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Growth and survival of microbes on different material surfaces: Current scenario and future challenges

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ABSTRACT

Biofilms can be defined as an organized group of micro-organisms living within a self-produced matrix of polymeric substances that get attached to several surfaces. It becomes apparent that these microbial collectives are present in practically all environments. Planktonic bacteria can exhibit a 10-1,000-fold increase in antibiotic resistance compared to their biofilm-dwelling counterparts. These bacteria' interactions with surfaces have significant effects on a number of different domains, including the creation of biofilms, biofouling, bioenergy, and infections in plants and animals. The microbial interactions have led to differential gene expression that affects cell behavior and morphology that comprise genes responsible for surface attachment and motility. The formation of biofilm structure is controlled by growth conditions, substratum, and cell surface that ideally provides an environment for the exchange of genetic material between the cells. So far, attention has been gathered on phenotypes as the system utilized by microbes for responding to surfaces is not well known. Hence, the mechanism underlying the promotion and inhibition of cell growth on new classes of materials will help in understanding complement studies and the physiology of microbes adhering to the surfaces.

1. INTRODUCTION

Microbial biofilms are composed of up of closely-knit populations of bacteria that are affixed to surfaces and covered in the extracellular matrix in the environment. Amongst the greatest areas of interest are the ways in which microbes aggregate on a surface and how they can become resistant to pharmaceuticals. Microorganisms create a special structure called biofilm to live in severe environments, including those treated with existing antibiotics. Biofilms are any association of microorganisms where the cells adhere to one another on a surface and are often embedded in an extracellular polymeric substance (EPS) matrix that the organisms themselves produce. This substance, also known as slime, is primarily composed of exopolysaccharides and traces of other organic compounds such as proteins, DNA, and polysaccharides, and it provides a safe environment for the microorganisms to grow [1,2]. The concept of biofilm is originated in 1947 by Antonie van Leuwenhoek, using his primitive but effective microscope found aggregates of animalcule [3]. Nearly all surfaces, including those of medical equipment such as catheters, contact lenses, prosthetics, and surgical implants, frequently develop biofilm. These cells may colonize and spread from the contaminated devices, which could be harmful to human health and raise the possibility of microbial

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infection [2]. Certain traits of biofilm-forming bacteria include greater resistance to antibiotics [1,4]. The majority of the time, bacteria may coexist in mixed-species biofilms, which makes intra- and interspecies interactions more complex. The coexistence of different bacterial species affects the collective behavior in multispecies biofilms, where interspecies interactions are essential to the formation, morphology, and characteristics of the biofilms. Microbes immobilize themselves onto hard surfaces to produce biofilms, which are then utilized by a variety of surfaces [5–7]. In contrast to naturally existing bacteria, this technique of immobilization of microorganisms includes the adhesion of germs that are helpful for a variety of diverse functions [8,9]. The stability of biofilms, their toxicity tolerance against harmful chemicals, their efficiency in treating high volumetric loadings, and the simultaneous existence of anaerobic and anoxygenic metabolic processes within the same unit process are all important characteristics of biofilms that are possibly associated with wastewater treatment [10–12].

Any surface can produce biofilms in three primary stages. Cells attach to a surface in the first stage, assemble to create microcolonies, and then differentiate into a mature structure called a biofilm. After the complete development of biofilm, its disassembly or dispersion takes place through both mechanical and active processes [13–15]. External factors that affect the formation process include temperature, pH, gravitational and hydrodynamic pressures, Brownian motions, the type of surfaces that are inhabited, quorum sensing (QS), secondary messengers, and other signaling molecules. The microbes then proliferate and integrate into a network made of extracellular polymeric molecules that it has created by assembling its own parts. The formation of biofilms, especially during the early attachment stages, is facilitated by a number of surface-related proteins, including OmpA, fibronectin binding proteins, 31 protein A, 32 SasG, 33, 34, biofilm-associated protein (BAP), 35, 36, and numerous additional elements. Some species cannot attach to a surface but can anchor themselves to the matrix or directly to the earlier colonies. Small signaling molecules with the help of cell-cell communication systems mediate this colonization [16,17].

On the other hand, the presence of surface proteins has been observed during the first stages of bacterial adhesion to the biofilm matrix [18]. The location of the biofilm is the most important element influencing its growth. It is possible for biofilms to grow in almost any place where there is moisture and a surface that has at least a modest nutrition supply [4,2,19]. The options are unlimited, but they can be categorized into a number of groups that have been well-researched [20]. The selection of biofilms from them, some of which occur naturally, and others have been influenced by human intervention [21].

The uncontrollably persistent nature of microbial infections is caused by persistent cells and antibiotic resistance, both of which are facilitated by the development of biofilms [22]. Infections that are persistent and recurring are caused by biofilm, which confers increased resistance to antibiotics and becomes resistant to host immune responses. It greatly complicates the therapeutic management of biofilm infections. The most likely causes of antibiotic resistance are decreased antibiotic molecule penetration through EPS, target site mutation, buildup of enzymes that degrade antibiotics, and increased expression of efflux pump genes [23]. Biofilms can be found practically anywhere and are associated with a variety of clinical symptoms. They can be found in living tissues, water channels, pipes, hospital floors, food processing units, and other biotic and abiotic surfaces [24]. Biofilm-associated bacteria are characterized by changes in phenotypic and gene expressions together with resistance to recognized antibiotics, decreased metabolic activity and growth rate, and production of virulence-associated proteins [25].

The scientific community has given biofilm-coated electrodes for microbial fuel cells (MFC)-based bioelectricity production a great deal of attention. It is impossible to overlook the fact that MFC technology appears to be a partial answer to the current energy issue. MFCs are a sustainable energy source that can reliably power modern society while also treating wastewater. This technology can be utilized to provide solutions for powering household appliances, other electrical equipment, and recharging biomedical devices since it recognizes the potential for large-scale conversion of organic waste and biomass into bioenergy [26].

