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REVIEW ARTICLE
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Harnessing Bacteriophages: A Promising Approach to Combat Foodborne Pathogen Biofilms

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ABSTRACT

A biofilm is a community of microorganisms that adhere to surfaces and are protected by a polymeric matrix they produce. Several pathogenic bacteria that form biofilms, such as *Clostridium perfringens*, *Staphylococcus aureus*, species of *Vibrio sp.*, *Bacillus cereus*, *Salmonella sp.*, *Clostridium botulinum*, *Shigella sp.*, *Escherichia coli, Campylobacter sp.*, *Yersinia sp.*, *Listeria sp.,* and *Aeromonas* sp. can cause foodborne disease outbreaks. The formation of biofilms by these pathogens increases their resistance to extreme environmental conditions and cleaning agents, posing significant challenges in the food industry. Biofilms not only threaten food safety but also increase production and handling costs. Conventional methods for eliminating biofilms are often ineffective, necessitating alternative approaches. The use of bacteriophages, viruses that specifically attack bacteria, shows excellent potential as antibiofilm agents. Bacteriophages can significantly reduce the number of biofilm-forming bacteria through lytic mechanisms on surfaces such as stainless steel, rubber, and fresh vegetables. Therefore, bacteriophages are expected to be implemented as innovative solutions to control biofilms in food and non-food industries, enhancing overall food safety. This review aims to explain in detail the potential of bacteriophages in combating biofilms of foodborne pathogens.

Keywords: Biofilm, Foodborne diseases, Food safety, Bacteriophage

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INTRODUCTION

The prevalence of unsafe food due to contamination by pathogenic bacteria leads to various foodborne diseases (Gallo et al., 2020). According to the World Health Organization (WHO), foodborne diseases are infectious or toxic diseases caused by consuming contaminated food or water. These diseases include intoxication (food poisoning caused by toxins produced by pathogens), infection (ingestion of food containing pathogens), and toxicoinfection (toxin production when pathogens grow in the human intestine) (Lennard, 2020; Gourama, 2020; Abebe et al., 2020). Several bacteria commonly contaminating food sources include *Clostridium perfringens*, *Staphylococcus aureus*, species of *Vibrio sp.*, *B. cereus*, *Salmonella sp.*, *Clostridium botulinum*, *Shigella sp.*, *E. coli*, *Campylobacter sp.*, *Yersinia sp.*, *Listeria sp.*, and *Aeromonas* sp. (Odo et al., 2021; Balta et al., 2021; Sheng & Wang, 2021; Bendary et al., 2022).

Pathogenic bacteria can survive in extreme conditions by forming biofilms (Liu et al., 2023). Biofilms are defined as accumulations of microbial cells that adhere to and grow on abiotic or biotic surfaces (Kumar et al., 2020).

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Typically, biofilms adhere to solid surfaces of materials such as stainless steel, rubber, or plastic (Carrascosa et al., 2021). The structure of biofilms consists of various components, including extracellular polysaccharides (EPS), proteins, and DNA (Treccani, 2023). In an industrial context, biofilm removal is often carried out using chemicals or antibacterial agents to lysing the biofilm. However, this approach presents new challenges, as bacteria can resist these agents and leave residues that are unsafe for consumption and harmful to the environment (Amankwah et al., 2021; Toushik et al., 2022). Therefore, there is a need for alternative solutions that are safer and more environmentally friendly, such as the use of bacteriophages (Tian et al., 2021; Stefani et al., 2021; Figueiredo et al., 2021). Bacteriophages, specific viruses that target bacteria, offer the potential as a more effective and safer method for biofilm control (Łusiak-Szelachowska et al., 2020).

Bacteriophages (phage) are viruses that specifically infect bacteria based on genus, serotype, or strain. Bacteriophages can be found in various environments, including soil, water, meat products, dairy products, and vegetables (Au et al., 2021). All bacteriophages are obligate parasites, meaning their survival depends on their bacterial hosts for growth and reproduction (Węgrzyn, 2022). Lytic bacteriophages, in particular, are used as biocontrol agents due to their ability to rapidly lyse bacterial cells without integrating into the bacterial DNA (Kassa, 2021; Elois et al., 2023). According to Chegini et al. (2020), bacteriophages can be used as antibiofilm agents against *Pseudomonas aeruginosa*, replacing ciprofloxacin antibiotics, which are often ineffective due to increasing resistance. Danis-Wlodarczyk et al. (2021) demonstrated the use of bacteriophages to destroy biofilms formed by *Staphylococcus aureus* on orthopaedic implants, as bacteriophages can replace cefazolin antibiotics that only target the biofilm surface. Kim et al. (2024) utilized bacteriophage pVa-21 as an anti-biofilm agent for *Vibrio alginolyticus*, providing an alternative to antibiotics. Additionally, Wu et al. (2024) used bacteriophages to eliminate biofilms of antibiotic-resistant *E. coli* and *Salmonella enteritidis*, replacing the commonly used Quaternary Ammonium Chloride (QAC) cleaning agents. This review highlights the importance of bacteriophages as antibiofilm agents that can contribute to combating antibiotic resistance and offer effective alternatives for biofilm control.

Biofilm

Biofilm is a collection of bacteria adhering to solid surfaces and encapsulated in an extracellular polymeric substance (EPS) matrix (Hooshdar et al., 2020). Biofilms can form on nearly any surface, including medical equipment, industrial machinery, and other solid substrates (Caldara et al., 2022). The biofilm matrix consists of EPS, which serves various functions, including adhesion, bacterial cell aggregation, biofilm cohesion, water storage, protection, absorption of organic compounds and inorganic ions, enzymatic activity, nutrient provision, genetic information exchange, electron donation and acceptance, export of cell components, storage of excess energy, and enzyme binding (Karygianni et al., 2020; Telegdi et al., 2020; Naaz et al., 2023). EPS is a hydrated biopolymer composed of polysaccharides, proteins, nucleic acids, and lipids secreted to envelop and immobilize cells. This biopolymer is often called slime (Priyadarshanee and Das, 2023).

