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Research Article

Using bacteriocin as an alternative preservative: A promising approach for Listeria monocytogenes control in canned foods and other food products

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Abstract

Due to the increasing demand for Ready-to-eat (RTE) foods that undergo minimal processing, there is a need for alternative methods of preservation that can ensure food safety without the use of chemicals or high temperatures. *Listeria monocytogenes* is a major safety concern in RTE food products. This pathogen can increase and multiply, simultaneously generating different virulence components like listeriolysin O, transcriptional activator, actin, and internalin. Additionally, the extended processing time and extended shelf life associated with certain ready-to-eat (RTE) foods, like cured meat and dairy products, create favorable conditions for the growth and proliferation of *L. monocytogenes* within the food itself. The review focuses on exploring the efficiency of bacteriocin and their potential to effectively manage *L. monocytogenes* within biofilms found in food production facilities. By targeting biofilms, the innovative techniques using bacteriocins have the potential to control and prevent L. monocytogenes contamination, thereby improving food safety standards in food industries.

Keywords: *L. monocytogenes*, *Lactobacillus* spp., bacteriocins, canned food, food biosafety

Introduction

Listeria monocytogenes is a versatile bacterium capable of surviving in diverse environments, including soil, plants, groundwater, and vegetation. This bacterium has been linked to several foodborne illnesses, especially those caused by consuming contaminated dairy products, meat, poultry, and ready-to-eat foods (Lopes-Luz et al., 2021). Although *L. monocytogenes* is non-

sporulating, it is widely distributed due to its ability to adapt and thrive in tough conditions. The bacteria have a notable ability to withstand and tolerate physicochemical stress. While it typically grows best at a temperature of 37°C, which is mesophilic in nature (Ranasinghe et al., 2021). This bacterial species also exhibits psychrotrophic tendencies and able to grow in cold temperatures leading to its classification as psychrotolerant (Lourenco et al., 2022).

In addition, it is capable of surviving in environments which has osmotic stress and low water activity and can tolerate both acidic and alkaline conditions. Exposure to a stressor can lead to cross-adaptation, which may serve as a protective mechanism for the bacteria in changing environmental conditions (Jacek et al., 2022). It is crucial to consider any object or surface that comes into contact with food as a potential source of microbial contamination. *L. monocytogenes* is of particular concern due to its ability to thrive as a common environmental pathogen in food processing facilities. The risk is especially high for ready-to-eat (RTE) meals that require significant processing and packaging after cooking. *L. monocytogenes* can proliferate in food products during storage and distribution, and consumers typically do not employ measures to inactivate the pathogen before consumption. Some types of bacteria could stay in food processing areas for a long time and may infect food during or after processing.

L. monocytogenes can produce biofilm and cause a huge challenge in food quality and safety. In addition to biofilms, the global food industry faces challenges such as the emergence of new pathogens, the expansion of supply sources, and changes in consumers' dietary preferences. In recent times, there is a growing consumer preference for fresh and natural food items that are free from preservatives and low in salt. To meet these demands and ensure the quality and safety of food products, it is crucial to seek alternative options to chemical additives, salt, and antibiotics. Implementing alternative practices to reduce the use of antibiotics in farming can not only contribute to sustaining the competitiveness of farms but also address concerns regarding antibiotic residues and the spread of resistance genes (Beata et al., 2022).

In an effort to enhance food safety and inhibit the growth of pathogens, the food industry frequently relies on chemical preservatives or aggressive physical treatments like high temperatures. Nevertheless, these preservation methods come with several drawbacks. For example, many of the commonly used chemical preservatives, such as nitrites, have been proven to be toxic (Crowe et al., 2019). Additionally, these techniques can result in the alteration of the sensory aspect and nutritional attributes of food products, which presents a challenge as consumers are increasingly seeking minimally processed and additive-free food options that are both safe and retain their natural qualities (Inetianbor et al., 2015). To meet the consumer's desire for minimally processed food products, with a need for food safety standards. The food industry is actively

exploring alternative methods to manage microbial spoilage and safety hazards. These alternative methods encompass the utilisation of innovative technologies, including the incorporation of biological antimicrobial systems like lactic acid bacteria (LAB) and their metabolites (Fedrick et al., 2023).