The United Nations established the 2030 sustainable development goals in January 2016 with the aim of attaining progress in the areas of the environment, society, and economy by utilizing cleaner and more environmentally friendly industrial techniques. Since the majority of people still lack access to basic essentials like food, clothing, shelter, and health care despite the rapid growth of the global economy, these aims' most important objectives are the fulfillment of basic human needs and desires. Furthermore, biofilm-producing microbes have a detrimental impact on a variety of food business sectors, including aquaculture, dairy, poultry, and ready-to-eat foods [27]. This can lead to food spoiling, disease outbreaks, and fatalities. Contaminants accumulate in milk processing equipment due to inadequate sanitization and cleaning, which leads to the formation of biofilm, which further becomes a major source of dairy product contamination. Due to the high frequency of biofilm-associated microorganisms and the ineffectiveness of the available antibiotics, it is necessary to develop non-toxic but highly effective antibiofilm agents that target signaling pathways that control a variety of biological processes, including QS, EPS synthesis, biofilm-related genes, microbial motility, adhesion, dispersion, and many others [24]. It will be helpful to examine all the traits connected to biofilm production in order to identify novel inhibitors for the treatment of biofilm and biofilm-forming illnesses. As a result, the microbial biofilm, its properties, and the range of surfaces on which it can grow are the main topics of this review article.

2. BIOFILMS ON SURFACES

It is possible for biofilms to grow in almost any place where there is moisture and a surface that has at least a modest nutrition supply. The options are unlimited, but they can be divided into a number of groups that have been well-researched. Biofilms have chemical and physical characteristics that can be studied. The biofilm matrix develops when the polymeric extracellular substances secreted by the organisms consist of proteins, polysaccharide macromolecules, lipids, nucleic acids, and other biopolymers [28]. They are highly hydrophilic molecules, as they form a three-dimensional (3D) [29]. It is possible for biodiversity to exist inside a biofilm because of the creation of the matrix along with homogeneous gradients, which provides a range of microhabitats. When microorganisms move from a free-living, i.e., nomadic stage to a multicellular sedentary state, continued development results in the establishment of organized communities characterized by cellular differentiation. Biofilm production happens as a result of extracellular environmental cues as well as signals produced by the organism itself [2,30–32]. Researchers who have looked into the production of biofilms have come to the conclusion that it is likely to create a global hypothetical model to describe how they arise.

There are five phases to this biofilm growth model: Individual plankton bacteria migrate and stick to the surface during the first phase [33]. The connected bacteria begin to build biofilms with a thin layer of exopolymeric material when the right conditions are met. A bacterial aggregation and matrix formation result from connected bacteria secreting extracellular matrix (EPS) and adhering to the surface during the second phase. Biofilms completely mature in the third phase, when they build water channel structures and microcolonies and becoming increasingly layered. Finalized biofilms attain the maximum density of cells and operate as three-dimensional communities during the fourth stage. Mature biofilms release bacterial microcolonies from the main population during the fifth phase, which allows the infection to spread to new locations. Antibiotics find it challenging to pierce the matrix and eradicate the buried bacteria because of these biofilms [4] (Fig. 1).

Individual microorganisms are placed on a surface in the case of mobile species, and this marks the beginning point for a major shift in their way of existence, from nomadic free to sedentary. Therefore, diverse constructions such as pilus, cilia, flagella, and fimbria, as well as sticky compounds, contribute to the development of the matrix, hence, the movement capability is reduced. In both scenarios (non-mobile and mobile microorganisms), tiny masses or microcolonies are created, resulting in increased cell-cell contact, cells clustered together are more likely to undergo adaptive phenotypic changes as a result of their increased cell-to-cell contact [34] (Table 1).

Hence, the formation of a monolayer resulted in the development of microcolonies in multi-layered systems. The creation of EPS starts, followed by the establishment of the first monolayer and the subsequent growth of the second and third layers. The formation of the extracellular matrix and the development of the 3D biofilm are two important steps [32]. Finally, the biofilm achieves its mature stage, exhibiting the existence of channels via which nutrients, water, communication chemicals, and nucleic acids may be transported [29]. The biofilm matrix keeps and holds the cells together, allowing for a greater degree of contact, intercellular communication, and the development of synergistic consortia to occur. Therefore, the cells of the biofilm cannot be totally immobilized as they have the ability to move inside it and to get disconnected from it.

Biofilms may also be classified as follows, depending upon the environment in which they are formed, such as natural, industrial, domestic, and hospitable [35]. It is also dependent on the kind of interface where they are created. They may be classified into the following categories, depending on the kind of contact at which they are created [36]. The genus *Lactobacillus* is composed of acidophilic bacteria that denature the proteins in dentin. Moreover, the genus Actinomyces contains bacteria that are aciduric and proteolytic in nature, such as *Actinomyces viscosus*, *Actinomyces odontoliticus*, and *Actinomyces naeslundii,* which are three of the species that have been identified. Biofilms are also present in a solution of black water such that treating home wastewater by nitrifying microorganisms can help in oxidizing nitrite, ammonium, and autotrophic nitrifying bacteria that dwell in biofilms adhering to tubes [37].

When it comes to the ammonium-oxidizing bacteria in these biofilms, the dominating species belongs to the genus *Nitrosomonas*, which can be found in abundance over the whole biofilm matrix [38]. The bulk of the components in this group of nitrite oxidants are members of the genus *Nitrospira*, which are found in the biofilm's interior. Unlike other types of biofilms, subaerial types of biofilms (SABs) are identified by patchy development on rock-solid material surfaces or urban structures. These biofilms include dominating families of algae, fungus, heterotrophic bacteria, protozoa, cyanobacteria, and tiny animals, among other microbes and fungi. SAB biofilms, are home to chemolithotrophic bacteria, which are capable of using inorganic mineral compounds as a source of food and energy [39,40].

The fact that the mineral–SAB interface affects ecosystem-scale processes like primary production, the stability and productivity of food webs, and biogeochemical cycling is also becoming more and more evident. These processes are governed by microscale interactions that take place within the mineralosphere. Thus, the ecological interactions between minerals and SABs within the framework of ecosystem function potentially reflect some of the most significant associations in dry terrestrial settings and land colonization, supporting a fundamental and pivotal shift in the development of microbes [41].

