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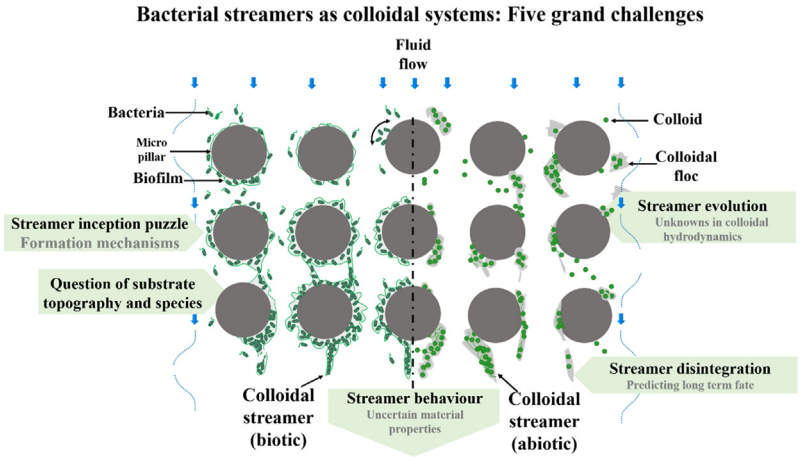
Feature Article

Bacterial streamers as colloidal systems: Five grand challenges ☆

Udita U. Ghosh [a], Hessein Ali [b], Ranajay Ghosh [b], Aloke Kumar [a,*]

[a] Department of Mechanical Engineering, Indian Institute of Science, Bangalore, India
[b] Department of Mechanical and Aerospace Engineering, University of Central Florida, Orlando, FL 32816, USA

GRAPHICAL ABSTRACT



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ABSTRACT

Bacteria can thrive in biofilms, which are intricately organized communities with cells encased in a self-secreted matrix of extracellular polymeric substances (EPS). Imposed hydrodynamic stresses can transform this active colloidal dispersion of bacteria and EPS into slender thread-like entities called streamers. In this perspective article, the reader is introduced to the world of such deformable 'bacteria-EPS' composites that are a subclass of the generic flow-induced colloidal structures. While bacterial streamers have been shown to form in a variety of hydrodynamic conditions (turbulent and creeping flows), its abiotic analogues have only been demonstrated in low Reynolds number (Re < 1) particle-laden polymeric flows. Streamers are relevant to a variety of situations ranging from natural formations in caves and river beds to clogging of biomedical devices and filtration membranes. A critical review of the relevant biophysical aspects of streamer formation phenomena and unique attributes of its material behavior are distilled to unveil five grand scientific challenges. The coupling between colloidal hydrodynamics, device geometry and streamer formation are highlighted.

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* Corresponding author.
E-mail addresses: ranajay.ghosh@ucf.edu (R. Ghosh), alokekumar@iisc.ac.in (A. Kumar).

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1. Introduction

Bacterial colonization of surfaces is ubiquitous in nature [1–3]. Such colonization often results in surface biofouling [4] with potentially devastating economic effects. Hence, science of the biofouling process has been under intense scrutiny over the last few decades [4–6]. Typically, biofouling proceeds via the formation of bacterial biofilms [7]. Biofilms [8–10] are surface-associated bacterial colonies encased in a matrix of self-secreted extracellular polymeric substances (EPS) and are excellent examples of active colloids [11,12]. Biofilms that form in the natural environment and in complex artificial systems such as membranes, can often be subject to a variety of external stresses [13–16], ranging from the physio-bio-chemical to hydrodynamic stresses. Particularly those that form in the presence of sustained hydrodynamic flow [16,17] are of significant interest to the scientific community; such an environmental condition is often automatically present in natural [18,19] and artificial systems such as river beds, biomedical devices [20–22] and filtration membranes [23,24]. Here sustained implies fluid flows over timescales that are greater than the relaxation timescale(s) of the EPS-bacteria composite. In the presence of sustained hydrodynamic flows, the EPS-bacteria composite often takes the form of elongated, flow-mediated slender structures called streamers [25], which are essentially soft slender composites with bacteria (Fig. 1).

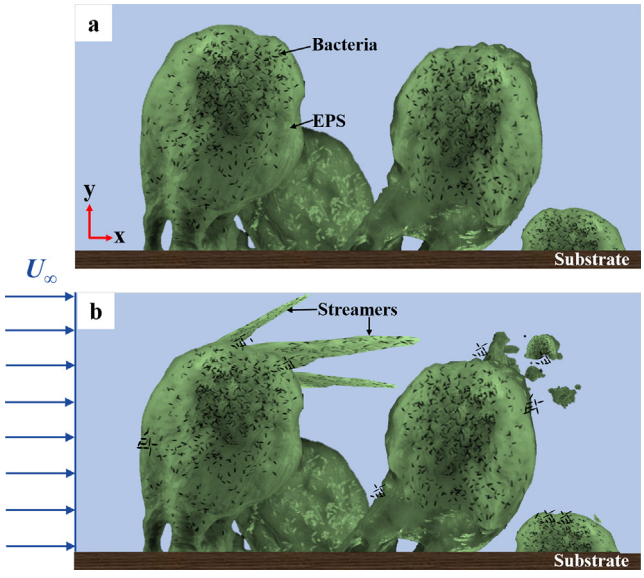

Fig. 1. Schematic showing the constituents of a biofilm where (a) bacteria (black) are encased in a matrix of biological molecules cumulatively called extracellular polymeric substances (EPS; green) (b) transformation of the biofilm into slender structures called streamers by the imposition of fluid flow.

Streamers, despite their relationship to biofilms, have distinctive properties, behavior, and impact on system flow and clogging dynamics. Drescher et al. [26] showed that streamers, unlike slow-growing biofilms, can lead to catastrophic clogging of curved channels and stents. Using microfluidic mimics for microfiltration membranes, researchers have now shown that streamer formation can lead to a new mode of fouling as compared to cake filtration and pore-blocking modes [27]. In the streamer formation regime, conspicuous mass transport downstream of membranes was observed due to constant streamer breakage. In another work, streamers forming on oil droplets could enhance fluid drag by 80% [28,29].

Recent studies indicate that streamer presence may not always be an adverse consequence. For example, oil spills [30–32] in the water bodies often generate micro-scale oil droplets which spatio-temporally conform with the inhabiting microbial populace. Streamers have been shown to prolong the residence time of the oil droplets, allowing sufficient interaction time between the microbe and the oil–water droplet thereby enabling degradation of oil droplets [28,29]. Structural analogues of streamers can also be found in food [33] and polymer processing. For example, processing of cotton candy, a food delicacy, involves spinning sugar solution or in the extrusion of polymeric fibers during electrospinning, thread-like structures have been observed. It must be noted that these are suggestive structural analogues and their fabrication process as well as material properties may be considerably different with respect to streamers. Streamers have created a distinct niche for themselves in the area of active colloids and characterization of these structures are essential to understand their behavior and predicting their evolution. However, significant challenges exist in this path. In this review, we outline five grand challenges that must be addressed to arrive at a matured stage of knowledge about streamers and the necessary factors that must be taken into account for developing predictive tools for the biophysical processes. These challenges underscore the most critical gaps in our understanding of this area, covering various aspects of streamer formation, evolution, maturation and terminal phases.

2. Bacterial streamers – structure, formation and impacts

Bacteria can colonize diverse interfaces [34] – the colonization process itself can be extremely complex with timescales (10^0–10^7 s) spanning several decades. Aggregative colonies at solid–liquid interfaces are called biofilms [35,36]; in open liquid wells, bacteria may adhere at the liquid–air interface, eventually generating chains and aggregates bound together by extracellular polymeric substances (EPS). Equivalents of the biofilm at the air–liquid interface are called pellicles. The cell-EPS aggregates or clumps dispersed from a matured biofilm or pellicle can give rise to floating aggregates in liquid media called 'flocs'. Mechanical response of these self-assembled composites is influenced by the bounding interfaces. For example, pellicles due to their access to a water body can swell by moisture absorption which leads to resistance in polymer cross-linking and acts as a protective barrier from complete dissolution [11]. It also alters the overall water content in the film which can modulate the mechanical response of the film to external perturbations. An increase in EPS content can also shift the biofilm behavior from the viscous fluid-like to the solid-like [11]. For example, *P. aeruginosa* biofilms exhibited a breaking point in compression tests beyond which the biofilm behavior was predominantly viscous fluid like. This distinctive transition was attributed to the entanglement of the EPS [37] components governed by the van der Waals and electrostatic interactions. The composition of EPS can also alter the stress relaxation timescale of the biofilm, ranging from 18 min [38] for environmental biofilms to a mere 13.8 s in *S. epidermidis* biofilms [39]. Such fluidity in EPS fabric may at times permit migration of housed organisms within the matrix providing a porous and heterogenous character to the biofilm [40]. Although, such internal movements are not universal since most organisms are fixated within the biofilm.