The objective of this review is to assess the presence of *L. monocytogenes* in various food products and evaluate the frequency and severity of illnesses resulting from the consumption of ready-to-eat (RTE) foods contaminated with this bacterium. Additionally, this review delves into the growth and survival of *L. monocytogenes* within food-related industries and outlines strategies aimed at mitigating the risks associated with its presence. Furthermore, the review looks at the use of safe and healthy technology to address consumer preferences for preserved canned foods. Specifically, the review examines the use of natural preservatives such as bacteriocins, antimicrobial peptides produced by lactic acid bacteria (LAB), which offer a promising alternative to traditional chemical preservatives. Bacteriocins are effective in inhibiting the growth of *L. monocytogenes* and other pathogens, providing a natural means of enhancing food safety while meeting consumer demands for minimally processed and additive-free food products. The application of bacteriocins in food preservation, particularly in RTE and canned foods, is explored, highlighting their benefits, mechanisms of action, and integration with other preservation strategies to ensure comprehensive control of foodborne pathogens.

Listeria monocytogenes and listeriosis

According to Jucilene et al. (2021), *Listeria monocytogenes* is a major cause of foodborne illness and is commonly found in environmental sources such as soil, water, and plants (Leong et al., 2016; Saraoui et al., 2018). It has been detected in a wide variety of food products, including raw and unpasteurised dairy, cheese, ice cream, fresh vegetables, cured meats, raw and cooked poultry, raw meat, and smoked or raw seafood (Jami et al., 2014). *L. monocytogenes* can grow across a broad pH range, tolerate high salt concentrations, and survive at refrigeration temperatures (4 - 10ºC) (Bortolussi, 2008). This makes it a persistent threat in food processing environments and retail outlets that handle ready-to-eat foods (Jucilene et al., 2021).

The pathogen primarily affects high-risk groups such as the elderly, immunocompromised individuals, and pregnant women, but it can also infect healthy individuals. It is commonly found in mammalian feces and is mainly transmitted through contaminated food. Studies estimate that 1% to 10% of the population are asymptomatic carriers of *L. monocytogenes*. Listeriosis can occur sporadically or during outbreaks and can range from mild gastroenteritis to severe conditions like bacteremia, sepsis and meningoencephalitis, where the bacteria invade the bloodstream and central nervous system.

Although listeriosis is relatively rare, its incidence has increased in recent years. This trend is likely due to the growing elderly population and individuals with chronic illnesses who are more vulnerable to infection. The disease's varied symptoms and incubation period make diagnosis challenging. *L. monocytogenes* can persist on surfaces in food-processing facilities such as floors, equipment, and drains for extended periods, sometimes months or even years, especially in the absence of strict hygiene practices (Ferreira et al., 2014).

Its ability to survive under harsh conditions such as low temperatures, dehydration, heat and high salt levels as well as its capacity to form biofilms, contributes to its persistence (Doijad et al., 2015; Zoz et al., 2017). Ineffective cleaning and disinfection, particularly in hard-to-reach areas, further support its colonization and long-term survival. Effective management of *L. monocytogenes* requires identifying contamination hotspots, verifying sanitation efficiency, and routinely monitoring for bacterial presence and recurrence in food-processing environments (Kim et al., 2021).

Mechanisms of virulence

Hemolysins

Harvey and Faber first demonstrated hemolysin production in Listeria species in 1941 (Va'Zquez et al., 2001). This activity is encoded by the *hly* gene, which produces Listeriolysin O (LLO) a pH-dependent toxin critical for *L. monocytogenes* virulence (Nguyen et al., 2019). LLO operates in various host environments, including extracellular spaces, phagosomes and the cytosol. By forming pores in host cell membranes, LLO enables bacterial entry into phagosomes and supports invasion by facilitating calcium influx (Ruan et al., 2016*) L. monocytogenes* can also infect epithelial cells, such as Hep-2 (Malet et al., 2018). In addition, LLO promotes intracellular survival by triggering apoptosis in immune cells and aiding the bacterium's escape from phagosomes into the cytosol, where it can replicate (Maury et al., 2017).