The Earth's crucial zone, a small layer where physical, chemical, and biological processes interact to support life on Earth, is home to the mineral SAB air interaction system [42]. The SAB's color, a ubiquitous

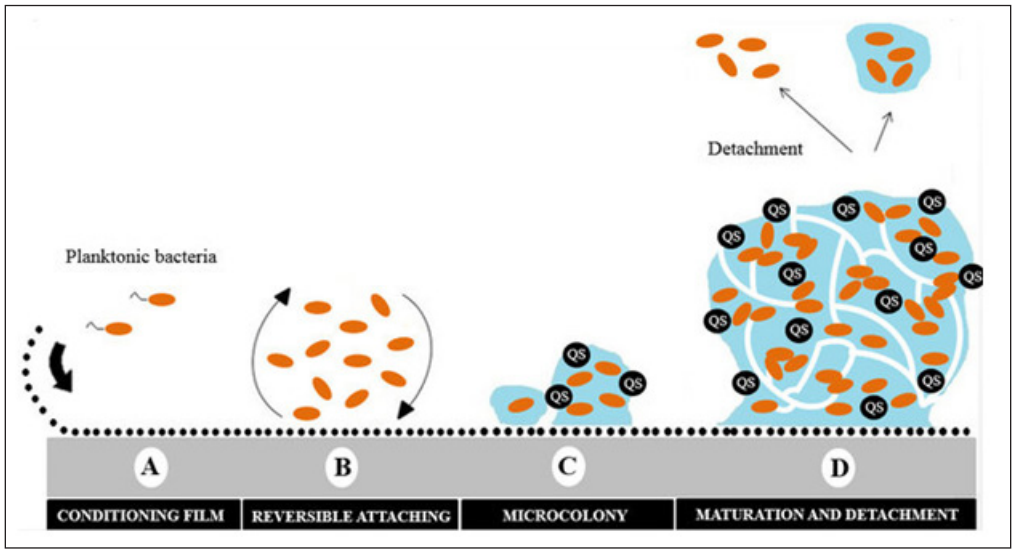

Figure 1. Schematic representation of biofilm development on a solid surface. Adapted from Moura *et al.* [120].

phenotypic trait in the microbial communities near the mineral–air interface, is crucial for determining the nature and function of these survival strategies. SAB communities exhibit the functional ability to sustain a self-sustaining community at the community level, even in the face of the aforementioned circumstances and low biomass. The current suite of omics-based technologies can be fully utilized to fully understand the complicated complexity of interspecies interactions in SABs [41]. SAB contains a variety of microbial species, such as *Blastococcus, Modestobacter, Apatococcus, Spirosoma, Rubellimicrobium, Thuepera, Deinococcus, Coccomyxa, Rubrobacter, Chroococcidiopsis, Halococcus, Kocuria, Salinimicrobium, Pontibacter, Halobacterium, Marinobacter, Halomarina, and Thuepera. Truepera, Chroococcidiopsis, Rubrobacter, Capnobotryella, Scytonema, Thiobacillus, Malikia, Ochrobactrum,*

Table 1. Survival of various microbes on different surfaces.

Class	Organism	Survival (Duration)	Surfaces	References
DNA virus	*Adenoviruses*	7–60 days	Aluminum	[122]
		1 hour–8 weeks	Stainless steel	[40]
		9–49 days	Plastic	[123]
		1 hour–12 weeks	Glass	[123]
		7–60 days	Paper	[123]
		1 hour–60 days	Ceramics	[123]
		1 hour–8 weeks	Vinyl asbestos	[124]
	Herpes simplex virus 1	48 hours–6 days	Plastic	[125]
	Herpes simplex virus 2	4.5 hours	Plastic	[126]
	Poxviruses	3–56 days	Glass	[123]
		1–56 days	Steel	
	Cytomegalovirus	1–8 hours	Plexiglass	
		15–240 minutes	Gloves	
		1–2 hours	Cotton blanket	
RNA virus	*Human CoV-OC43*	2 hours	Aluminum	[127]
	SARS-CoV-1	72 hours–9 days	Plastic	[128]
		2 days	Disposable gown	
		24 hours	Cloth	
		24 hours	Paper	
		48 hours	Stainless steel	
		8 hours	Copper	
	MERS-CoV	8–48 hours	Steel	[129]
		8–48 hours	Plastic	
	SARS-CoV-2	4 hours	Copper	
		24 hours	Cardboard	
		72 hours–8 days	Stainless steel	
		72 hours–4 days	Plastic	
		30 minutes–2 days	Paper	
		1 day	Wood	
		1 day	Cloth	
		4–7 days	Surgical masks	
	Hepatitis B-virus	More than 7 days	Silanized tubes	[130]
		More than 14 days	Cotton	
Gram-positive bacteria	*Staphylococcus epidermidis*	6–28 days	Cloths	[131]
		More than 7 hours	Glass	
		41–90 days	Plastics	
	Streptococcus pneumoniae	3 days–1 month	Plastic	[132]
	Streptococcus pyogenes	2–24 hours	Tomatoes	[133]
		2–24 hours	Ceramic	
		2–24 hours	Stainless steel	
		2–88 hours	Metal	

Continued

Class	Organism	Survival (Duration)	Surfaces	References
Gram-negative bacteria	*Proteus mirabilis*	4 hours–9 days	Cloths	[134]
		1–26 days	Plastics	
	Pseudomonas aeruginosa	5 hours	Glass	[135]
		9 hour–10 days	Plastics	
		5 days	Stainless steel	
		2 hours	Cotton	
	Shigella dysenteriae	4 hours	Cloth	[136]
		1.5 hours	Plastic	
		2 hours	Aluminum	
	Serratia marcensens	1 hours–7 days	Cloths	[137]
		1–10 days	Plastics	
		7 hours–11 days	Glass	
Fungi	*Candida auris*	Less than 14 days	Plastic	
		Less than 7 days	Steel	[123]
	Candida krusei	1–30 days	Cloths	
		3–7 days	Plastics	
	Candida parapsilosis	2–30 days	Cloths	
		More than 14 days	Glass	
		More than 28 days	Plastics	
	Candida tropicalis	1–30 days	Cloths	
		6–18 days	Plastics	
	Fusarium spp.	More than 120 hours	Aluminum	
		4–10 days	Cloths plastics	
		6–30 days	Maize stalk residue	
	Saccharomyces cerevisiae	More than 48 hours	Cardboard fibres	
		More than 48 hours	Plastic	
		Less than 0.5 minutes	Copper	
		5 minutes	Stainless steel	

Knufia, Leptolyngbya, Sarcinomyces, Nitrogenbacter, Thioclava, Thiobacillus, Rhodovulum, Desulfuromonas, Chroococcidiopsis, Leptolyngbya, Nostoc, Trebouxiophyceae, Nitrososphaera, Nitrospira, Novosphingobium, Nitrobacter, Stenotrophomonas, Pseudomonas, Crosiella, Rhodobacter, Aurantiamonas, Acidimicrobium, Ferrimicrobium Bacillus, Phormidium, Aurantiamonas, Thiobacillus, and *Thioclava* [43]. In a study, photocatalytically reactive subaerial surfaces revealed the presence of novel fungus strains recognized as *Constantinomyces oldenburgensis* [44].