Any of these aggregative forms can be a precursor to bacterial streamer formation, which have been observed to form under a variety of flow conditions ranging from turbulent [41–45] to creeping flow regimes ($\mathrm{Re} \ll 1$) [23,24,28,29,46–55] where Re is the Reynolds number, $Re = du\rho/\mu$, d is the characteristic length of the device, u is the flow velocity, ρ and μ are the density and dynamic viscosity respectively of the fluid. Streamer formation in turbulent flow situations represents a more classical aspect of streamer related research. Streamer formation under low Reynolds number ($\mathrm{Re} < 1$) conditions has recently [52,54] attracted attention due to interest in understanding bacterial colonization in micro-scale systems. In these micro-scale devices, the filamentous structure of streamers can extend significantly with flow, thereby spanning several disconnected surfaces [54] otherwise not easily possible for precursor aggregative modes of bacteria – flocs, pellicles or biofilms. This can make colonization rapid, pervasive and resistant to erosion with flow having a significant impact on the performance of filtration units [27] and biomedical devices.

At the core of streamer formation processes is the viscoelastic response of an aggregated state (floc or biofilm) to the traction forces generated by hydrodynamic flows. This is similar to flow-induced structure formation in complex fluid flows [56] that arise due to a variety of forces such as van der Waals and electrostatic forces, Brownian motion and hydrodynamic interactions. It is well known that colloidal suspensions subjected to flow can give rise to aggregation states [56,57] and such structures have been observed even for dilute concentrations in non-Newtonian media [57,58]. Particle-laden complex fluids also exhibit flow-induced alignment and/or aggregation of microscale particles in viscoelastic fluids for diverse flows [56,58]. Initially these were ascribed to normal stress effects [59–61]. Later, alignment was reported in shear-thinning viscoelastic fluids [62,63] but absent in Boger fluids, indicating that shear thinning may be the dominant cause. However, the roles of fluid elasticity and viscosity were both found to play a role (contrasting) in flow-induced aggregation of dispersed colloidal nanoparticles in complex fluids. An increase in the lower limit shear viscosity accelerated the aggregation whereas an increase in elastic character opposed aggregation [58]. On the other hand, the flow velocity profiles of nanoparticle dispersions in disordered porous media remained unaffected by polymer addition [64]. These studies imply that predicting flow-induced structure formation in complex fluid flows through porous layouts is still ambiguous. This can be attributed to difficulty in accurate determination of the characteristic length scale in porous architectures and it is this length-scale that further dictates the rheology of the complex fluid [65,66]. Therefore, despite extensive research, flow-induced structures for particle-laden flows of complex fluids remains poorly understood. This is further elaborated in Section 4.2.

Macroscopic aggregates of bacteria trapped in EPS broadly referred to as 'acid streamers' [68–70] were the first accounts of streamers found in effluent treatment reports of acid mine water resources [71] (Fig. 2a). Such macroscopic streamers [68–74] (Fig. 2b) are abundantly found in natural environments [22,74] such as in hydrothermal vents[73], and in spring channels of the Arctic [72]. For example, Niederberger et al. [72] found macroscopic microbial streamers, with characteristic length-scale (l_s) in the order of 10^{-1} m attached to rocks and sediments within run-off channels of the cold saline springs of the Canadian high Arctic. These macroscopic streamers [51] have significant biological complexity often comprising of mixed- species, and very little mechanistic understanding of these is available in the current literature. It must be stated here that microbial communities comprise of archae, bacteria, fungi and eurkaryotic microbes [9] and thus a natural biomass composite is diverse in composition. The biogeochemistry of the environment heavily influenced the evolution of the microbial community [75,76] within the streamers. For example, in abandoned sulfide mine [75], species distribution was found to be a function of the lateral depth of the sample with microalgae

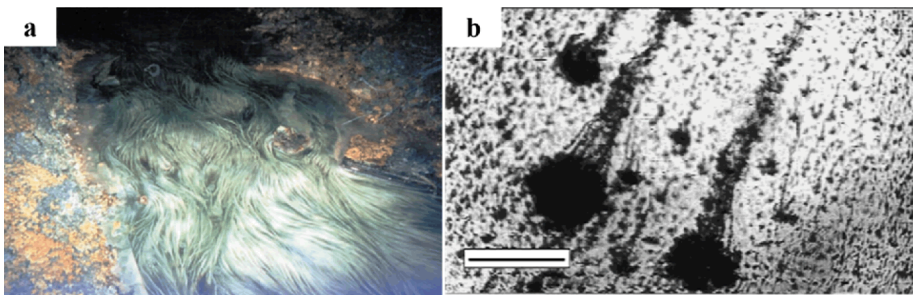

Fig. 2. Streamers in turbulent flow (a) "From [Microbial Geoengineers, Lesley A. Warren, Mary E. Kauffman, Science, [67]]. Reprinted with permission from AAAS." (b) Confocal microscopy image showing streamers emanating from biofilm. Scale bar: 500 μm. "Creative Commons 'Oscillation characteristics of biofilm streamers in turbulent flowing water as related to drag and pressure drop' by Stoodley et al. [43] is licensed under CC", Copyright © 1998 John Wiley & Sons, Inc.

dominating the streamer biomass at the surface followed by heterotrophic acidophilic bacteria (*Acidobacteriacae* and *Acidiphilium* spp.) as the intermediate layer and sulfidogenic bacteria forming the lowest rung. In the late 1900s, in an attempt [77] to simulate microbial growth in laboratory conditions, a porous construct was etched on silicon wafer and subjected to effluent flows. Long filaments (few ~ mm in length, 6.5 ± 2.3 μm wide) were observed to emanate from the microbial colonies which sparsely populated the pores in the downstream direction. These filaments were probably the foremost report on microscopic streamers although the nomenclature 'streamers' seeped into literature much later, with the development of biofilms and subsequent work by Stoodley et al. [42,43]. The advent of microfluidics [23,26,53,54] in recent times enabled study of streamer formation at the laboratory scale i.e. the microscale streamers.

Structure and length-scale of the streamers are a function of the imposed flow regime (laminar/turbulent) and inception mechanisms (floc/ biofilm) as discussed later (Section 4.1). Correlation between the mechanism, flow regime and the final structure of the streamer is still poorly understood, but these factors subsequently determine the timescale (τ_s) of streamer formation.

3. Streamers as colloidal structures

Although streamers were originally almost exclusively associated with bacterial flows, more recently [48] streamers were observed in microfluidic devices with particle-laden polymeric flows. This has led to their generalization into the abiotic realm. Creating the abiotic equivalent artificially at the laboratory scale was recently achieved for a system comprising of polyacrylamide solutions mixed with polystyrene colloidal suspensions [48]. The particle-polymer aggregates formed by flocculation bear close resemblance with the bacterial flocs [46] and the generation of colloidal streamers also requires a sustained hydrodynamic flow like its biotic counterpart. Recently, similar structural analogues were also reported for Re > 1, by Chandra et al. [78] with aged polymeric solutions of polyethylene oxide solutions and food particles. These underlying similarities (and dissimilarities) will be critically examined in the light of colloidal physics in Section 4.2. Any generalization represents a significant scientific advancement in a field, and thus the idea that streamer-like morphology can be recreated in colloidal suspensions has opened new vistas of research.

Streamers are an amalgamation of several entities, with length-scales ranging from few nanometers to microns. At the lower end of the length-scale spectrum are the macromolecules and at the other end of this length-scale spectrum are bacteria or other passive colloids. Thus, streamers cover the entirety of colloidal length-scale spectrum, and interactions between the colloidal particles such as bacteria or microbeads in suspensions are governed by forces that are of interest to the colloidal science community. This encompasses the attractive Lifshitz-van der Waals [79,80] and the repulsive electrostatic [81], which forms the framework of DLVO (Derjaguin, Landau, Verwey and Overbeek) theory [82]. However, interactions between colloidal particles and polymers also bring into account the polymer conformation and extent of polymer adsorption on particle surfaces where in DLVO theory is no longer applicable. Adsorbed polymers act as steric barriers, preventing penetration during inter-particle interactions [83]. For example, when two surfaces covered with polymer approach each other, the entropy of chains that are freely suspended into the solution results in a repulsive force known as the steric force [79]. There is no simple theory for steric forces because they are complex and difficult to explain [84,85]. However, an empirical formula for repulsive steric energy is available which has the form,

$$V_{steric} = \frac{K}{H^m} \quad (1)$$

where H is the distance between interacting particles, K is a constant and m is an exponent and ranges from 3.4 to 20 for particles with grafted polymer [86].

