stoodley et al. (1998) investigated the behavior of streamers in high flow velocities. The path of motion of the streamers was visualized by staining the biofilm with neutral density fluorescent latex spheres and time-exposed fluorescent images were taken to show the range of streamer motion. Amplitude and frequency of streamer oscillations are the two most important characteristics studied in this section.

Figure 5 compares the maximum amplitudes of the streamer vibration calculated numerically with those experimentally measured. Similar to the experimental results, the streamer started to oscillate only for $Re$ larger than a specific value, and the amplitude of oscillations reached a plateau value.

The value of the critical velocity at which vortex shedding begins depends on the shape as well as the size of the biofilm cluster. A larger biofilm characteristic length, here the diameter $D$ of the circular head, translates to a higher $Re$ number, which implies that the onset of oscillatory behavior shifts to slower flows. Slowly increasing the velocity, the larger biofilm clusters start to shed vortices earlier.

To obtain the frequencies of streamer oscillation, the displacements of the streamer tips were used for time-domain analysis using Fast Fourier Transform (FFT) method. For the circular base without tail, the frequencies were extracted from the drag force oscillations measured on boundaries of the circular base. Figure 6A shows the frequencies of vortex shedding for a circular base and various streamer lengths. It can be observed that when the flow velocity is increased (larger $Re$), the frequency of streamer oscillation and vortex shedding increase as well, which is in agreement with the experimental observations.

The periodic flow is characterized by the Strouhal number ($St$), that is, the dimensionless frequency of the oscillations, defined as:

$$St = \frac{fL_C}{U_{\text{mean}}}$$

where $f$ is the frequency of flow oscillations, $L_C$ the characteristic length (here the base diameter $D$), and $U_{\text{mean}}$ the mean velocity of fluid passing the body. Figure 6B presents the calculated Strouhal number versus $Re$ derived
from our simulations. The Strouhal number can be used together with the object size and fluid velocity to predict the frequency of vortex shedding.

The oscillation of an object induced by vortex shedding might have considerable consequences, that is, breakage, when the object is flexible and the rate of shedding is close to some natural oscillatory frequency of the object (Vogel, 1996). In our simulations, the natural frequency of the biofilm streamer was occasionally in the vicinity of vortex shedding frequencies which, together with complex wake interactions, can partly account for the irregular behavior of the streamer in some simulations and also the sloughing events in the experiment. The natural frequencies calculated using eigenfrequency analysis of the streamer tail for $L/D$ ratio of 4.5 were approximately 28.8, 129.4, 317.2, 484.7 Hz.

Several factors have strong effects on the deviation of the simulation results from the experimental results, apart from measurement errors. The assumed material properties, local turbulence effects, outlet boundary condition, and 2D assumption are few of these factors. In addition, our simulations were focused on a single streamer, while flexible bodies in the actual environment may interact with each other (Ristroph and Zhang, 2008). Nevertheless, the case of biofilm streamers in flow is a three-dimensional problem.

**Figure 2.** Flow patterns behind biofilm streamers of different lengths. The motion of the tail is upward. $L/D$ ratios are 0, 1, 2.5, 4.5, and 7, ordered descending. Inlet velocity is 0.4 m/s ($Re = 133$).
and a 3D model is required to investigate further aspects such as presence of the substratum in future.

**Effect of Streamer Length on Drag**

Further, this work investigated the effect of the special streamer form, here correlated to length, on the overall biofilm drag. Figure 7A shows the drag coefficients for various streamer lengths and flow velocities. At low flow velocities ($Re = 33$), the drag increased with the tail length. However, at high flow velocities, where the pressure drag becomes more significant, the streamer tail helped to streamline the body and reduce the drag. Remarkably, there was a maximum 23% drag reduction by a streamer tail ($L/D = 4.5$) compared to the circular biofilm base without a tail, at the highest flow velocity used for simulations ($Re = 167$).

In addition, to measure the effect of the streamer flexibility and reconfiguration on drag at higher flow
velocities, the $G$ parameter related to speed-specific drag was calculated. For the circular base, the value of the calculated $G$ ($G = -0.24$) is close to the experimental value reported in literature for cylinders in $Re$ range of 10–120 ($G = -0.29$; Table 6.1, Vogel, 1996). Figure 7B shows that at $Re$ larger than 133, the circular shape ($L/D = 0$) has a $G$ value close to zero, as expected from the rigid bodies. The lowest $G$ value corresponds to $L/D = 4.5$, where it experiences the lowest drag scaling compared to rigid bodies. To be specific, the drag of a streamer with $L/D = 4.5$ ($G = -0.46$, $Re = 133$–167) increases by the power of 1.54 with respect to the flow velocity, in contrast to power of 2 for the circular base (or cylinders). Hence, it is expected that at higher flow velocities ($Re > 133$), the streamer with $L/D$ ratio of 4.5 will experience the lowest drag with the increase of flow velocity amongst others.