Many of the bacteria that are known to be the causal agents of human illness may be found living in biofilms [45,46]. *Vibrio parahaemolyticus, Vibrio cholerae, Vibrio fischeri, Streptococcus mutans,* and *Legionella pneumophyla* are only a few of the bacteria that may cause disease [47]. Another class of microbes is present in venous catheters used in hospitals. Explanted central venous catheter biofilms constitute an incredible variety of gram-negative bacteria and gram-positive bacteria, as well as other microorganisms, which have been identified from the biofilm. Furthermore, biofilms formed by gram-positive bacteria have been found in venous catheters by several scientific studies, including *Corynebacterium* spp. *Enterococcus faecium* spp., *Enterococcus* spp., *Staphylococcus* spp. *Staphylococcus aureus,* and *Streptococcus* spp. [48].

In the world, we wonder how biofilms interfere with the functioning of industry, and we can say that they cause clogs in pipes, damage to equipment, interference with processes like heat transmission while covering exchanger surfaces, and corrosion of metal components. The formation of film in the food sector has the potential to cause serious public health and operational issues [49]. Pathogens associated with biofilms have the potential to infect food items with pathogenic microorganisms, resulting in major public health consequences for consumers. Flagella and membrane proteins are utilized by this pathogen in the early stages of biofilm development [50,51].

Food-borne diseases can result from infections or intoxications linked to bacterial biofilms on food matrixes or industrial equipment. Plants that digest food have biofilms that can produce toxins. As a result, plenty of food-borne bacteria might attach themselves to the contact surfaces found in these places, raising the possibility of bacterial food-borne disease [52]. From there, they have the potential to contaminate a food matrix, leading to one or more intoxications (in the event of an outbreak). Its potential as a foodborne pathogen in a number of food groups, including water, milk, meat, fruits, and vegetables, has been underappreciated. Food safety issues can arise from the use of chemical preservatives, which are frequently employed to inhibit the growth of microbes found in food sources [53].

Biofilm-associated diseases encompass both tissue- and device-related infections, such as endocarditis, meningitis, kidney infections, periodontitis, osteomyelitis, rhinosinusitis, and nonhealing chronic wounds [54]. The European Centre for Disease Prevention and

Control reported that up to 37,000 persons die as a result of healthcare-associated infections, which affect approximately 4.1 million patients yearly on average in European hospitals [55]. The National Institutes of Health estimates that biofilm-forming microbes are responsible for around 65% and 80% of human acute and chronic infections, respectively [56–58]. As biofilms are formed on steel surfaces of slicing machines, preventing them from being cut. Biofilms formed by *Listeria monocytogenes* have been found in liquid milk and dairy products obtained from milk in the dairy sector. The presence of dairy wastes in containers, tanks, pipes, and other equipment encourages the formation of biofilms by this pathogen, which utilizes the residues as accessible nutrition [59,60]. It is possible to find bacterial biofilms in food industry facilities, like on floors and drains, as well as on food surfaces like vegetables, fruits, meats, and in low-acid dairy products such as yogurt [61,62].

When *Pseudomonas aeruginosa* produces extracellular chemicals, they are utilized in the production of the polymeric matrix that adheres to a significant quantity of inorganic materials, such as stainless steel, resulting in the formation of a biofilm. *Pseudomonas* may cohabit in a biofilm with other dangerous bacteria, such as *Salmonella* and *Listeria*, and this is known as coexistence [34]. They are the initial causative agents of bacterial etiology and outbreaks of foodborne illness because they are the most prevalent. Several scientific investigations have shown that *Salmonella* may attach itself to concrete, plastic surfaces, steel, and food processing plant facilities, forming biofilms on these surfaces [63].

One of the key elements in the development and maintenance of the structure and properties of the biofilm is the extracellular matrix. The extracellular matrix is made up of water and EPS, primarily polysaccharides, proteins, and DNA [64]. The rdar morphotype, so called because of the red, dry, and rough look of colonies formed on agar plates containing Congo red dye, has been identified as the most well-studied biofilm phenotype for Salmonella. Congo red concentrates within the rdar colony due to the presence of cellulose, the β1-4-linked glucose polymer, and proteinaceous curli fimbriae, which are functional amyloid structures resistant to pH, detergents, and proteases. Together, curli and cellulose serve as the extracellular matrix scaffold, facilitating short-range connections between cells and long-range interactions spanning the colony's whole length. It has been demonstrated that BapA, a large Salmonella protein with several repeating sequences, contributes to the pellicles' strength and integrity [65] (Fig. 2).

2.1. Surface-Associated Growth

The mechanism followed by microbes for adherence differs depending upon the method of attachment. There are three phases to the production of biofilms: early, medium, and late. Reversible and irreversible adhesion steps make up early stage biofilms. Planktonic bacteria use surface appendages like flagella and pili to approach and connect to the surface during the reversible adhesion stage. The bacteria-surface interaction can be readily overcome by the bacteria's motility, allowing them to revert to their planktonic condition. To covalently connect to the surface and gradually complete the firm attachment, initially attached bacteria release EPS during the irreversible adhesion stage [66]. EPSs are used by connected bacteria to attach to surface-associated cells, and they can also aggregate via type IV pili-mediated twitching motilities in the early stages. Bacteria grow in number and release more EPSs, which eventually coat the bacteria's surface in a thin layer of water and produce microcolonies [67]. Microcolonies develop into mature colonies. The final phase involves the biofilms reaching maturity and separating. When a biofilm reaches maturity, its compact structure and coordinated functions resemble a 3D network structure. Once fully developed, biofilms burst, allowing bacteria to spread out into planktonic forms and initiating a fresh cycle of biofilm formation. A similar report documented that *Pseudomonas fluoresces* has been observed on glass surfaces [68]. Further, in the case of continuous culture growth, kinetics on the surface differs from that of the bulk phase. In the case of high dilution rates, the productivity of microbes increases by itself [69,70]. It happens because of the fact that microbes still remain intact to the surface, i.e., beyond the maximum dilution rate. Bacteria in huge amounts can be utilized as a buffer to reimburse the biomass loss as it changes dilution rates.