The above discussion motivates us to christen the generic class as, 'colloidal streamers' which can be broadly divided into the biotic and abiotic streamers based on the origin of the soft composite. We will also elucidate how bacterial streamers can be looked upon as an example of the generalized concept of 'colloidal streamers' under the umbrella of biotic streamers. It is the interplay between above stated intermolecular forces that determines the possibility of aggregation (bridging/depletion) and therefore formation of flocs in a floc mediated streamers (details on mechanism pathway in Section 4.1.2). The research challenges and questions that lie ahead in these subclasses will be discussed in tandem.

4. Grand challenges of bacterial streamers

In this section, we outline five grand challenges that still exist in the broad domain of streamer research. Each section begins with a thorough literature review of the existing body of work and critically examines the lacunae in our current understanding.

4.1. The puzzle of streamer inception

The question of streamer inception, despite being one of the most obvious lines of enquiry, remains a puzzle till now. As shown in Fig. 3, streamer formation can occur over a wide range of Reynolds numbers (Re) and characteristic streamer formation timescales (τ_s). This diversity makes any universal theory of streamer formation very challenging; indeed, one may doubt if a universal theory even exists. In this section, we address some of the knowns and unknowns of streamer inception, by categorising streamers into various groups.

4.1.1. Streamers in turbulent flows

In laboratory models, initial investigations reported bacterial streamer formation [23,41,43–45,51,55,67,90–92] (l_s, length-

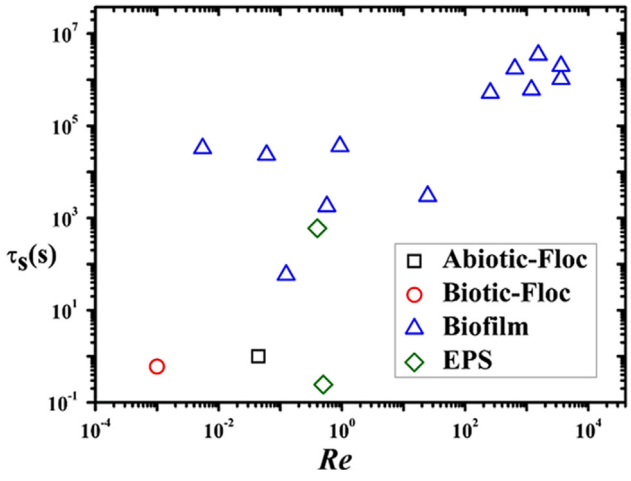

Fig. 3. Diversity in streamer formation timescales, τ_s (*s*) pertaining to flow regimes characterized by the flow Reynolds numbers, *Re* for studies reported in literature till date. Each study is represented as an individual data point identified by its distinct mechanism (i) abiotic-floc (□) [48] (ii) biotic-floc (O) [24,45–46,74,75] (iii) biofilm (Δ) [23,39,41–44,50–52,56,64,66–70,70–73] (iv) EPS (◇) [28,29,89].

scale, $> 10^{-3}$ m) exclusively in the turbulent flow regimes. Streamers were found to shed vortices after attainment of such millimetric length-scales [90,92]. This adversely affected device efficiency due to the accompanying substantially high pressure drops [42,43]. It has been proposed that such bacterial streamer development occurred through a multi-staged process. The first stage comprised of firm and secure attachment of aggregative forms of bacteria (biofilms and microcolonies) onto the solid surfaces. The imposed turbulent background flows, created a pressure difference between the upstream (high) and downstream (low) borders of the bacterial microcolonies, triggering the formation of wakes in the downstream section. Under the action of the high shear stresses originating from the turbulent flows, the growth of the bacterial colonies gets streamlined. Such repeated cycles of streamlining or elongation with simultaneous mass accrual at the downstream lead to generation of streamers. The streamer formation time scale, τ_s, in such situations has been found to be of the order of several hours. Unfortunately, such a proposed mechanism remains a purely qualitative proposition. Quantitative evaluation of the streamer formation processes in turbulent flows, along with the concomitant mass transport and other biophysical phenomena, remain an unaccomplished goal.

4.1.2. Streamers in low-Re flows

Earlier research had suggested that bacterial streamers form only in turbulent flows, and not in laminar flows [41,45]. The claim of streamer formation only in the turbulent regime came to be refuted in later studies and this was feasible with the advent of microfluidics which allowed experiments in the very low *Re* regime [46,54]. Microscale streamers, just like their macroscale counterparts, have a slender morphology resulting from an interaction between fluid flow and the associated stresses that act on the 'active matter'.

The biophysical origins of microscopic streamers can be extremely diverse and one important pointer in this direction is the diversity of streamer formation timescales reported by different researchers. Across these studies, two distinct mechanisms have been identified, which include (i) biofilm mediated streamers [23,26,41,43–45,51–55,67,90–93,93–96] (ii) floc-mediated streamers (biotic and abiotic) [24,46–48,87,88]. A third ill-understood mechanism [28,29,49] of EPS driven streamers also likely exists and it will also be discussed herein.

In the low *Re* regime (Re < 1), the characteristic timescale (τ_s) of streamer formation varies widely from 6 to 7 h in biofilm mediated streamers to 2–3 h in EPS driven [28,29,49] streamers to relatively instantaneous (~few seconds) in floc mediated streamers (biotic and abiotic). Let us delve into these mechanisms briefly.

Microfluidic channels, when subjected to continuous flow of planktonic bacterial solutions, can allow irreversible attachment of the freely flowing bacteria on the surfaces. This eventually leads to the formation of biofilm. Interestingly, if the infusion of the bacterial solution into the microfluidic channels is further continued, then after few hours (~7–9) filamentous structures can be observed. Figure 3 indicates an underlying commonality in the biofilm mediated pathway studies which is the higher timescales (τ_s) of formation (~$O(10^5)$ s). This can be attributed to the fact that the biofilm formation precedes the streamer formation which requires ~6–8 h (~$O(10^4)$ s). In the specific example [54], demonstrated in Fig. 4**a**, continuous infusion of fluid through a microchannel with