Phospholipases

Listeria monocytogenes produces two types of phospholipase C enzymes: phosphoinositol-specific phospholipase C (PI-PLC or PLC-A) and broad-specificity phosphatidylcholine phospholipase C (PC-PLC or PLC-B), encoded by the *plcB* gene (Sibanda & Buys, 2022). These enzymes, along with Listeriolysin O (LLO), play key roles in the bacterium's escape from the phagosome into the host cell cytosol. PI-PLC inhibits pre-autophagosomal autophagy, while both PI-PLC and PC-PLC contribute to the disruption of the double-membrane vacuole, facilitating the pathogen's release. This coordinated action enables *L. monocytogenes* to evade clearance by autophagy a host defense mechanism that targets and degrades intracellular pathogens (Coelho et

al., 2019). Autophagy is a critical innate immune process that degrades damaged organelles and pathogens, particularly upon cell stress or death (Lavious & Anthony, 2020). By interfering with this pathway, *L. monocytogenes* enhances its intracellular survival and replication.

ActA

The *ActA* gene in pathogenic Listeria species encodes a protein that initiates actin recruitment and polymerisation, enabling actin-based intracellular motility. *ActA* activates actin polymerization near the phagosomal membrane, and polymerized actin enters through pores formed by Listeriolysin O (LLO), further widening them and disrupting the phagosome (Radoshevich & Cossart, 2018). This allows *L. monocytogenes* to escape into the cytosol.

Once in the cytosol, actin polymerisation continues at one pole of the bacterium, propelling it toward the host cell membrane. This results in the formation of elongated protrusions often referred to as actin comets or fibroids which extend into neighboring cells, facilitating cell-to-cell spread (Vasquez & Martin, 2016). Additionally, ActA helps the bacterium evade the host immune system by mimicking host proteins, allowing it to hide within epithelial cells and resist autophagy-mediated clearance (Radoshevich & Cossart, 2018).

***Listeria monocytogenes* contamination in food**

Listeria monocytogenes can be found in a wide range of food products, although its levels are generally low and rarely exceed the European safety threshold of 100 CFU/g throughout the product's shelf life (Figure 1 & Table 1). Raw materials and unprocessed products are often contaminated; however, standard heat treatments or other control measures typically prevent these foods from transmitting listeriosis before consumption. The bacterium is more commonly associated with minimally processed or lightly heat-treated products, where it can survive and, under certain conditions, proliferate (Kureljusic et al., 2019).

Key risk factors that promote the growth of *L. monocytogenes* in foods include extended refrigerated storage and the absence of reheating before consumption. Based on their susceptibility to contamination, ability to support bacterial growth, and documented links to past outbreaks, food items are categorized as high-, medium-, or low-risk (Wagner et al., 2007). Most listeriosis cases are associated with ready-to-eat (RTE) foods that are stored under refrigeration and consumed without reheating. The increasing popularity of RTE products and their prolonged shelf life have created favorable conditions for *L. monocytogenes* to persist and multiply (Loessner et al., 1996; Kayode, 2022). High-risk foods include soft cheeses, smoked fish, pâté, non-reheated frankfurters, deli meats, and unpasteurised milk, which have all been significantly linked to *L. monocytogenes* contamination and listeriosis cases (Sauders & D'Amico, 2021).