Bacteria in biofilms exhibit higher antibiotic resistance than bacteria in their planktonic form. This increased resistance can be attributed to several factors, including the slow penetration of antibiotics through the extracellular polymeric matrix of the biofilm, reduced bacterial growth rates, increased genetic transfer, and the expression of resistant genes within the biofilm (Abushaheen et al., 2020; Pinto et al., 2020; Roy et al., 2022). The biofilm's maturation level also significantly affects bacterial resistance to antibiotics (Grande et al., 2020). A study by Chen et al. (2020) found that *Pseudomonas aeruginosa* biofilms grown for 5-12 hours remained sensitive to gentamicin, while biofilms grown for 24 and 48 hours showed high resistance to the same antibiotic. Aquaculture farmers often rely on the preventive use of antibiotics in farmed fish to reduce pathogenic *Vibrio* and its biofilm, which has gradually led to the emergence of *Vibrio* resistance and increased the burden on the aquaculture industry. Matamp & Bhat (2019) identified a characteristic lysin in *Vibrio parahaemolyticus* phage with lytic activity against various *Vibrio* species, making it a promising bio-bactericide for treating *Vibrio* resistance and addressing the problem of antibiotic overuse in the aquatic industry.

Formation and Biofilm Role

Bacteria living in biofilms are protected from conditions that can damage cells, making this a crucial factor in the disease cycle caused by pathogenic bacteria in both animals and plants (Vestby et al., 2020). Biofilms have specific functions and roles for each microorganism (Table 1).

Bacteria can adapt based on their environment, transitioning between single cells (planktonic) and forming biofilms consisting of more than 1,000 bacterial cells. The biofilm formation process occurs in five stages, as illustrated in Fig. 1. The first stage involves the initial attachment of cells to solid surfaces such as iron, rubber, or plastic. The second stage is characterized by the production of extracellular polymeric substance (EPS), which results in more robust, more "irreversible" bonds. The third stage marks the early development of the biofilm. The fourth stage involves the maturation of the biofilm. In the fifth stage, single cells are dispersed from the biofilm to form new biofilms. Environmental and physiological triggers influence the transition from single cells to biofilm formation, such as quorum sensing, nutrient availability, and cell stress levels (Chirathanamettu & Pawar, 2020).

The formation and spread of biofilms are regulated by three main factors quorum sensing (QS), bis-(3'-5')-cyclic diguanosine monophosphate (c-di-GMP), and various small RNAs (sRNAs) (Sionov & Steinberg, 2022). QS involves molecular signals known as autoinducers. When bacterial populations reach a critical density and autoinducer concentrations exceed a threshold, bacteria respond by repressing or activating specific target genes.

Table 1: Differences in the function/role of biofilms for each microbe

Microbes	Function/Role	Source
Listeria monocytogenes	a. Self-defense from antibiotics and cleaners b. Media for sticking to surfaces c. Intercellular communication d. Chemical sensing e. Balancing nutrients and toxins in cells	Balaure & Grumezescu (2020); Byun & Kim (2023)
Salmonella spp	a. Protection from the environment, antibiotics, disinfectants, and the immune system b. Has the ability to adapt to an environment without a host c. Protection from UV, osmotic changes, dehydration, pH variations and metal toxins	Harrell et al. (2021) Pradhan et al. (2023)
Escherichia coli	a. Producing amyloid called curli is useful for stabilizing the environment, producing pigment b. Adapt to extreme environments c. Perform quorum sensing d. Produces autoinducers that can secrete virulent factors, modulate the host immune system, and produce genetic changes	Li et al., (2022) Ballén et al., (2022)
Staphylococcus	a. Can survive in environments with limited nutrients b. Can be attached to biotic and abiotic surfaces c. Has adhesin intercellular polysaccharides which can produce enzymes	Nandhini et al., (2022) Schilcher & Horswill, (2020)
Pseudomonas aeruginosa	a. Has amyloid as a building material and strengthens the extracellular matrix and prevents the spread of chemical and mechanical substances b. Increases resistance to antibiotics c. As a place for quorum sensing d. Amyloid fibrils in biofilms can polymerize in the absence of an energy source and can function as a molecular scaffold with limited resources	Li et al., (2022) Tuon et al., (2022)

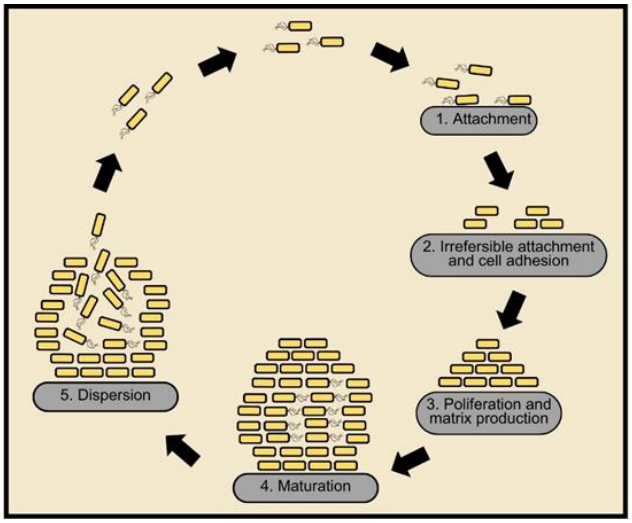

Fig. 1: Biofilm formation process (Source: Canva)

QS plays a crucial role in developing and disseminating biofilms (Tan et al., 2020). The second regulatory factor in biofilm formation is c-di-GMP, which influences bacterial transcription, enzyme activity, and the formation of larger cellular structures (Liu et al., 2022). c-di-GMP regulates the synthesis of exopolysaccharides, adhesive pili, adhesins, and extracellular DNA (eDNA) secretion and modulates cell death and motility, forming three-dimensional biofilm structures. The third factor is sRNA, which is involved in post-transcriptional gene regulation in bacteria. sRNAs participate in metabolic processes, stress adaptation, and microbial pathogenesis (Quendera et al., 2020; Felden & Augagneur, 2021).