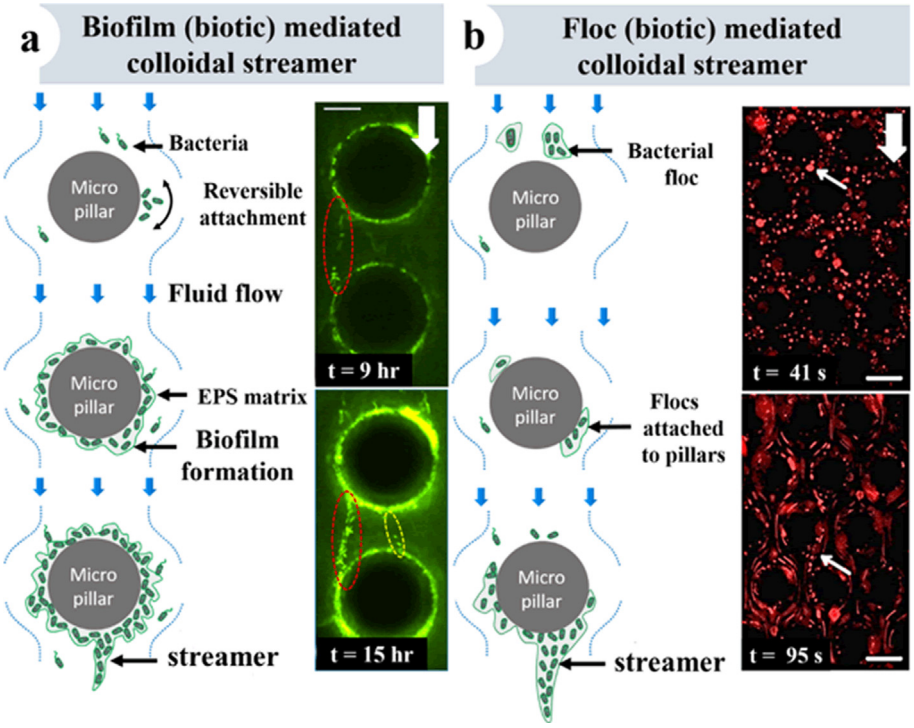

Fig. 4. Streamer formation mechanisms segregated into three categories. Representative confocal images of (a) biofilm (biotic) mediated streamers (indicated by the dashed ellipse, red -parallel streamers, yellow – transverse streamers) formed by *P. fluorescens* bacteria observed in green fluorescence at t = 9,15 hr resp. These images are for a flow rate = 8 μL/h, corresponding to a representative Reynolds number ~10^{-3} through a microdevice comprising of uniformly placed micro-pillars of equal size and diameter of 50 μm with an inter-pillar distance (pitch) of 25 μm. Scale bar: 20 μm, [54] – Adapted with permission of The Royal Society of Chemistry (b) floc (biotic) mediated streamers bacterial streamers formed by *P. fluorescens* bacteria tagged with 200 nm fluorescent red polystyrene beads. The arrow specifies a floc, which is advected through the channel (t = 41 s), followed by its attachment to the micropillar and then its transformation into a slender streamer at t = 95 s. "Creative Commons 'Bacterial floc mediated rapid streamer formation in creeping flows' by Hassanpourfard et al. [46] is licensed under CC BY" Scale bar: 50 μm. The events in streamer generation mechanisms in the original confocal images are also indicated in the accompanying corresponding schematics.

PDMS micro-pillars led to the formation of a biofilm. Fig. 4**a**, represents a confocal laser scanning image of a cross-section of the device, where the green fluorescent protein (GFP) expressing bacteria appear green. Streamers spanning the inter micro-pillar distance are seen to appear after several hours. It has been reported that in curved microchannels, the imposed fluid flow of bacterial suspensions can give rise to secondary flows [52,53] at the curved corners that promote local accumulation of bacteria. These flows promote local accumulations of biomass near the mid-section of the channel and the eventual shearing of the biofilm transforms them into filamentous structures or streamers. Other reports, however, have indicated that in other channel geometries, streamers can form throughout the height of the channel [54].This suggests, that the role of secondary flows remains an unsettled challenge in this field.

Delineation of biofilm mediated streamers has been carried out based on the very long streamer formation timescales that have been reported. Yet, the exact mechanics of streamer formation remains an extant challenge both experimentally and theoretically. Currently, only the genesis of floc mediated streamers has been explored with some rigor. Floc mediated streamers have been shown to form when bacterial flocs – which were infused into a microfluidic channel – adhere to channel walls and are subsequently 'extruded' by hydrodynamic traction forces into a slender morphology i.e. a streamer **(**Fig. 4**b)** [24,46,47,87,88]. The nature of their genesis implies that such streamers have a very short streamer formation timescale (~$O(10^{-1}$–10 s)). Even in creeping flow conditions, floc-driven streamer formation have been shown to be characterized by very large strains (~600%) and creep response [88] and failure through necking. Some of these issues are discussed in the subsequent sections. A third mechanism involving jetting of highly viscous fluids in a multi-phase flows has been proposed [97]; however such a mechanism remains ill-understood and strong experimental verification of the same remains desirable. Streamer formation at intermediate timescales has also been observed [7,29,49]. Sheng and co-workers [28,29,89] have reported streamer formation to be mediated by preformed EPS threads ($\ll$1 μm in diameter**)**. Bacterial solutions were allowed to flow through a microfluidic device and in close contact with pinned oil droplet. Transient attachment-detachment events of preformed EPS threads onto the droplet were touted to form a net for trapping bacteria. This was followed by eventual shearing of the oil–water interface leading to streamer initiation at timescales of ~O(10^1) while its development into a streamer bundle occurred in ~40 mins (O(10^3). Further quantification and identification of the relevant fluid mechanical phenomena are desirable for a thorough understanding of this mechanism.

It is evident from the preceding discussions that streamers represent a complex class of structure and its quantification [23,48,54,55,96] has focussed only its observable physical characteristics like length, width or a combination of the linear dimensions i.e. the slenderness ratio etc. For example, porosity [96] of a streamer indicated the amount of biomass carried by each of these filaments but this is a dynamically evolving property closely related to the EPS production. Streamer count has also been employed in certain studies although it varies widely across the device. It is proposed that porosity and streamer count may foretell the clogging capacity of the generated streamer bundles. However, these existing quantifications provide an incomplete picture of the streamer in terms of its material and biophysical minutiae.

The formation of streamers has been generalized recently, to particle-laden flows of polymeric fluids, where it has been shown that similar morphological structures are created from a polymer-particle composite. Here too, the mechanism of streamer formation was identified as being one with where a polymer-particle floc formation takes place; these flocs are advected by hydrodynamic flow and later attach to channel walls and are extruded to form streamers by hydrodynamic traction forces. Such abiotic colloidal streamers are discussed in more detail in the subsequent section.

4.2. Unknowns in the colloidal hydrodynamics of streamer evolution

Biological streamers are now understood to be a common occurrence in several natural and artificial systems. Despite their broad applicability, bacterial streamers allow researchers little room to probe the underlying colloidal hydrodynamics principles. The bacterial EPS is a blend of several biological macromolecules such as proteins, polysaccharides and DNA in a highly hydrated environment [8,9]. Production of EPS is not exclusive to bacteria; algae [98], fungi [99] and archaea [100] can also generate EPS. There can be variegation in EPS composition even between strains of a species [101,102], thus providing very minimal control to the experimentalist towards artificially mimicking this blend. In other words, arbitrary variations of the blend are not possible. It is a dynamically evolving entity and its composition is a function of several factors (but not restricted to) (i) species origin (ii) growth condition (temperature, nutrients) (iii) external perturbation e.g. hydrodynamic shear [8,9,103–105]. Determining the composition of EPS is a humongous scientific enterprise for it involves the obstacle of EPS isolation. A portion of EPS will be bound to the cells and loss of water content may alter the composition during isolation. Thus, till date there exists no universal procedure for EPS isolation that is, it is specific to the species and should be adapted depending on the objective of the investigation. Extreme care needs to be taken during the isolation process such that the method is non-invasive and prevents mixing of the intracellular material with the extracellular polymeric substances. In this light, the discovery of abiotic colloidal streamers has special significance for it allows researchers room to tweak the parameter space of the experiments. Variability and complexity in EPS composition, gaining consistent structural parameters with such synthetic systems is a challenge; yet, simple polymer-colloid analogues provide a suitable pathway to conduct systematic and parametric studies on streamers.

Debnath et al. [48] showed that a critical concentration of particles to polymer was required for abiotic colloidal streamer formation **(**Fig. 5**a)**. Since in this study, the amount of polymer added in the system or polymer dosage is an externally controllable parameter, the investigators were able to develop state diagrams demarcating regimes of streamer formation. Their state diagrams show that in certain flow regimes, streamer formation only occurred when $c_{particle}/c_{polymer} > 0.6$ and this ratio correlates to the size of floc formed. The streamer formation timescales observed by Debnath et al. [48] are close to the floc-mediated bacterial streamer timescales reported by Hassanpourfard et al. [46]. It must be reiterated here that these two studies have been conducted in the $Re < 1$ regime. Interestingly, while investigating streamer formation for Re > 1, Chandra et al. [78] found that streamers (Fig. 5**b**) were not observed with fresh polymeric solutions but formed readily with aged polymer solutions. Fig. 5a and 5b show the colloids embroiled in a network of polymers in salvaged abiotic streamers, as observed by *insitu* microscopy. The experimental device comprised of Couette flows of food particles and polymers with a needle placed in the flow path for visualization of the attached streamers. This apparent contradiction concerning the ageing of the polymer solution between Debnath et al. [48] and Chandra et al.'s [78] studies suggests that floc mediated streamer formation route still remains ill-understood.