2.2. Surface Properties and Mechanisms Used by Bacteria for Sensing Surfaces

The bacteria follow a chemotaxis system to measure the concentration of ions and small molecules and to study the mechanism affecting bacterial mobility. A study suggested that bacteria can sense variations in spatial changes in particular conditions [71]. The intriguing topic of "How does a microbe know it is on a surface?" is raised by the fact that the initial stage in the formation of a bacterial biofilm is contact with the surface on which the microbe would eventually build this community.

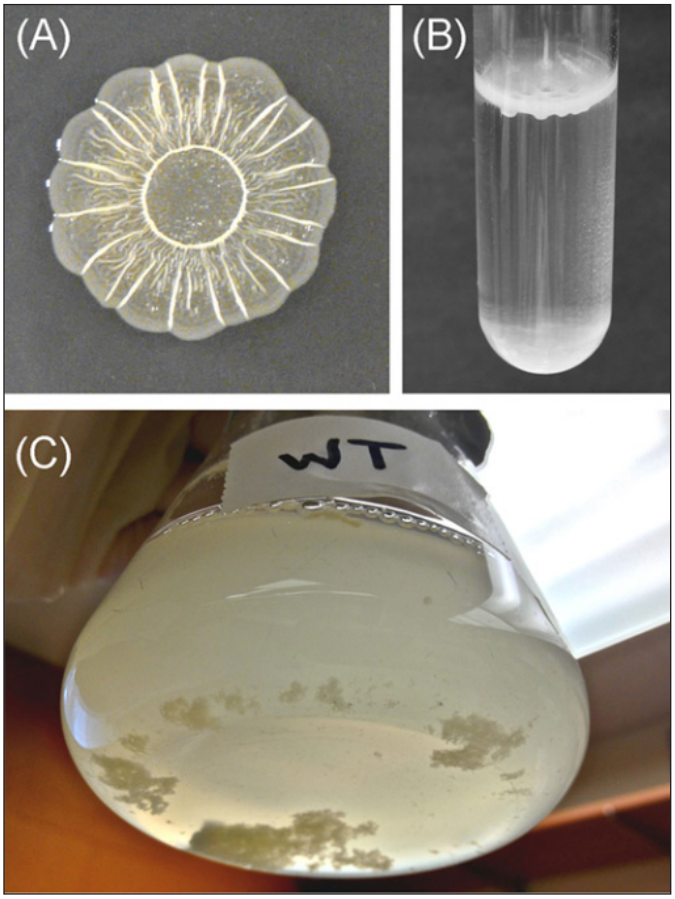

Figure 2. Examples of *Salmonella* biofilm formation. (A) Colonies grown for 48 hours at 28°C on solid 1% tryptone media form the characteristic surface patterns of the red, dry, and rough (rdar) morphotype. The colony appears red when the media is supplemented with the dye Congo red. (B) Pellicle formation at the air–liquid interface of a 1% tryptone liquid culture. (C) *Salmonella* form multicellular aggregates and planktonic cells within the bulk liquid phase of a flask culture. Adapted from MacKenzie *et al.* [65].

For decades, researchers studying biofilms have been deeply intrigued by this query. According to Zobell and Allen [72] theory, bacteria may require a bacterial film or nutrients to convey the signal that allows them to choose an appropriate surface for attachment. Swarms and biofilms are examples of bacterial communities where cells interact with one another in a variety of ways.

The term "surface sensing" refers to a wide range of behaviors, such as the mechanisms underlying the device that permits the perception of a surface's close proximity, the device that selects various surfaces for attachment, the biochemical chain reaction, and the physical effects that ensue from surface recognition. Bacterial communities with tight cell packing allow for a concentration rise of tiny molecules that facilitate information flow between cells and cause physiological changes [73]. Certain bacteria changed how they produced polysaccharides and even how their cells looked. Numerous other physiological variations have been discovered thanks to developments in high-throughput screening techniques, global transcriptome and proteome analysis of bacteria, and identification of the genes necessary for biofilm formation. In addition, modifications in the extracellular polysaccharide and organelle formation that take place in bacteria in response to the biofilm community's presence and expansion linked with a surface [71].

The development of chemical gradients near surfaces facilitates the chemical information transmission between biofilms and surface-attached communities. Comparing biofilms to planktonic cells that are free to float in liquids, there is also an increase in lateral gene transfer. It should come as no surprise that surface sensing has historically been interpreted differently depending on the type of microorganism. Although the mechanics of surface sensing in microbes have not been thoroughly studied, this subject has been discussed in the literature using a range of model microorganisms [74]. Additionally, surface-associated growth induces phenotypes that promote "natural competence" in *Vibrio cholerae*. Myxobacteria cells that are associated with biofilms even exchange outer membrane proteins and lipids [75] (Figs. 3 and 4).

McCarter *et al.* [76] concluded that *Vibrio parahaemolyticus* has a "flagellar dynamometer," or a mechanism by which, upon surface contact or in conditions of high viscosity, decreased rotation of the polar flagellum starts a signal transduction pathway that in turn causes swarming motility with lateral flagella. The concept behind this model is that when this appendage binds to the substratum, it restricts the rotation of the flagella, signaling that the microbe has made contact with a surface. This conclusion is corroborated by the finding that planktonic cell incubation in a highly viscous liquid also initiates the "surface" programme. *Staphylococcus aureus* makes strong binding with surface ligands to receptors on one side of the cell surface and further responds by localizing the receptors to the associated surface. It is also reported that cells have the ability to sense and allow spatial changes that modify the attachment of ligands to receptors by surrounding the receptors in nearby regions [77]. This indicates the ability of bacteria to recognize signals from different subsets where the receptor lies. This study truly explains the association of bacteria and chemical gradients during the formation of biofilm. As *E. coli* attaches to the surface, the pH shifts in decreasing order reaches below the bulk liquid phase, and stays for at least 72 hours. A Cpx two-component system plays a critical role in maintaining cell surfaces and pH-sensing responses [78].