Fig. 2 illustrates biofilm formation in *Vibrio cholerae*, highlighting the roles of QS, c-di-GMP, and sRNA. At low cell density, the concentration of autoinducers is also low. Under these conditions, the histidine kinases LuxP and CpqS undergo phosphorylation and can phosphorylate the regulator LuxO. LuxO-P activates the expression of Qrr 1-4 RNA, which represses HapR by inhibiting c-di-GMP synthesis and increasing the production of enzymes synthesising c-di-GMP. Subsequently, c-di-GMP activates the proteins VpsR and VpsT, which regulate biofilm-related genes, leading to mature biofilm formation (Teschler et al., 2022).

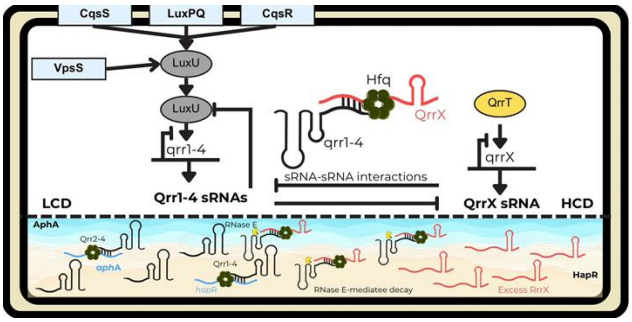

Fig. 2: Biofilm formation process in *Vibrio cholerae* (Source: Canva)

Foodborne Bacteria-Forming Biofilm

Pathogenic bacterial biofilms are one of the biggest challenges in the food industry. Biofilms are thin layers formed by communities of microorganisms that adhere to various surfaces and are enclosed within an extracellular matrix. Forming biofilms on equipment, processing facilities, and food products can lead to persistent and difficult-to-eliminate contamination (Carrascosa et al., 2021). Table 2 details various pathogenic bacteria commonly found in biofilm form in food, the types of media that support biofilm growth, optimum conditions for biofilm formation, and effective mitigating strategies to prevent and control contamination.

Food Safety Concern

Food contamination by pathogenic microorganisms is a significant public health issue and a major cause of economic loss worldwide (Abebe et al., 2020). Microbial biofilms, which include food-damaging bacteria and pathogens, can lead to contamination after processing, reducing product quality and shelf life and potentially spreading disease (Bhadra et al., 2023). The formation of biofilms on both biotic and abiotic surfaces increases risk by exacerbating pathogen circulation in food production

Table 2: Various Pathogenic Bacteria Commonly Found in Biofilm Form in Food

Bacteria	Material	Optimum condition	Mitigating strategy	Reference
Listeria monocytogenes	Stainless steel and polycarbonate	Temperature increases up to 30-37°C and pH 7	The use of CDC Biofilm Reactors represents a new approach to assist in the implementation of sanitation control strategies	Mendez et al. (2020)
Salmonella enterica	Stainless steel	Temperature increases up to 30-37°C	The tolerance to sanitizers and ability to form biofilm	Chaves et al. (2024)
Pseudomonas aeruginosa	Stainless steel surfaces	Temperature increases up to 11-47°C	The efficiency of sanitizers used in the food industry against the biofilms formed was also evaluated	Castro et al. (2021)
Escherichia coli	Glass and stainless-steel surfaces	Temperature increases up to 30-37°C	Alternative therapy that uses enzymes to degrade biofilms	Nahar et al. (2021)
Bacillus cereus	Can form biofilms on food contact surfaces or in food-processing environments	Temperature increases up to 30-37°C	Biofilm inhibition or removal using enzymes	Lim et al. (2021)
Campylobacter jejuni	Stainless steel, copper, glass, and plastic surfaces	Temperature increases up to 30°C	By reducing the adhesion of microorganisms	Šilha et al. (2021)
Staphylococcus aureus	Stainless steel and plastic	Temperature 30-37°C, neutral pH	Good hygiene practices, temperature control, use of biocides	Argudin (2021)
Vibrio spp.	Stainless steel and plastic	Warm temperature, saline conditions	Thorough cooking, cold storage, use of antimicrobials	Su et al. (2022)
Clostridium perfringens	Stainless steel and plastic	Warm temperature, anaerobic conditions	Rapid cooling, adequate heating, good sanitation practices	McClane (2023)
Enterococcus spp.	Stainless steel and plastic	Warm temperature, high humidity	Good sanitation, use of probiotics, temperature control	Giraffa (2021)

environments, thereby causing severe contamination (Araújo et al., 2024). Biofilms formed by pathogenic bacteria harm food, processing operations, and other areas directly impacting human health (Guzmán et al., 2020; Nikolaev et al., 2022). Pathogenic microorganisms adhering to surfaces that come into contact with food can pose sanitation problems because they can persist for extended periods in hostile conditions and serve as sources of contamination (Mazaheri et al., 2021; Sehgal et al., 2024). Biofilm formation on stainless steel surfaces in food processing plants, which can lead to foodborne illness outbreaks, occurs due to pathogens adhering and getting trapped in microscopic cavities with rough surfaces. Microorganism attachment to food processing surfaces facilitates the formation of biofilms that become sources of contamination (Abebe, 2020).