A major line of enquiry could be what are the factors governing floc-formation in these systems? There are a multitude of factors

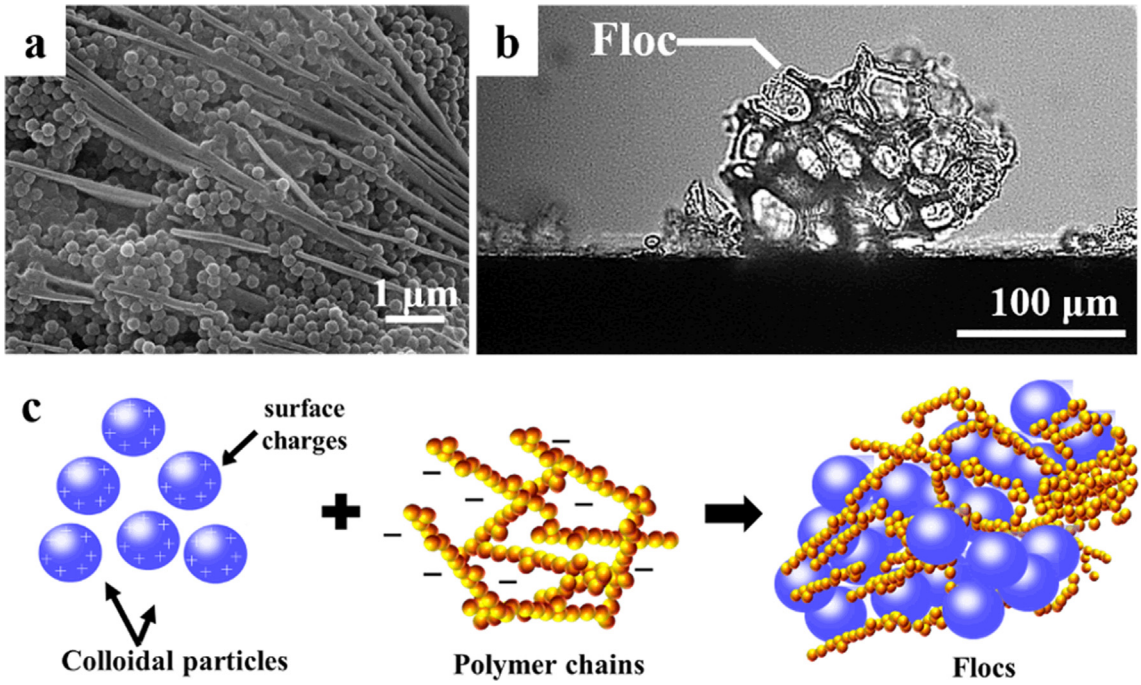

Fig. 5. Scanning electron microscopy image and microscopic image resp. showing the internal structure of salvaged abiotic streamers formed in a (a) micro-device [48] – Reproduced by permission of The Royal Society of Chemistry. (b) milli-scale laboratory setup. Image courtesy – Chandra et al. [78]. The intricate network of colloids wrapped in polymer can be seen in both the images. (c) Schematic illustrating the mechanism of flocculation with colloidal particles and polymers possessing opposite surface charges that result in the formation of flocs.

ranging from (a) polymeric properties like conformational state [106], relaxation timescale, inherent polydispersity, (b) particle orientation and shape (c) solvent properties [107,108] (d) histories of the imposed flow [109]. 'Polymer bridging' [110] may be the backbone of floc mediated streamer formation as shown schematically in Fig. 5**c**. Simply put, high molecular weight polymers (>10^4 g/mol), tend to get adsorbed on multiple particles [80,111] forming a bridge that connects an array of particles, embroiling them into the polymer matrix and eventually shaping them into colloid-polymer aggregates or flocs. Insights into the flocculation mechanism [106,112–114] are necessary to determine its extent of influence on the flow behavior [115] of the flocs and may hold the key to the route of its transformation to streamers.

It is the interplay between the intermolecular forces (van der Waals, electrostatic and steric) that determine the possibility of aggregation (bridging/depletion) and therefore formation of flocs. For example, in the study of Debnath et al., [48] alteration of the colloidal suspension pH from acidic (or neutral) to basic adversely affected floc size. The requirement of particle/polymer for streamer formation increased by an order from$c_{particle}/c_{polymer}$ > 0.6 to$c_{particle}/c_{polymer}$ > 3. Another instance is the stretching of colloid-polymer composite during streamer initiation and detachment, wherein electrostatic and steric forces arise due to alignment/orientation of the polymer strands within the composite. In addition to these forces, SEM images [48] have confirmed that presence of stretched filaments that play a crucial role in holding the colloidal aggregates in streamers. These provide structural integrity while maintaining long-range order inside streamers.

As stated previously (at start of this Section, 4.2), EPS is a mixture of polymeric substances but so far, experimental attempts at replicating abiotic streamers are limited to a single polymer added to a colloidal suspension. To address this scientific gap, cues may be drawn from commercial processes like sludge dewatering, where often, a combination of polymers [106] is employed to increase efficiency of the flocculation process. The colloidal

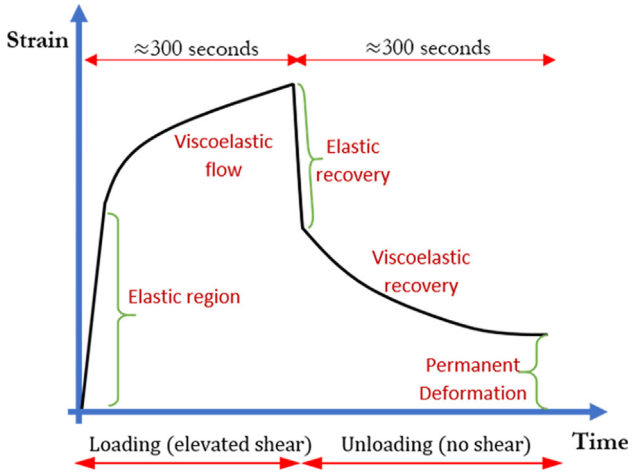

Fig. 6. An illustration of viscoelastic behavior of *S. aureus* biofilm through creep curve. Adapted from [125].

dynamics governing particle-polymer interaction with a polymer blend and imposed flow is a complex question as discussed before (Section 3).

Moreover, while the mechanics of colloidal suspensions in Newtonian media has been extensively studied over decades, the same cannot be said for colloids dispersed in non-Newtonian fluids like polymers [116]. This is related to the complexity of describing the highly non-linear stress–strain relationship of non-Newtonian fluids even when devoid of particles/colloids. Our physical understanding of experimental estimates of even basic rheological properties like viscosity of a viscoelastic fluid such as, high molecular weight polymers, EPS etc., is still in its infancy. An additional complexity is introduced in the case of streamers, wherein the imposed fluid flow may modulate the overall rheological response of the

suspension (particle-polymer). Therefore, correlation between the morphology of flow- induced polymer-colloid structures with the hydrodynamic parameters [117] and system constituents needs further exploration to understand the origin of colloidal streamers.

4.3. The uncertain material properties and behavior of streamers

Streamers are slender structures, which form *in situ*, by the combination of multiple factors including colloidal hydrodynamic conditions of the ambient, initial aggregate state, EPS, bacterial properties and physiology. Therefore, their material properties are strongly dictated by their formation and media environment of the device. This presents a unique difficulty in quantifying their material behavior under well controlled and well defined 'standard' loading conditions, typically done in material science or rheology literature. Yet their material and rheological behavior is of critical significance in predicting their behavior. Note that biofilm by themselves are known to be viscoelastic materials [38,42,118], exhibiting a time-dependent response to a sustained mechanical perturbation [71] along with an intricate range of behaviors [12,42,119–123] comprising deformation, fracture, and strain hardening [11,124] as shown in Fig. 6.

Streamers have been observed in considerable detail under creeping flow conditions, ($Re \ll 1$) in microfluidic systems mimicking porous media. This is because of their similarity to a number of critical engineering systems such as biomedical devices [26,93,95] and filtration units [23,126]. In early research streamers were assumed to be homogenous linear elastic for modeling purposes [92,127]. However, later detailed observations clearly showed that streamers are not homogenous and can exhibit significant nonlinear viscoelastic behavior [26,97,128]. Specifically, the EPS acts as a viscoelastic matrix with biological macromolecules that can introduce nonlinear mechanical response [94,129], whereas the embedded stiffer biological cells [11] make them complex soft heterogeneous materials. More significantly, considering the size of the bacteria and their random distributions inside the soft EPS matrix, streamers are inherently colloidal in nature bearing some resemblance to particle-laden polymeric flows [48]. The overall behavior therefore exhibits many features depending on their lifecycles and overall hydrodynamic conditions.

Such complexities are reflected in early literature on the topic. In contrast to the homogenous linear elastic assumption, subsequent research claimed fluid like behavior by fitting droplet breakup model [97] to streamer disintegration data [54]. However, in reality this hypothesis turned out to be very restrictive as further experimental evidence showed considerable elastic recoil behavior of streamers formed via flocs at their initial stages of formation [46]. Specifically, very large strains (~600%) were observed at the formation stage of the streamers, which were observed to undergo repeated cycles of stretching and relaxation without disintegration. This unambiguously indicated that streamers possessed significant nonlinear elasticity and were not dominated by viscous behavior. Interestingly, this same study also demonstrated and quantified the viscous nature of the streamers after they were formed. Here, pairwise tracking was used to compute the strain rates on the streamers at various flow rates. The results unambiguously showed shear thickening rheological behavior of the streamers.