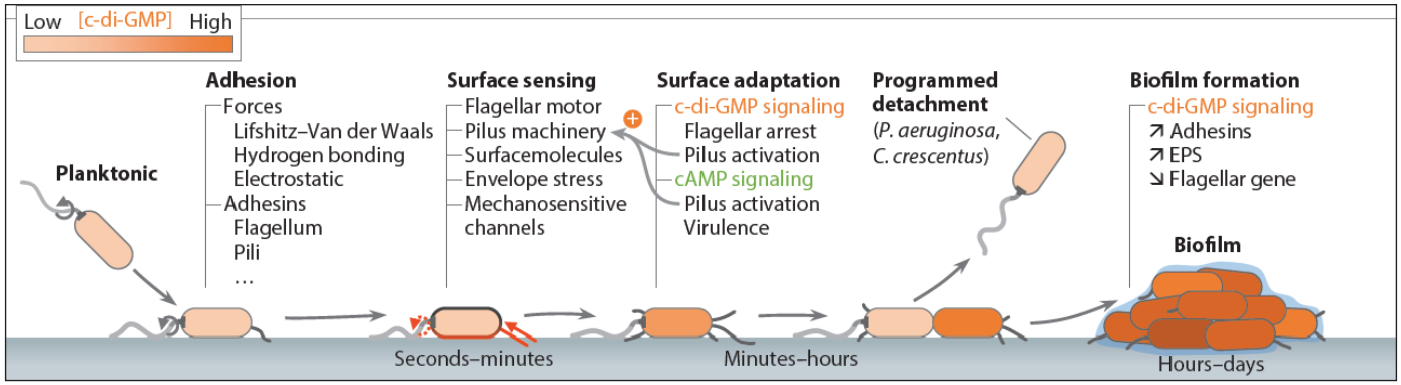

Figure 3. Timeline of bacterial surface adaptation leading to biofilm formation. Adopted from Laventie and Jenal [121].

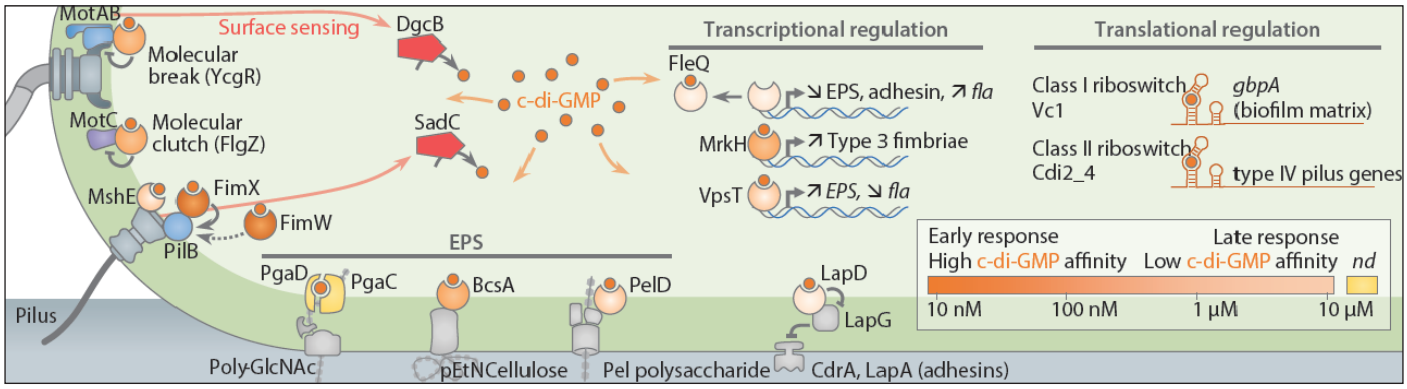

Figure 4. Overview of surface-sensing and adaptation mechanisms. Adopted from Laventie and Jenal [121].

Moreover, similar works have been concluded that *E. coli* controls the assembly of pili and regulates its expression [79]. Another study showed sensing of osmolality in gram-negative bacteria by using OmpA which brings variation in other genes that are involved in transcription. Furthermore, repression in cellulose production is regulated by the OmpA gene via the Cpx pathway and enhances the formation of *E. coli* [80–82]. The presence of extracellular fibrils is polymeric in nature that involved in attaching bacteria to different surfaces [83]. Water and EPS, mainly polysaccharides, proteins, and DNA, make up the extracellular matrix. Identification of the matrix's constituent parts is necessary for its characterization, as is the calculation of the relative concentration of each EPS component and an explanation of their physicochemical characteristics and interactions. Infrared spectroscopy examination of biofilm provides details on the chemical composition of the matrix and the relative amounts of various EPS. The biofilm's reactivity to several EPS-targeting hydrolytic enzymes provides information about the matrix's composition and the roles that matrix constituents play in maintaining the structure's integrity. Determining the matrix composition can also be accomplished through the extraction and purification of EPS from the biofilm using both chemical and physical methods [84].

Another study revealed that anionic material could be used for attaching freshwater bacteria and cations, which influences contractions in initial adhesives, thereby decreasing the distance between the cell and substratum [85]. Hence, cross-linking of cations with anionic polymer leads to contraction. However, a study suggests the role of lectins in inhibiting attachment, whereas glucosidases reduce attachment for *Pseudomonas fluorescence*. Also, lectins showed affinity to bind with polysaccharides on the cell walls and would decrease the attachment sites [86]. Another study revealed the effect of polysaccharides on studies and interaction with *P. fragi* [87]. Furthermore, a study on non-motile and motile strains of *P. fluorescens* depicted increased cell attachment and flow in motile strains as compared to non-motile. The study also showed vacant seed areas that no longer recognize substratum as mobile strains, which results in the formation of biofilm by non-motile organisms. This suggests a critical role of flagella attachment during the early stages, thereby turning off the force exerted by the substratum [88].