Additionally, biofilms can reduce production efficiency and the use of materials in food processing (Yuan et al., 2020). Since biofilms embedded in extracellular polymeric substances (EPS) are difficult to remove from food production facilities (Huang et al., 2022), developing effective methods to prevent, reduce, control, and eliminate biofilm formation on food surfaces and processing equipment is crucial. Food contaminated by foodborne pathogens due to biofilm formation can be seen in Table 3.

Bacteriophage as AntiBiofilm

Bacteriophages are viruses that replicate inside bacterial cells. The first scientist to discover these viruses was French researcher Félix d'Hérelle. Bacteriophages have a more complex structure than other viruses, consisting of several meticulously arranged parts (Letarov, 2020). Their structure includes a hexagonal-shaped head, a neck, and a tail. The head contains two twisted strands of DNA (Farooq et al., 2022). The neck connects the head and tail, while the tail functions to inject the viral DNA into the host cell (Zinke et al., 2022). The tail portion of a bacteriophage features receptor-binding proteins, which can be located on tail fibres, tail spikes, or the tail tip. These structures enable the bacteriophage to recognize receptors on the host, such as lipopolysaccharides, teichoic acids, and porins (Dunne et al., 2021; Filik et al., 2022; Leprince & Mahillon, 2023). The structure of a bacteriophage is illustrated in Fig. 3.

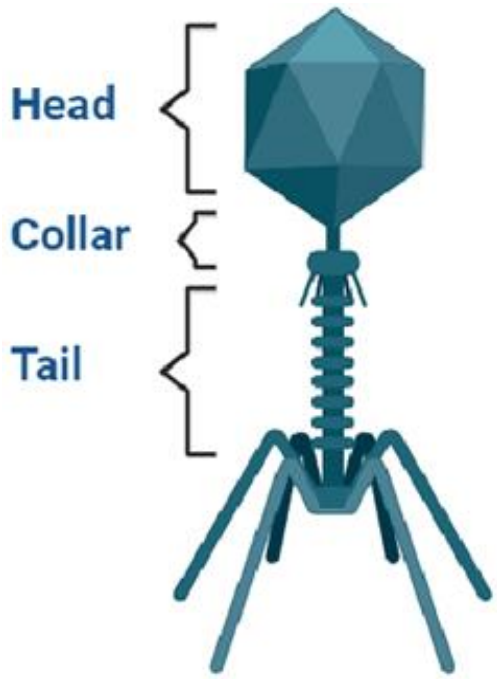

Fig. 3: Bacteriophage structure (Source: BioRender).

Mechanism of Action

One application of bacteriophages is their use as biocontrol agents against biofilm-producing bacteria, also known as antibiofilm agents (Amankwah et al., 2021). This is because bacteriophages are viruses that infect bacteria in a specific manner. Moreover, bacteriophages are readily available in nature, given their abundance. All bacteriophages are obligate parasites, meaning they depend on their hosts for survival (Naureen et al., 2020). The Biofilm destruction by bacteriophages can be seen in Fig. 4.

Table 3: Food contaminated by foodborne pathogens as a result of biofilm formation

Foodborne Pathogens	Characteristics	Contaminated Food	The Main Symptoms of Food Poisoning	Examples of Harmful Spoilage Effects	References
Listeria monocytogenes	Gram-positive, facultative anaerobic bacterium	Soft cheeses, pate, and unpasteurized milk	Gastroenteritis, fever, and in severe cases, bacteraemia and encephalitis, especially in high-risk individuals	Decreased product quality and shelf life, potential fatal listeriosis in vulnerable groups	Valenti et al. (2021)
Salmonella enterica	Gram-negative, rod-shaped, facultative anaerobic, flagellate, non-spore forming	Poultry and produce	Gastroenteritis, abdominal cramps, bloody diarrhea, fever, and vomiting	Spoilage of fresh produce and animal products, economic loss	Ehuwa et al. (2021)
Pseudomonas aeruginosa	Gram-negative, rod-shaped, motile, aerobic, endospore negative, oxidase and catalase positive	Fruits, vegetables, meat, low-acid dairy products	Nausea, vomiting, and diarrhea	Spoilage of raw vegetables and dairy products, economic losses	Urgancı et al. (2022)
Escherichia coli	Gram-negative, rod-shaped, non-spore forming, metabolically active	Consuming undercooked meat, unpasteurized milk, or contaminated water	Characterized by symptoms such as nausea, abdominal cramps, diarrhea, vomiting, headache, and fever	Gastrointestinal infections, urinary tract infections, septic infections, hemorrhagic colitis, hemolytic uremic syndrome, thrombotic thrombocytopenic purpura, kidney failure	Guptaa & Chaudhary (2022)
Bacillus cereus	Bacteria that can live in both oxygen-rich (aerobic) and low-oxygen (facultatively anaerobic) environments, and it forms spores, which are tough, dormant forms that can survive harsh conditions	Spices, dairy products, and meats, food products, including cereals, vegetables, spices, ready-to-eat foods, meats, milk, and dairy products	Nausea and vomiting, diarrhea, abdominal pain and cramps, fever, weakness and Fatigue, Headache, Loss of Appetite, Muscle aches	Meningitis, brain abscess, cellulitis, endophthalmitis, pneumonia, endocarditis, and osteomyelitis	Jelena et al. (2021)
Campylobacter jejuni	Gram-negative, rod-shaped, microaerophilic, flagellate, non-spore forming, motile	Undercooked poultry, unpasteurized milk, and contaminated water	Diarrhea, abdominal pain, fever, and vomiting	Gastrointestinal infection, acuteenteritis, septicemia, meningitis, arthritis, pelonephritis	Manaa et al. (2022)
Staphylococcus aureus	Gram-positive, spherical, facultative anaerobic, flagellate, non-spore forming, non-motile	Foods such as meat, milk products, poultry, eggs, fish, salads, and pastries due to poor food handling practices.	Nausea, vomiting, abdominal cramps, and diarrhea	Osteomyelis, endocarditis, chronic wound infection, eye infection, multimicrobial biofilm infection, renal abscess	Pal et al. (2022)
Vibrio spp.	Gram-negative, rod-shaped, halophilic bacteria	Quality of water and seafood, especially in high-risk environments like oyster production	Gastroenteritis to sepsis	Contamination of seafood, potential for severe illness	Martins et al. (2021)
Clostridium perfringens	Gram-positive, spore-forming, anaerobic bacterium	Meat and meat products	Diarrhea, necrotic enteritis, enterotoxemia, and gangrene in humans	Production of toxins leading to food poisoning, spoilage of meat products	El Bayomi et al. (2020)
Enterococcus spp.	Gram-positive, lactic acid bacteria	Cheese, fermented foods	Opportunistic infections, particularly in immunocompromised individuals	Spoilage of cheese and fermented foods, potential health risks	Giraffa (2021)