Further quantitative investigations on the mechanical behavior confirmed that the streamers were indeed highly nonlinear viscoelastic materials. This mechanical behavior was more precisely observed [87] in the case of *P. fluorescens* thin streamers (ratio of longitudinal to transvers length > 10) by tracking two adjacent 200 nm fluorescent polystyrene particles embedded in the EPS, and calculating their stretch (Fig. 7**a**). Surprisingly, in spite of a relatively stable background flow, the streamer stretch (or strain) was found to slowly increase with time **(**Fig. 7**b)** [130]. This is akin to a creep like behavior where a material deformation increases even when held at a constant stress. This creep behavior was analyzed by plotting it against time. The resultant creep behavior showed three distinct regions –an initial linear increase, a second plateau region and a final exponentially increasing creep which leads to failure.

These impressive advances have answered several fundamental questions about streamer material behavior. However, they have also unambiguously exposed the steep challenges for further quantification, especially those that can lead to multiscale linking of structure-properties. Bacterial streamers are biological structures, which exist inside the media and any extraction for microstructural characterization would lead to desiccation and irreversible changes in material properties. Thus, characterizing the fluid–structure interaction of a streamer cannot depend on build up

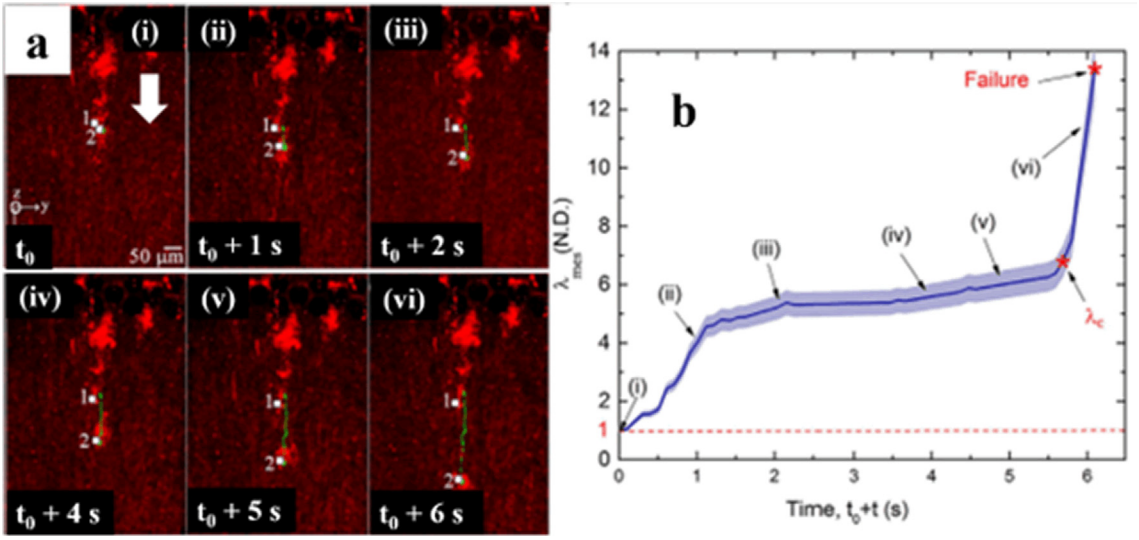

Fig. 7. (a) Time-based tracking of two Lagrangian points placed inside a *P. fluorescens* streamer until failure of the streamer. (b) An illustration of three phases of deformation for the same streamer through stretch ratio against time. Note that $\lambda_{mes} = 1$ refers to the completion of formation and initial deformation of the streamer, and thus the inception of creeping stage. The shaded line represents the error envelope. The flow velocity is U = 8.9 × 10^{-4} m/s and initial time t_0 = 30.4 min. "Creative Commons 'Nonlinear deformation and localized failure of bacterial streamers in creeping flows' by Biswas et al. [87] is licensed under CC BY"

models of individual components, as they co-exist by their very nature. This adds considerable complexity in their measurements when compared to traditional fluid–structure engineering problems. Therefore, standard careful mechanical tests such as ASTM [131] cannot be used, and only indirect information about their microstructure can be obtained [46].

For such structures to be evaluated *in situ*, the fluidic conditions and fluid–structure interaction problem must be solved, and mechanical properties obtained indirectly. This remains a formidable challenge since such indirect calculations can be accurate only when the colloidal hydrodynamics of the background flow, streamer geometry and boundary conditions are precisely obtained. Some physical information has been gleaned so far by tracking embedded fluorescent PS beads as mentioned earlier (Fig. 7). However, several limitations exist extending this method for greater accuracy. Clearly, higher bead densities are necessary to obtain precise streamer geometry information (streamers are nearly transparent otherwise), but this can begin changing the streamer properties due to the high stiffness of the beads compared to the EPS matrix. Also, pairwise particle tracking has inherent inaccuracies due to tracking errors, optical artifacts, error cancellations, and lack of spatial resolutions. Typically, full field, noninvasive optical techniques such as digital image/volume correlations (DIC/DVC) [132] can provide alternatives to this class of embedded particle measurements.

DIC measurement systems rely on putting a 'speckle pattern' on the reference configuration and then using correlation functions to obtain displacements. Such patterns are typically sprayed on or referred from some natural patterns in the material. These patterns are assumed to not affect the mechanical indices of the material tested. Unfortunately, for streamers, using these techniques remains a challenging affair. The microscale nature of these systems mean that quantity of matter is small and can be easily perturbed by addition of particles. Secondly, finding a natural non-invasive and stable marker for such *insitu* systems to carry out correlations is not easy due to reasons outlined earlier. Finally, there is the issue of signal distortion from optical fluorescent signatures coming from different planes of the streamer depth when observing from the top of the chip. Other characterization techniques such as atomic force microscopy (AFM) are also difficult to integrate into these systems due to the inherent flow-structure coupling, complex material behavior and possible sensitivity issues due to complicated local traction forces. Additional problems surface when standard rheometric techniques are sought for investigating streamer rheology. The fragile nature of biofilms has led to researchers creating novel microfluidic based rheometric platforms for mechanical analysis of biofilms [39,133,134]. Unfortunately, even these microfluidic techniques cannot be easily extended to streamers and other than a few studies [46,87,88], rheological investigation of streamers is still very much in infancy.

These issues would be even more difficult to resolve for higher *Re* flows, where the background flow can become turbulent. Typically in turbulent flow, biofilm streamers oscillate rapidly proportional to the flow velocity [43]. To implement the transient coupling between the streamers and the fluid, a 2D computational model of the fluid–structure interaction was developed [92] see Fig. 8 **(a)** for illustration. They found that streamer oscillation occurs due to vortex street formation and drag reduction at higher flow velocity. Another approach consists of modelling the streamers as a sequence of particles [135] with decreasing particle diameter along the vertical axis (head to tail) as shown in Fig. 8 **(b)**. Here, discrete element method with computational fluid dynamics is employed where the inter-particle contact forces are given by the Kelvin-Voigt model, for outlining flow patterns as well as oscillation amplitudes for single and multiple streamers. These reports however capture only a singular aspect of streamer mechanics i.e., its oscillation. Correlation of streamer material properties with its mechanics in turbulent flow conditions is unexplored. There is a dearth of analytical models that can capture the material response of the streamer especially in turbulent flows.