Further findings on different cell surfaces like EPS, LPS, proteins, and fimbriae display an essential role in the processes of attachment. There are different cell surfaces having nonpolar sites that are attached to hydrophobic substrata, whereas lipopolysaccharides play an essential role in attachment to materials that are hydrophilic in nature.

The hydrophobic–hydrophilic structure of interacting surfaces is a key factor in microbial adhesion, as demonstrated by a body of experimental evidence. Enhanced hydrophobicity of the cell surface may facilitate surface approaching and activate the specific forces responsible for the irreversible adhesion. There was an increase in cell-to-cell adhesion when bacteria became more hydrophobic; hence, cell surface hydrophobicity may have contributed to the cells' immobilizing power [89]. The role of hydrophobic interactions between microorganisms and supports in the microbial adhesion process has not received much attention in research to date, and little data is currently available to characterize quantitatively how much the hydrophobicities of bacterial and support surfaces contribute to microbial adhesion. A model that describes how microbial adherence depends on the system's relative hydrophobicity was created using the idea of the relative hydrophobicity of cell-to-support interaction. The suggested model has the ability to establish a clear link between microbial adherence and the surface thermodynamics related to hydrophobicity. It was found that increased cell surface hydrophobicity would favor cell adhesion on both hydrophilic and hydrophobic support surfaces [90].

However, the role of flagella is only highlighted to surpass the opposing forces rather than to perform as adhesives [91]. Therefore, the attachment will take place on surfaces that are more hydrophobic, rougher, and coated by surface “conditioning” films. An increament in water temperature, flow velocity, and nutrient concentration also adds to the increased attachment. Cell surface properties, mostly the presence of surface-associated polysaccharides, flagella, and fimbriae, are essential and can possibly give a competitive advantage for one organism where a mixed community is present [46,92].

Bacterial cell appendages adhere to surfaces when they get close to them. Flagella facilitate adhesion; they stick especially to hydrophobic surfaces because they are hydrophobic. Adhesion depends on both the rotational ability and the presence of flagella, since *E. coli* mutants without functioning flagella have trouble forming biofilms and separate more quickly than the wild-type. On the other hand, it was discovered that the presence of flagella decreased adherence in *Caulobacter crescentus*, demonstrating the intricacy of the adhesion mechanism. Once connected, flagella which result from impeded rotation can communicate with the cell to indicate surface contact [93].

3. PHYSICAL SURFACE PROPERTIES OF VIRAL PERSISTENCE

In 1892, the discovery of the first virus was accomplished [94]. Efforts have led to understand the viral survival in various environments and to evaluating the impact of surface properties on their viability. Various factors influencing surface properties are absorption, porosity, surface hydrophobicity, and so on. All viruses have their own way of interacting with the surface in a unique way. So, there is no prerequisite for designing a specific type of virus with an altered design having a specialized antiviral surface. The persistence of the virus is influenced by a number of factors that not only include environmental conditions but are also altered by relative humidity, temperature, and how they differ in absorbing onto different surfaces. These factors can be considered in designing an antiviral surface [95,96].

Biofilms have already been recognized as a common cause of bacterial infections from the perspective of public health [46]. Additionally, generated EPS has been proposed as a potential defense against viruses, particularly phage penetration, in biofilms [97]. Recent research has shown that viral particles can enter the EPS structure of mucoid biofilms even in the absence of particular enzyme processes. Once inside the polymeric matrix, the viruses may benefit from the unique "biofilm lifestyle" and defence against environmental stressors such desiccation or other antimicrobial agent effects [46]. Furthermore, protected immobilized viral particles may be released into the environment by biofilm erosion or sloughing. These particles will then come into touch with their intended host, starting the viral infectious cycle. The speeds at which viruses attach to biofilms can differ significantly and rely on a variety of parameters, including the properties of the biofilm or virus (size, shape, and isoelectric point), as well as the concentration of viral particles [98].

According to a variety of studies, biofilms have the ability to capture and hold onto virus-sized particles, creating a possible reservoir for bacterial or human infections. Biofilms are seen in natural settings where microbial cultures are typically composed primarily of prokaryotes with a little amount of eukaryotes. Though there has been experimental evidence of virus attachments to biofilms and very little

pathogenic virus contamination of natural biofilms, biofilms should be viewed as a reservoir of protection from pathogenic viruses, which may be the cause of many chronic viral infections. Various studies have been reported the antiviral surface properties that show virus absorbance [95]. Also, absorbent surfaces like cardboard and cotton provide more protection against droplets containing the virus. A study reported the survival of SARS-CoV on two different personal protective equipment (PPE) gowns were in the hospital, gowns were in the hospital, which are cotton and fluid-repelling disposable gowns. The results confirmed the presence of virus droplets absorbed by cotton cloth, and there was no evidence of viable virus after 1 hour. However, the persistence of the virus was seen on disposable gowns after 24 hours. Further, an outer fluid layer in medical devices and PPE gowns can offer more advantages [99]. Another study on SARS-CoV-1 and SARS-CoV-2 showed virus persistence on cardboard at 21°C–23°C and 40% humidity as compared to stainless steel and plastic [100].

A significant role is played by porous inmate surfaces in the survival of the virus and studies have distinguished the time and persistence of viruses on different types of surfaces, such as porous and non-porous surfaces [101]. There are some reports which suggest longer persistence of the virus on non-porous materials than on porous surfaces, but few exceptions still exist. A study on the influenza A virus reported that in the case of humid conditions (35%–40%), the virus stayed longer than 24–48 hours on plastic and stainless-steel surfaces [102]. However, on porous surfaces, the number of particles was less after 8–12 hours, such as paper or cloth. A study concluded from the observations that because of complete drying on porous surfaces resulted in less virus persistence. The report further suggested the persistence of the SARS-CoV-2 virus on a surgical mask even after 7 days, while no virus was detected on surfaces like plastic or stainless steel after a week [31,103].

Surface hydrophobicity factor can also alter viral persistence on different surfaces [104]. It is also known that the outer layer hydrophobicity of proteins present in capsids can alter interactions with the environment and solid surfaces [105]. An understanding can be developed through these interactions, which is essential for regulating and designing antiviral strategies and environmental transmission. Different computational and environmental experiments have helped in determining the hydrophobicity of viruses [106]. Various studies have been reported the sorption of hydrophobic viruses on surfaces coated with hydrophobic sorbents preferred by viruses having hydrophobic protein outer layers. However, hydrophilic surfaces are favored by hydrophilic viruses for absorption [107].