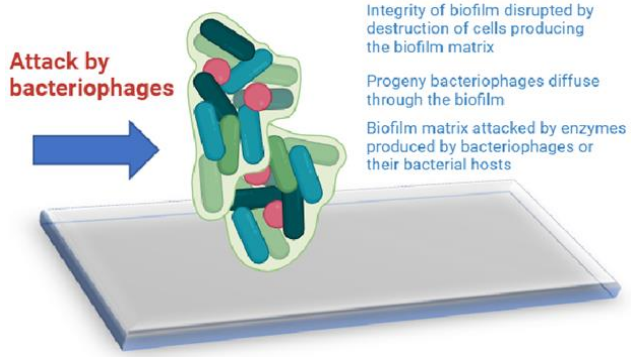

Fig. 4: Biofilm destruction by bacteriophages (Source: BioRender).

The mechanism by which bacteriophages eliminate biofilms differs from chemical antibiotics or biocides due to their co-evolution with host bacteria (Singh et al., 2022). Bacteriophages attack host bacteria with at least four distinct mechanisms (Hussain et al., 2021; Teklemariam et al., 2023). As illustrated in Fig. 5, the first mechanism involves replicating bacteriophages inside the host cell, increasing the number of bacteriophages (amplification). Once dispersed within the biofilm and targeting bacteria that produce extracellular polymeric substances (EPS), bacteriophages progressively dismantle the biofilm and reduce the likelihood of its regeneration. The second mechanism involves bacteriophages carrying depolymerase enzymes that can degrade EPS. The third mechanism includes bacteriophages inducing depolymerase enzymes from the host genome, contributing to EPS degradation. The fourth mechanism addresses persister cells. Although bacteriophages cannot replicate or destroy these inactive cells, they can remain inside until the cells become active again. Once reactivated, bacteriophages can initiate a productive infection that ultimately destroys these cells (Dennehy & Abedon, 2021).

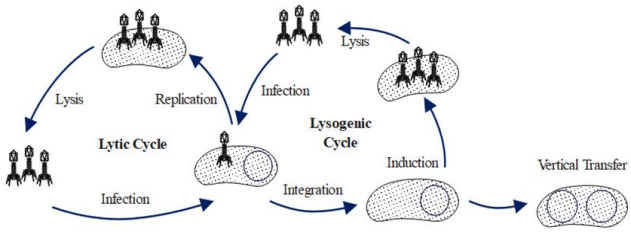

Fig. 5: Mechanism of bacteriophage in lysing bacterial cells (Source: BioRender).

Bacteriophages have two types of life cycles: the lytic cycle and the lysogenic cycle. However, the lytic cycle is the most effective antibiofilm agent (Latka & Drulis-Kawa, 2020; Amankwah et al., 2021; Singh et al., 2022). The lytic cycle consists of several stages. Initially, the bacteriophage undergoes adsorption, attaching to the host cell's surface. During this stage, the bacteriophage tail fibres bind to specific receptors on the cell surface. Next, the bacteriophage injects its nucleic acid into the host cell's cytoplasm. The phage genome then replicates and increases in number within the cytoplasm. The early genes expressed regulate the host cell's metabolism to facilitate bacteriophage replication. Subsequently, new bacteriophages are formed, with the late genes directing their assembly. These new virions assemble by joining the head and tail, encapsulating the nucleic acid within the head, and undergoing virion maturation. Finally, the bacteriophages lyse the host cell, releasing new bacteriophages ready to infect other cells within the biofilm and initiate a new lytic cycle (Elois et al., 2023).

Isolation of Bacteriophages

Bacteriophages can be isolated from various samples, as summarised by several literature sources in Table 4.

Based on the examples in Table 4, isolating bacteriophages, viruses that specifically infect bacteria, is a crucial step in developing phage therapy as a potential alternative to antibiotics, particularly in combating drug-resistant bacteria. As concerns about antibiotic resistance continue to grow, research in this field has expanded, and various studies have successfully demonstrated the effectiveness of bacteriophage isolation using various methods. These methods are designed to target various types of bacterial pathogens, including highly resistant ones, thereby opening up new possibilities for treating infections that are difficult to manage with conventional approaches.