From this discussion, it is clear that obtaining precise physicochemical properties of streamer system would be extremely challenging. Improvements in measurement systems and protocols might alleviate some of these issues, but such promise does not look imminent. The grand challenge is thus not only in improvement measurement of mechanical properties but a new paradigm of reporting and quantifying the data obtained from the experiments, which are likely to be fundamentally imprecise. There is a need to develop useful correlations between mechanical behavior, approximate regimes of response and the colloidal hydrodynamic conditions of the media. The existence and extraction of universal features must be postulated and verified. A measure of uncertainty

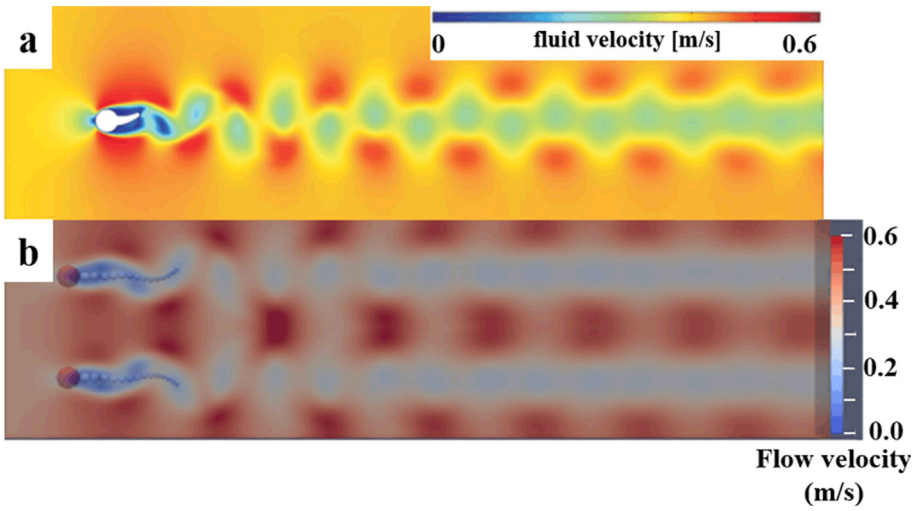

Fig. 8. Biofilm streamer modelled as a (a) combination of circular biofilm base of diameter, D and length, L. Flow patterns behind by a single biofilm streamer of *L/D = 1*, corresponding to inlet velocity of *U* = 0.4 m/s, *Re = 133*. Adapted from 'Computational study of the drag and oscillatory movement of biofilm streamers in fast flows' by Taherzadeh et al. [92] Copyright © 2009 Wiley Periodicals, Inc. (b) group of 15 particles with consecutively decreasing diameters. Flow patterns behind two streamers in tandem, with the ratio of spacing distance to biofilm streamer length *l/L*, corresponding to inlet velocity *U* = 0.4 m/s, Re = 136 and at t = 0.1 s. Adapted from "Creative Commons 'CFD–DEM modelling of biofilm streamer oscillations and their cohesive failure in fluid flow' by Chen et al. [135] is licensed under CC", © 2020 Biotechnology and Bioengineering published by Wiley Periodicals LLC."

and their propagation into the final predictive algorithms need to be developed. Interestingly, experiments on these systems generate very large data sets. Such large data sets along with certain fundamental physical insights about microstructure and mechanics make machine learning and statistical learning a potentially revolutionary tool to develop flow-property correlations [136–140]. These insights can come from complementing quantitative and qualitative measurements, flow and structure properties, and both in and ex-situ characterization. For instance, the microstructure of streamers have only been recently probed via ex-situ isolation and SEM [48]. It showed fascinating networked architecture where nano-strands of polymers connected embedded particles to provide elasticity to the structure. Unfortunately, no *insitu* analog exists for this study. However, such microstructural characterization will be necessary to gain insights into the more complex material behavior of streamers including anisotropy, emergent mechanical properties and regime changes in performances. These insights can then be baked into machine learning algorithms for greater predictive accuracy. Developing such a paradigm shift in measurements, computations and analytics highlight the most important grand challenges in this area.

4.4. Predicting the long-term fate of streamers

In creeping flow, biofilm streamers exhibit various failure modes. For example, Valiei et al. [54] had reported failure (not discussed in detail) of biofilm formed streamers (with time formation $t_s \gg \tau_{ve}$) in a microfluidic device. Such failure was theoretically investigated [97] via hypothesizing streamers as liquid jets that fail due to the instability of the jet. Note that this hypothesis is too restrictive for rapid floc-meditated streamers (t_s seconds) [46] which forms with initial and residual elasticity. Biswas et al. [87] presented another mode of failure of streamers, which occurs far from the wall. The failure was mainly due to a localized failure that happens via necking-type instability and not the global instability of the hydrodynamic instabilities. The behavior is similar to ductile material under creep response. This failure phenomenon was further clarified through developing a nonlinear simplified model assuming localized failure incorporating surface tension and inelasticity. The model provides a power law between the strain at failure and the flow background. In addition, Hassanpourfard et al. [46] reported that failure could also be due to the clogging phenomena that occur in the device due to the stick–slip phenomena observed through the evolution of 'mature streamer', thereby an instability of the clogged mimic is possible and marked by localized streamer failure and leakage leading eventually to extended water channels throughout the mimic. The stick–slip mechanism is expected because the presence of instability in viscoelastic material can experience such mechanisms or spurt flows [141,142]. Gashti et al. [94] also noticed non-monotonic behavior of the velocity of biofilms when they are sheared by flow and they interpreted that as a non-Newtonian behavior of the biofilm. Later on, Biswas et al. [88] presented that streamers could fail due to the biomass void growth which initiates near the pillars of microfluidic devices but not far. These voids/cracks were initially observed to be in the mesoscale (>bacteria scale and <streamer scale) and grow through the thickness of the streamers and it could be characterized into short and long timescale. Interestingly, the crack went through cycles of propagation and arrests and eventually leading to a failure of the streamer. This type of failure contrasts with the necking-like failure [87] mentioned earlier.

Despite the above-mentioned advances, there remain important barriers to understanding the long-term fate of streamers. There are several overlapping challenges with materials quantification issues highlighted earlier. However, other challenges arise from the dynamic and evolving nature of the entire system. Here defects due to localized pressure cavities, tearing, and particle losses can suddenly nucleate and precipitate dramatic instabilities. No proper classification or correlation of such defect nucleation, evolution and annihilation are currently unknown. At the same time, the time evolution can span multiple length scales, and with time, the streamers begin to thicken. This can fundamentally change the fluid–structure interaction between the background flow and biomass. The emergence of localized water channels and stick–slip motions are only topically known at this point. Although streamer formation has been demonstrated in the abiotic regime, with several similarities at the inception and intermediate timescales, in the long timescale their behavior can dramatically differ. This is because the biological life processes will begin to affect all aspects of the system via growth, secretion and signaling. This presents an exciting unknown frontier of research.

4.5. Question of media topography and species on streamer formation

Streamers are products of fluid-biofilm/floc interaction, and hence it is not surprising that channel geometry plays an important role in determining the maturation of streamers.

4.5.1. Question of substrate topography

Streamers can form in straight channels, but their spatio-temporal evolution can be challenging to quantify since they can be difficult to distinguish from their surrounding biological mass. The advent of microfluidics [25,143] has made it possible to investigate the impact of complicated geometries on bacterial growth and proliferation. Rusconi et al. [52] used curved microchannels to study biofilm and streamer formation under sustained flow conditions. They found that in low Re flows, transverse secondary flows generated by wall curvature dictates biomass aggregation leading to the formation of a single streamer at mid-height. In a subsequent work, they showed that the formation of streamers correlates to the strength of the secondary flows around the curved sections [53].

However, Valiei et al. [54] later showed that in a microfluidic device containing micropillars, streamer formation was not dictated by these secondary flows and streamer formation occurred throughout the transverse height of the channel. Such contradictory results suggest that the mechanism of streamer formation remains poorly understood, and its relationship to channel geometry needs to be investigated further. Valiei et al. [54] used cylindrical micro-posts and also provided preliminary results on the impact of other post geometries such as square pillars and the effect of pillar spacing (Fig. 9). As discussed earlier, Hassanpourfard et al.[47] used cylindrical micro-post geometry to show that maturation of streamers leads to the formation of distinct clogging front, which advanced via a pronounced 'stick-slip' motion over the micro-pillar surface. The streamer, the geometry (micro-posts) and the fluidic media defined a three-phase front influencing these dynamics. These studies quite clearly show that the role of the interface and channel geometry can be critical factors governing streamer formation and maturity. However, these experiments are quite preliminary, and an in-depth investigation of complicated channel geometries remains desirable.