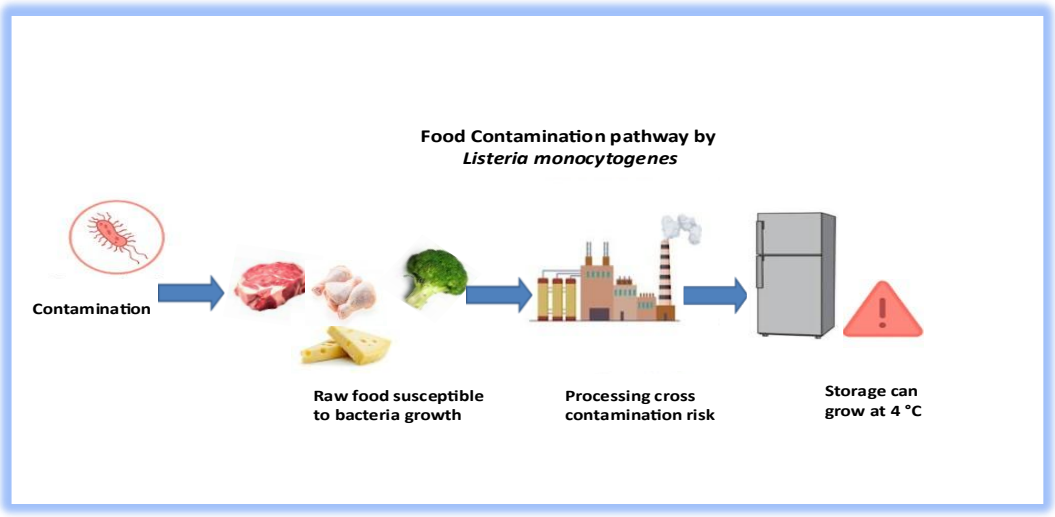

Figure1. Contamination of various food samples by *Listeria monocytogenes* and its potential implications for food safety.

Table 1. Occurrence of *Listeria monocytogenes* in raw and processed foods in Europe.

Country	Product	Number samples/number positive	Percentage (%)	No with > 100 CFU/ga (% of total)	Reference
Austria	Ready-to-Eat meat products	553/23	(4)	0 (0)	(Wagner et al., 2007)
Spain	Ready-to-Eat (RTE) fish products	140/9	(6)	0 (0)	Cabedo et al., 2008
Austria	Ready-to-Eat (RTE) fish products	96/18	(19)	5 (5)	(Pichler et al., 2009)
Belgium	Smoked fish	90/25	(28)	4 (4)	(Uyttendae et al., 2009)
Spain	Ready-to-Eat meat productS	Not specified	17.1–36.8% at manufacturing; 2.7–5.7% at end of shelf life	(0.78)	(Gómeze et al., 2015)
Denmark	Preserved fish products (Not heat-treated)	335/35	(11)	6 (2)	(Schjørring et al., 2017)
France	cold-smoked salmon	510/30	(6)	2 (<1)	(Schjørring et al., 2017)
Estonia	Ready-to-Eat foods (various)	30,016/1,081	(3.6)	0.3%	(Täht et al., 2019)
Sweden	Raw fish Salmon Products	310/40	(13)	7 (2)	(Schirone &Visciano, 2021)
Italy	Salmon Products	90/20	22	4 (3)	(Schirone &Visciano, 2021)
Italy	RTE delicatessen foods	132 / 23	17.4%	Not specified	(Rossi et al., 2024)

Food-borne outbreaks caused by *L. monocytogenes*

The relationship between food consumption and human illness has been recognized for centuries. Hippocrates (460 B.C.) was among the first to suggest a direct connection between food and disease (Hutt, 1984; Zhang et al., 2021). Foodborne pathogens such as viruses, bacteria, and parasites are biological agents capable of causing food poisoning. A foodborne disease outbreak is defined as the occurrence of two or more cases of the same illness resulting from the ingestion of contaminated food. Pathogens can cause disease either by being ingested and establishing infection within the human host or by producing toxins in food that are later consumed, leading to illness. Accordingly, foodborne illnesses are classified into two main types: (a) infection and (b) intoxication. Infections typically have a longer incubation period compared to intoxications, which cause a more rapid onset of symptoms. To date, more than 200 distinct foodborne diseases have been reported. The most severe outcomes usually occur in the elderly, very young, immunocompromised individuals, and in otherwise healthy individuals exposed to a high pathogen load (McLauchlin et al., 2020).

In China, a surveillance study involving 1,036 retail food samples, including vegetables, mushrooms, raw meat, seafood, and frozen products, revealed that *L. monocytogenes* was present in 20% of the samples (Wu et al., 2015). Although China lacked a national clinical surveillance system for listeriosis before 2013, several cases were reported in the medical literature. A retrospective study covering 1964 to 2010 examined the clinical and epidemiological features of listeriosis and found that 52% of cases were pregnancy-related, with septicemia (46%) and gastroenteritis (23%) as the most common presentations. The overall case-fatality rate was 26% (Feng et al., 2013). In the United States, the Centers for Disease Control and Prevention (CDC) estimates that listeriosis causes approximately 1,600 cases and 260 deaths annually (Morrison et al., 2018). In the European Union, the incidence of listeriosis is reported at 0.46 cases per 100,000 population, with a 17.7% case-fatality rate. In Asia, although fewer outbreaks are documented, several listeriosis incidents have been reported in different countries (Table 2).