Characterization of Bacteriophages

The obtained bacteriophages are then characterized to determine their properties in Fig. 6. According to Abdelrahman et al. (2022), who isolated *E. coli* specific bacteriophages, various types of characterization can be performed. This characterization includes morphological observation using an electron microscope, determination of host range by testing several bacterial species in a double-layer medium, and creating a one-step growth curve by infecting bacteria in the exponential phase using a Multiplicity of Infection (MOI) value of 1.0 (Lukman et al., 2020). Additionally, phage resistance testing is conducted by culturing phages on bacteria in the exponential phase and testing at MOIs of 0.01, 0.1, 1, and 10, as well as pH and temperature stability testing at various temperatures and pH values. In the study by Jamal et al. (2019) on *Enterobacter cloacae*-specific bacteriophages, characterization involved assessing the phage's effect on calcium and magnesium adsorption by adding $CaCl_2$ and $MgCl_2$ to determine adsorption capacity and the number of non-adsorbed phages. Protein expression characterization was also performed using ultracentrifugation at 187,000xg for 4 hours and mixed with PBS (pH 7). This study also involved DNA isolation, which resulted in a genome size of 40kb. Chen et al. (2020) focused on expressing and purifying depolymerase enzymes produced by specific *E. coli* bacteriophages. Therefore, bacteriophage characterization should be tailored to the specific research objectives, but general characterization such as morphology, host range, pH and temperature stability, and growth curve should be included (Zurabov & Zhilenkov, 2021; Abdelsattar et al., 2022; Karaynir et al., 2022).

The morphology of bacteriophages can be observed using a specialized tool called Transmission Electron Microscope (TEM), as shown in Fig. 6. Fig. 6 (A) depicts the morphology of bacteriophage JBP901, which infects *Bacillus cereus*. This bacteriophage, isolated from various traditional fermented foods, is classified in the Myoviridae family with a capsid dimension of 95 ± 5 nm and a tail length of 170 ± 5 nm (Matamp & Bhat, 2020). Fig. 6 (B) presents the appearance of bacteriophage LPST94, which infects *Salmonella*, isolated from aquatic environments. This bacteriophage features an icosahedral head and a long tail, with a head diameter of 67.60±2.30nm and a tail length of approximately 116.30±4.10nm. Based on its morphology, this bacteriophage belongs to either the Ackermannviridae or Myoviridae family (Islam et al., 2020). Fig. 6 (C) illustrates the morphology of bacteriophage PS5, which targets both *E. coli* and *Salmonella* isolated from poultry products. This bacteriophage is classified in the Myoviridae family and has an isometric head with a diameter of 84nm and a tail of 106nm (Duc et al., 2020). Fig. 6 (D) shows the commercial bacteriophage Listshield™ that targets *Listeria monocytogenes*. The image indicates that the commercial bacteriophage Listshield™ belongs to the Myoviridae family (Wintachai & Voravuthikunchai, 2022).

Table 4: Effectiveness of isolation method on the bacteriophage recovery

Bacteriophage method	Bacteria	Sample	References
Double agar layer method	*Campylobacter sp*	Chicken skin	Nafarrate et al. (2020)
Agar overlay assay method	*Bacillus cereus, Bacillus subtilis, enterotoxigenic Escherichia coli (ETEC),* and *enterohemorrhagic Escherichia coli (EHEC)*	Soil	Artawinata et al. (2023)
Double-layer agar method	*VibrioParahaemolyticus*	Clam (*Meretrix meretrix*)	Cao et al. (2021)
Double-layer agar (DLA)	*Pseudomonas Aeruginosa*	Wastewater	Sharma et al. (2021)
Double agar overlay plaque assay	*Vibrio parahaemolyticus*	Seafood samples	Tan et al. (2021)
Hydrodynamic countercurrent chromatography	*Escherichia coli*	Water sources, effluent, or fecal samples	Friedersdorff et al. (2022)
Membrane chromatography	*Escherichia coli*	Wastewater	Roshankhah et al. (2023)
Double-layer agar method	*Escherichia coli, Staphylococcus aureus, Acinetobacter sp, Pseudomonas aeruginosa*	Wastewater Treatment	Alilesh et al. (2024).
Plaque assay	*Staphylococcus spp., Escherichia coli,* and *Klebsiella pneumoniae*	Pasteurized milk and wastewater	Imklin et al. (2024)
Plaque assay	*Bacillus cereus*	Such as soil, water, or food samples	Wang et al. (2024)

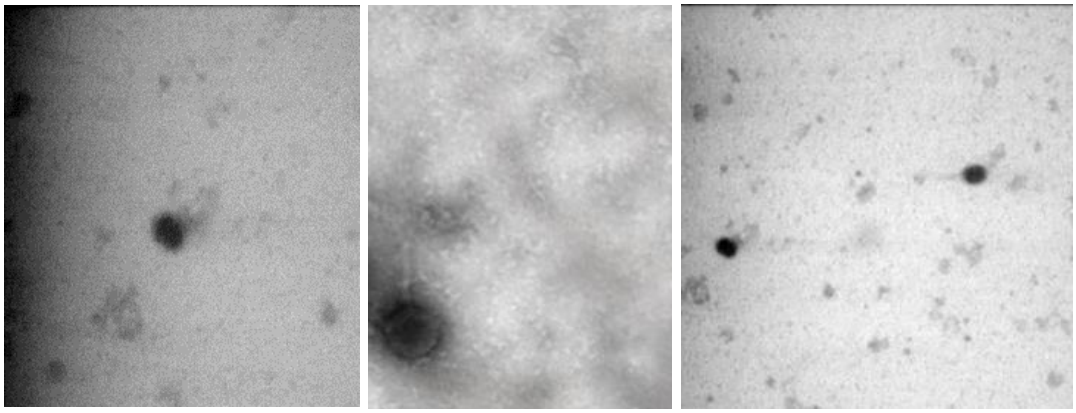

Fig. 6: The morphology of bacteriophages was observed using TEM ordo *Caudovirales* (Source: Personal Results).