Biofouling can be defined as the colonization of microorganisms such as bacteria in the aquatic environment [108]. An understanding of this process and how it can be prevented has been a keen interest in various biofilm studies, yet it still lacks more research so far [109]. Microorganisms like barnacles, mollusks, encrusting bryozoans, and tube worms are a few examples of calcareous fouling microbes, whereas non-calcareous fouling organisms include hydroids, seaweed, and slime [110]. It poses a serious threat to the maintenance of mariculture, cooling large industrial equipment by repeated water cycles. This phenomenon occurs in oil pipelines carrying oil, cutting oils, and hydraulic oils. The attachment of microorganisms can be prevented using nontoxic anti-sticking coatings, which are made of organic polymers [111].

4. MOLECULAR BIOLOGY PROCEDURES

Earlier, scanning confocal laser microscopy was used to scan the specimen in one plane using a laser beam. Also, the image is processed and analyzed by a computer. Nowadays, various reports display a variety of molecular methods to study the composition and diversity of biofilm communities [112]. Techniques such as hybridization with 16S/23S rRNA probes can be used to characterize bacteria forming biofilms in oil fields, trickling filters, and drinking water [113]. Furthermore, if biofilm structures can be preserved, then taxonomic types can be identified through their distribution, and the characterization of individuals will be possible within the community. Different approaches, diversity, and composition of a community are applied in a hydrothermal vent system, such as microbial mats made from sea sediments and wastewater treatment reactors. A study concluded by Muyzer and Ramsing [114] reported that, hydrothermal vent biofilms in an experiment where restriction fragment length polymorphism analysis was carried out using 16S rRNA genes.

Microelectrodes are very beneficial in providing information on biofilm activity and structure. A precision current is passed to provide a spatial resolution of concentration in the range of 25–100 [115]. Measurements from the microsensor include pH, sulfide, and oxygen. Moreover, physiological processes can be evaluated by measuring environmental and nutrient gradients from the sensor. These evaluations can help to link the chemical microenvironment in the presence of specific taxonomy of organisms. The levels of hydrogen sulfide, along with pH and oxygen gradients, are analyzed using microelectrodes followed by cold freezing the samples in liquid nitrogen. Later, the section probed with fluorescently labeled phylogenetic 16S rRNA probes [116].

5. NEW OPPORTUNITIES FOR MATERIAL SCIENTISTS, CHEMISTS, AND ENGINEERS

An understanding of microbes with different surfaces is yet not much studied. This topic deals with multidisciplinary approaches as it creates a platform for microbiologists, chemists, material scientists, and engineers to collaborate and study different areas such as classifying properties of surfaces sensed by microbes, exploring molecular mechanism and their biochemical responses to sense various surfaces, determining how to alter surface properties by changing morphology and varying energetics to get the desired response. The area that holds an advantage from the development of physical sciences is the conditioning layer of protein that promotes bacterial attachment to a surface. However, conditioning layers can lead to the rendering of surface chemistry, which results in the short lifespan of antimicrobial surfaces [117]. Studies require bacterial-surface interactions to prevent the formation of conditioning layers. So, engineers, along with material scientists, can solve this issue but might face difficulty in measuring cellular responses, at the time of microbe-surface interaction, i.e., changes in gene expression. However, with advancing technology, fluorescent reporters can be measure varying levels of gene expression. A study was conducted to measure the yellow fluorescent protein expression, which controls the changes in the gene coding for flagellin protein [118]. Nowadays, surface-enhanced Raman scattering helps in localizing peptide-guided nanoparticles to the bacterial membrane and exploring the chemistry of how bacterial communities and genetic profiling work. The role of microbes surface sending is not well understood at the cell biology, biochemistry, and physical chemistry levels. The use of physically and chemically defined substrates, along with the latest biochemical and analytical techniques, can help us guide applications in the fields of biomedicine, food safety, industrial processing, and agriculture [119].

6. CONCLUSION

The intricate process of bacterial adhesion and biofilm formation is governed by the interaction of topographical surface features,

physicochemical, mechanical, and environmental factors. This review offers an in-depth overview and understanding of the characteristics that influence bacterial adhesion. The effects of various surface characteristics, bacterial motility, or the surrounding hydrodynamic conditions on the bacterial sensing and binding behavior on surfaces have not been taken into account in a large portion of the studies conducted to date. Crucially, before bacteria bind, bare surfaces are really covered in conditioning films of organic and inorganic materials. This has a substantial impact on the binding behaviors of bacteria. Thus, research projects that assess the effect of many surface parameters on bacterial adhesion are essential to improve understanding rather than focussing on a single surface characteristic and its effect on adhesion. Moreover, the identification of strategies and mechanisms that biofilms adapt to evade powerful antibiotics and the application of environmentally benign biological, physical, and chemical techniques to disrupt biofilm communities are equally noteworthy. Surface nanopatterning and its hybrid approach with bactericidal chemicals hold considerable potential to offer more sophisticated treatments for biofilm-related fouling in commercial or medical fields.

7. AUTHOR CONTRIBUTIONS

All authors made substantial contributions to conception and design, acquisition of data, or analysis and interpretation of data; took part in drafting the article or revising it critically for important intellectual content; agreed to submit to the current journal; gave final approval of the version to be published; and agree to be accountable for all aspects of the work. All the authors are eligible to be an author as per the international committee of medical journal editors (ICMJE) requirements/guidelines.

8. CONFLICTS OF INTEREST

The authors report no financial or any other conflicts of interest in this work.

9. ETHICAL APPROVALS

This study does not involve experiments on animals or human subjects.

10. PUBLISHER'S NOTE

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11. USE OF ARTIFICIAL INTELLIGENCE (AI)-ASSISTED TECHNOLOGY

The authors declares that they have not used artificial intelligence (AI)-tools for writing and editing of the manuscript, and no images were manipulated using AI.

12. DATA AVAILABILITY

All the data is available with the authors and shall be provided upon request.

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