All streamer research so far has exclusively dealt with rigid walls. However, extremely slender and hair-like media can show significant deformations and elastic energy absorption [144]. The natural world already points to such possibilities. Semi-aquatic mammals provide an interesting path for further exploring nature's solution to biofilms. Their furs escape this burden because of the intricate multiscale nature of the fur interacting with fluid–structure [145]. At this microscopic scale, fouling will depend on the surface chemistry and topography [146–148], propagating its rule to larger scales. Despite the length scale, smooth surfaces

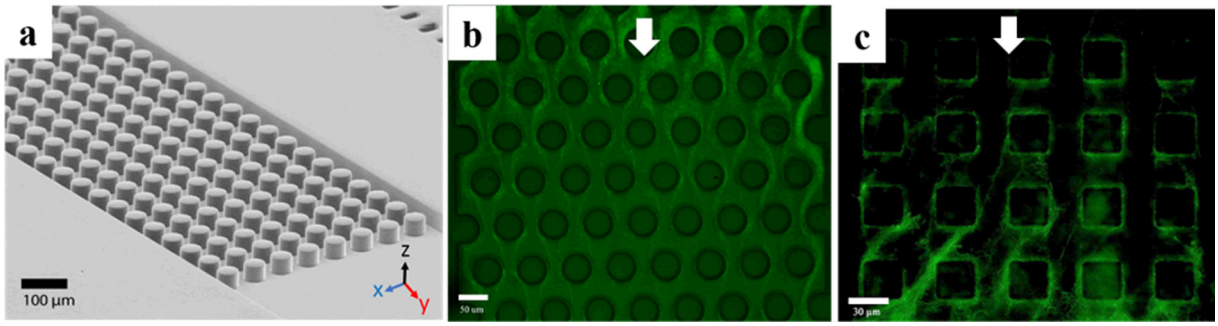

Fig. 9. (a) shows a scanning electron microscopy (SEM) image of a typical microchannel with micropillars of diameter ~50 µm linearly spaced arrangement, pitch 25 µm. [54] – Reproduced by permission of The Royal Society of Chemistry. Confocal microscopy imaging of bacterial streamers formed in diverse porous architectures (b) with staggered geometry. Image courtesy: Amin Valei (c) with square post pattern. [54] – Reproduced by permission of The Royal Society of Chemistry. Scale bar: (a) 100 µm (b) 50 µm (c) 30 µm. *P. fluorescens* bacteria expressing green fluorescent protein (GFP) appear green. White arrow indicates the direction of imposed hydrodynamic flow in all the images.

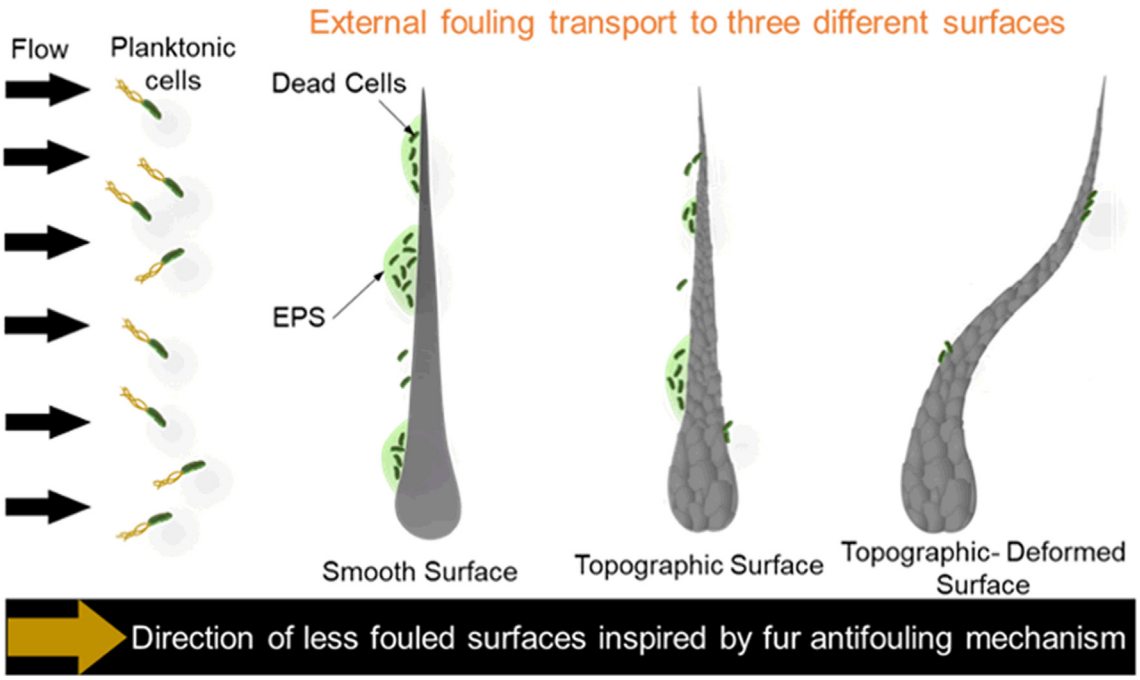

Fig. 10. Schematic illustrating the influence of surface topography and deformation on surface hugging biofilms and streamers. Black arrows indicate the direction of imposed fluid flow.

are typically attractive to biofilms, which in turn leads to streamer generation through shearing of biofilm.

Fur surfaces, on the other hand, consist of rough topography whose fluid flow-induced deformation can effectively change local topography and roughness [149–153], thus changing the initial stages of biofouling, illustrated in Fig. 10. Currently, the role of surface topography and deformation in inducing and affecting biofouling or streamer formation remains unexplored [7]. Scientific knowledge in this arena will provide a promising avenue for designing tailored surfaces fibrous surfaces to control biofouling.

4.5.2. Question of species

The discussion of streamers has been limited to the pure culture of bacterial species; however aggregative forms like biofilms may often comprise of mixed-species [96,154–157]. Thus, accounting for inter-species interactions, along with intra-species interaction will be an interdisciplinary challenge involving the development of experimental imaging techniques to track individual species and its influence in conjunction with other species on streamer morphology. Cell to cell signalling [158] can be expected to impact streamer formation. Moreover, biopolymers or EPS synthesized by each bacterial species has unique material composition [159,160] with respect to water content, nutrients etc. EPS is also pliable with the propensity to deform under hydrodynamic stresses. The structural integrity of the EPS is intimately linked with its origin and flow hydrodynamics. Such deformability may even cause detachment of the streamers. Therefore, the housing of the microconsortia is an intricately complex material of biophysical origin [96] with properties that change dynamically over the course of streamer formation.

5. Conclusions and future perspectives

Previous review articles [11,12,14,15,25,36,157], which addressed the issue of bacterial biofilms, have lacked a thorough and comprehensive take on the phenomena of bacterial streamers. This review article, for the first time, addresses this unique phenomenon of soft, slender flow-mediated structures, *streamers* in-depth, with a cogent identification of the colloidal hydrodynamic fundamentals involved as well as the outstanding grand challenges

remaining in this domain. Based on the identification of these fundamental colloidal hydrodynamic questions, we have proposed the coinage of the generic term "colloidal streamers", which encompasses bacterial/biological streamers as a subset.

Each sub-section of Section 4 is dedicated to an outstanding grand challenge, spanning the evolution of streamers from its initiation to maturation and eventual failure. This emerging domain of research had its beginnings as a biophysical problem concerning fluid–structure interaction; the discovery of abiotic streamers in particle-laden polymeric flows has now significantly expanded this emerging domain. Given the very wide range of streamer formation timescales, a universal understanding of bacterial streamer formation has proved to be elusive, yet the principal pathways of its origin stem from distinctly different aggregative forms of bacteria such as biofilms and flocs. We highlight the critical relationship between the genesis pathway, streamer formation timescales and imposed flow regime through an extensive literature review spanning several decades. Employing the principles and concepts of colloidal physics, we draw parallels between the origin, evolution and morphology of bacterial and colloidal streamers. This juxtaposition is so far restricted to the floc-mediated pathway, and equivalents of biofilm mediated have not yet being reported in the colloidal realm. A critical discussion of the existing characterization techniques of streamers unveils the dearth of non-invasive probing methodologies, which is an interdisciplinary challenge involving spheres of physics, chemists, biology and materials sciences. To reiterate here, understanding the material behavior of bacterial and abiotic streamers is a subject that is still in its infancy. Interestingly, channel geometry can play a critical role in the formation and proliferation of streamers, thus bringing a new dimension into the problem. Such challenges and open questions in the domain of streamers has informed our attempt at this review. Scientific challenges have been identified by distilling and critically analysing the literature spanning across multiple domains of colloids and interfacial science, material behavior and fluid–structure interactions.

Streamers are now understood to impact industrial piping systems, biomedical devices and water filtration units – these applications are likely a severe underestimate of the true economic impact of streamers. As scientific recognition for this emerging domain increases, it is very likely that new and previously left out applications will come to the fore.

CRediT authorship contribution statement

Udita U. Ghosh: Writing - original draft, Writing - review & editing. **Hessein Ali:** Writing - original draft, Writing - review & editing. **Ranajay Ghosh:** Conceptualization, Writing - original draft, Writing - review & editing. **Aloke Kumar:** Conceptualization, Writing - original draft, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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