Application of Bacteriophage as Antibiofilm

Bacteriophages play a significant role in molecular biology and biotechnology, with a range of developed applications. They are commonly used in agriculture, healthcare, disease diagnosis, livestock biocontrol, and food safety. Examples of bacteriophage applications include their use as therapeutic agents, pathogen detection tools, and biocontrol agents in the food industry (Wang & Zhao, 2022). Bacteriophages have been applied therapeutically in plants, animals, and humans, with varying degrees of success. The benefits of using bacteriophages as therapeutic agents include their narrow antibacterial spectrum, which makes them highly specific to targeted bacteria, their applicability to both gram-negative and gram-positive bacteria, fewer side effects compared to traditional antibiotics, increased efficacy, and cost-effectiveness (Huang et al., 2021; Liu et al., 2022; Ahmed et al., 2023).

Bacteriophages can also detect pathogenic bacteria due to their specificity in infecting bacterial host cells. This detection process may involve using green fluorescence or reporter genes to visualize bacteria that bacteriophages have infected. Additionally, bacteriophages are used as biocontrol agents to replace antibiotics, considering many bacteria have developed resistance to various antibiotics. Several studies have demonstrated the success of bacteriophages in reducing the number of bacteria such as *Salmonella* sp., *Listeria* sp., and *Pseudomonas* sp. Certain bacteriophages have been commercialized and are considered safe (GRAS) by regulatory bodies like the FDA and USDA, including products such as Agriphage™, Ecoshield™, ListShield™, Listex™ P100, and Salmonellex™ (Costa et al., 2023). To effectively eradicate bacterial biofilms, it is recommended to use a combination therapy approach with phages, either simultaneously or sequentially, along with other alternative antibiofilm agents. This combination therapy involves phages and/or phage-derived enzymes with nanoparticles, chemical compounds, antimicrobial peptides, and disinfectants (Table 5).

One application of bacteriophages is as antibiofilm or biocidal agents that effectively lyse biofilm-forming bacteria. According to Tian et al. (2021), using bacteriophages as antibiofilm agents can be categorized into two main areas: medical and industrial applications. In the medical field, biofilms often form on medical equipment, increasing patients' risk of significant infections. Bacteriophages can target these biofilm-forming bacteria, disrupt the biofilm matrix, and reduce infection risks (Ferriol-González & Domingo-Calap, 2020). In industrial settings, bacteriophages are commonly applied to stainless steel surfaces, as biofilm-forming bacteria can adhere to various surfaces, both biotic and abiotic, including stainless steel (Jamal et al., 2019; Figueiredo et al., 2021; Lila et al., 2023). Bacteriophages can infect biofilm and planktonic bacteria and disrupt the stability of extracellular polymeric substances (EPS) by producing enzymes (Azeredo et al., 2021).

Future Concern

a. Specificity

Bacteriophages typically have a narrow host range, meaning they infect only specific strains or species of bacteria. This specificity can pose a challenge in clinical applications due to the limited ability of phages to target a wide variety of pathogenic bacteria. To address this issue, one approach being explored is using phage cocktails containing multiple phages, each capable of simultaneously targeting several bacterial strains. Research by Glonti et al. (2024) successfully identified and classified phages targeting *Pseudomonas aeruginosa* and *Klebsiella pneumoniae*, demonstrating various host specificities. Testing these phage cocktails on different bacterial strains effectively inhibited phage-resistant mutants. Therefore, using phage cocktails containing diverse phages to combat antibiotic-resistant bacterial infections is a promising strategy.

Genetic engineering techniques are also being developed to broaden the host range of phages, enabling them to treat a broader range of bacterial infections more effectively. Research by Lewis et al. (2024) has demonstrated that genetic engineering can expand the host range of phages by creating phage variants optimized for increased infectivity or broader host specificity. Advances in genetic engineering play a crucial role in paving the way for more efficient phage therapies by allowing the development of phages that can target a broader spectrum of bacterial species, ultimately enhancing the effectiveness of phage therapy against antimicrobial-resistant strains.

Table 5: Examples of combination of phages or phage-derived products and antimicrobials applications against bacterial biofilm formation

Bacteriophage	Antimicrobial Agent Used	Biofilm-Bacteria	Biofilm Reduction	Reference
Environmental phage-based cocktail	Antibiotics (Ciprofloxacin, sulfamethoxazole/ trimethoprim, Gentamicin, Tobramycin, Meropenem, Imipenem)	*Acinetobacter baumannii* in a human urine mode	Reduction of biofilm biomass and clearance of persister cells	Grygorcewicz et al. (2021)
Bacteriophage Brsv	Amikacin	*Proteus mirabilis* 3059	Eradication of biofilm	Maszewska et al. (2021)
Commercially available phages Sb-1 and PYO	Ciprofloxacin	Dual-species of *Staphylococcus aureus/Pseudomonas aeruginosa*	Complete eradication of dual-species biofilms	Tkhilaishvili et al. (2020)
Phage EFLK1	Vancomycin	Vancomycin-resistant *Enterococcus faecalis*	Reduction of biomass by 87%	Shlezinger et al. (2019)
Phage E79	Aztreonam lysine	*Pseudomonas aeruginosa* PA01	Reduction in biofilm growth over 3-fold	Davis et al. (2021)
Phage-encoded endolysin LysP108	Vancomycin	Methicillin-resistant *Staphylococcus aureus* XN108	Inhibition of biofilm	Lu et al. (2021)
Bacteriophage (Xccϕ1) - hydroxyapatite complex	Saturated long–chain fatty acids	*Xanthomonas campestris* in a flow cell system	Removal of biofilm	Papaianni et al. (2020)
phage ϕ44AHJD	Green synthesized silver nanoparticles	*Staphylococcus aureus*	Rapid dispersion of biofilm	Manoharadas et al. (2021)
T7Select phage	Antimicrobial peptide 1018	*Escherichia coli*	Eradication of biofilm	Lemon et al. (2019)
Phage SA46-CTH2	Nisin	*Staphylococcus aureus*	Reduction in biofilm	Duc et al. (2020)
Phages PN05 and PN09	Carvacro	*Pseudomonas syringae* pv. actinidiae	Prevention of biofilm regrowth	Ni et al. (2020)

b. Regulatory and Safety Concerns

The regulatory framework governing the production and application of phage-based products is a crucial aspect that requires special attention. As support for phage therapy as a potential solution to combat antibiotic-resistant bacteria increases, resolving regulatory and safety issues is critical to ensure its successful application in various sectors, including agriculture, food safety, and healthcare. Efforts to streamline regulatory processes and improve public understanding are essential to maximize the effectiveness of phage use in combating bacterial diseases.