The drag coefficient of the streamer with $L/D$ ratio of 7 is found to be close to the drag coefficient of circular base ($L/D = 0$) at the highest flow velocity studied. This shape also exhibits a $G$ value close to zero at high flow velocities ($Re > 133$). Thus, there is an optimum streamer length to minimize the drag, which in our case is $L/D = 4.5$.

The effect of density on drag was also investigated. However, it was found (see Table II) that the density does not have a significant effect on the oscillating characteristics of the streamer and the drag in the range of common biofilm densities.

**A Closer Look at the Forces, Stresses, and Growth Conditions**

Besides evaluating the effect of streamer oscillations on the drag, the reverse analysis is also interesting: what could be the effect of flow-induced oscillations on the biofilm streamer itself. Figure 8 shows the fluid viscous (shear) forces acting on the body and the stress conditions inside the tail. For the streamers, the highest shear force is experienced...
at the tip of the streamer and the front side of the base facing the flow. Other sections of the streamer are protected from the fluid shear forces, as seen by force vectors acting on the boundaries. Similarly, the circular clusters without tail \((L/D = 0)\) experience the shear force only on the front side downstream of the flow.

Especially, the simulation result presented in Figure 8 gives an idea on how hydrodynamic conditions and growth/development of biofilm streamers may interact. As long as substrate is available, the microorganisms will divide and grow. Therefore, they will need space. Growth in the lateral direction \((y\)-direction, and also \(z\)-direction in 3D) will somehow be limited due to exposure to high shear forces and thereby forced detachment (Böl et al., 2009; Horn et al., 2003; Picoreanu et al., 2001). Growth in the \(y\)-direction will also decrease the availability of substrate as the diffusion distance will increase with increasing size of the aggregate. Hence, a favorable direction to propagate would be in \(x\)-direction behind the base, as it is protected from the shear forces. Moreover, biofilm growth in streamers may also benefit from the enhanced mass transfer due to the flapping movement of the streamer and also the mixing in the wake behind the base. The development of a streamer-like structure oscillating in the flow seems to be a very good strategy for microorganisms to obtain the highest possible supply of substrates out of the bulk phase, while reducing the detachment probability. The increasing stress in the \(y\)- (and \(z\)-) direction will force the microorganisms to grow in the flow direction and, by doing so, streamer-like structures will develop. This “shear stress induced growth of streamers” hypothesis can be proved using fluid–structure interaction models adapted for biofilm growth (Küttler et al., 2009).

High values of the von Mises equivalent stress are shown in Figure 8 at the bent segments of the streamer as well as where the tail is attached to the base. These regions with stress concentrations are likely to detach, similar to the streamers experimentally observed by Stoodley et al. (1998). As mentioned earlier, streamer structures will have a benefit compared to larger circular structures. But this will only be valid up to a certain ratio \(L/D\), depending on the internal strength developed by the microorganisms and other factors.
As a final point, achieving the lowest drag itself may not be the foremost reason to form streamers, but can be a strong factor when considering detachment. The simulations presented provide an idea on how the biofilm structures behave in the flow field. Future work should couple fluid–structure interaction, time-dependant material models, mass transfer, and biofilm development to provide better insight into the transient nature of the biofilm lifecycle seen in the experiments. In this respect, numerical tools may help to increase the knowledge, as currently the lack of methods for reliable measurement of local biofilm dynamics and physical properties is a challenging problem.

**Conclusion**

In this work, a numerical FSI framework was employed to simulate streamer oscillations measured in previous works. It is shown that above a critical velocity the flow becomes unsteady and a vortex street forms, which is the main driving force behind the streamer oscillations. Moreover, it is shown that at higher flow velocities the streamers help to reduce the fluid drag force on the biofilm structures up to a critical tail length.

The authors thank Luoding Zhu for the helpful discussion on subjects of drag of flexible structures. This work was funded by Oswald Schulze Stiftung. The work of C. Picioreanu was financially supported by the Netherlands Organization for Scientific Research (NWO, VIDI grant 864.06.003).

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