The safety of bacteriophages is well-established, as they exhibit high specificity and only infect bacterial hosts within a very limited range, thereby minimizing the risk of secondary infections (Imklin et al., 2024). Bacteriophage therapy does not contribute to antibiotic resistance (Ghani et al., 2024). Bacteriophages can be directly applied to food surfaces, integrated into packaging materials, or used during food processing. Several commercial bacteriophage products have been declared safe for consumption and have been granted Generally Recognized as Safe (GRAS) status by the FDA (Food and Drug Administration) (Dellalibera-Joviliano et al., 2020; Ranveer et al., 2024). Applying bacteriophages as a natural treatment to prevent bacterial growth in fresh produce, dairy, and food products is promising (Imran et al., 2023). Their targeted action and safety profile make them valuable bioadditives for enhancing food safety and quality (Narayanan et al., 2024).

c. Stability and Storage

Bacteriophages face several environmental challenges that can affect their stability as antimicrobial agents. Phages can be sensitive to temperature variations and maintaining an optimal temperature range is crucial for their survival and functionality in antimicrobial applications (Sae-Ueng et al., 2022; Choi et al., 2022). Acidic conditions can damage phages, as they are often less stable in low pH environments, which can reduce antimicrobial activity (Wdowiak et al., 2022; Bagińska et al., 2024). Ensuring a neutral or slightly alkaline pH can help maintain phage stability and efficacy. Exposure to UV light can damage the nucleic acid components of phages, resulting in a loss of infectivity (Yu et al., 2023). UV irradiation poses a significant challenge for phages, particularly in outdoor or unprotected environments where they may be employed as antimicrobial agents (Vitzilaiou et al., 2022; Liu et al., 2023).

Developing stable formulations and ensuring the long-term storage of phages are crucial for effective phage therapy. Effective phage formulations are needed to protect them from degradation and maintain activity. Encapsulation techniques, such as using excipients like lactose, trehalose, mannitol, PEG, and leucine, have shown promise in protecting phages (Bolsan et al., 2024). These formulations play a vital role in ensuring the survival and effectiveness of phages, especially in combating antibiotic-resistant bacteria. By employing appropriate protection and delivery strategies, phages can be utilized as powerful tools against bacterial infections, addressing the challenges posed by resistance (Choudhary et al., 2023; Flint et al., 2023).

d. Production and Scale-up

Large-scale production of bacteriophages requires specialized facilities and expertise to maintain consistent quality and high phage titers, which are crucial for effectively combating bacteria (Davydov et al., 2023). Additionally, maintaining strict production standards is essential to ensure the purity and safety of phage products for therapy. Enforcing rigorous controls at every stage of production, including phage and bacterial strain identification, fermentation, purification, formulation, quality inspection, and documentation, can assure the purity and safety of phage products (Mutti & Corsini, 2019).

The costs of producing and purifying phages can be high, which may limit the widespread adoption and use of phage therapy (Luong et al., 2020). Efforts to reduce production costs without compromising the quality and effectiveness of phage products are one of the critical challenges. This can be achieved by optimizing growth

conditions for host bacteria and phages, such as temperature, pH, and nutrient supply, to maximize yield and efficiency (Mäkelä et al., 2024). Implementing automated systems to monitor and control the production process can reduce labour costs and improve consistency and quality, leading to cost savings (João et al., 2021).

e. Public Perception

Public perception and acceptance of phage therapy can pose obstacles to the adoption of this technology. A lack of understanding regarding the safety and benefits of phage therapy can lead to doubts among consumers and stakeholders. Therefore, proper and comprehensive education about phage therapy is crucial to enhance its acceptance and adoption in clinical applications and food safety. Despite these challenges, ongoing research and technological advancements play a significant role in overcoming these barriers, ensuring that phage therapy remains a promising tool in improving food safety and addressing antibiotic resistance in the future.

Conclusion and Future Prospects

In the effort to combat foodborne pathogen biofilms, the use of bacteriophages emerges as a highly promising approach. Bacteriophages, viruses that specifically infect bacteria, have proven effective in targeting and addressing biofilms that are difficult to remove using conventional methods, such as antibiotics and biocides. Research results indicate that bacteriophages can disrupt biofilm matrices and reduce the risk of infection from pathogens like *Listeria monocytogenes, Salmonella*, and *Pseudomonas aeruginosa*. Looking to the future, the development of more specific bacteriophages and genetic engineering has the potential to enhance the efficiency of this therapy. Integrating bacteriophages with advanced technologies, such as nanoparticles and enzymes, is expected to improve further effectiveness in combating biofilms. Establishing regulations and safety standards will also be crucial for the widespread application of bacteriophages. With advancements in production technology and a better understanding of bacteriophage mechanisms, the use of bacteriophages in controlling foodborne pathogens holds the promise of being a safer and more environmentally friendly alternative to conventional methods. Broader education and ongoing research support will accelerate the adoption of this technology, making bacteriophages a vital tool in enhancing food safety and addressing the challenges of pathogen biofilms in the future.

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