Table 2. Documented cases of food-borne listeriosis in certain Asian nations.

Country	Case Description	Reference
Malaysia	• A 56-year-old immunocompetent man presented with cerebritis and infective endocarditis due to *L. monocytogenes*.	(Mohan et al., 2023)
Vietnam	● Three adults were presented with *L. monocytogenes* meningitis. ● Three of them experienced fever, headache, and vomiting ● Consumption of contaminated raw milk and soft cheese might be one of the reasons for the outbreak	(Chau et al., 2017)
China	● Eighty-two cases caused by contaminated egg products during preparation and packaging. ● Four pregnant women were infected through the consumption of roast meat, dairy products, seafood, and preserved vegetables	(Weiwei et al., 2018)

Japan	● Eighty-six persons had been infected with *L. monocytogenes.* ● Forty-four percent of patients developed gastroenteritis. ● Outbreak was caused by cheese	(WHO, 2016)
Thailand	● An immunocompromised patient had a brain abscess due to *L. monocytogenes* ● Most probably due to exposure to contaminated shrimp product in the company	(Vongkamjan et al., 2017)
Bangladesh	● A novel virulent strain of *L. monocytogenes* (CT 11424) was identified as the cause of a stillbirth.	(Alam et al., 2025)

Incidence and survival in foods and metabolic pathways

Most studies on *L. monocytogenes* have focused on its responses under aerobic conditions. However, *L. monocytogenes* is a facultative anaerobe, meaning it can adapt to varying oxygen levels, particularly during food processing. Studies show that the growth rate of *L. monocytogenes* strains is generally unaffected by oxygen concentration in the gastrointestinal tract (Couvert, 2019). A summary of the growth limits of *L. monocytogenes* is provided in Table 3. Changes in oxygen availability also impact the host's response to stressors, such as pH, osmolarity, invasiveness, and bile. These stressors are often used as protective measures in food processing. However, a phenomenon known as "stress hardening" can occur, in which pathogens like *L. monocytogenes* develop increased resilience to typically harmful conditions. This adaptation allows *L. monocytogenes* to withstand exposure to specific stress factors (Matereke & Okoh, 2020).

Table 3. Limiting conditions for growth of *L. monocytogenes* (Lado and Yousef 2007)

Growth parameters	Minimum limit	Optimum	Maximum limit
Temperature (°C)	-1.5°C	30–37	45°C
Salt (%)	10%	0.5-2%	25%
Water activity	0.90	0.97	-
pH (HCl as acidulant)	4.4	6.0–8.0	9.6

The growth of *L. monocytogenes* is enhanced by both glucosamine and N-acetylglucosamine, regardless of whether the conditions are aerobic or anaerobic. When cultivated anaerobically in glucose-defined media, *L. monocytogenes* produces lactate, acetate, formate, ethanol, and carbon dioxide (Nathan et al., 2017). Anaerobic conditions lead to increased lactate production, with 17% of the carbon from glucose metabolism used to synthesize other end products, suggesting that *L. monocytogenes* is not exclusively homofermentative. Additionally, metabolites like formate, ethanol, and carbon dioxide are generated, with lactate production being higher in anaerobic conditions compared to aerobic ones. In an anaerobic setting, lactate addition enhances the production of Listeriolysin O (LLO) (Wallace et al., 2017). Propionate, a natural food preservative and a significant fermentation acid in the intestine, has been shown to reduce adherent growth

under aerobic conditions without affecting planktonic growth (Ricke, 2003). Under anaerobic conditions, increasing pH levels decreased planktonic growth while promoting adherent growth.

Listeria monocytogenes and the formation of biofilms

L. monocytogenes can persist in food environments, posing a significant risk of contamination that may lead to food spoilage and disease transmission (Wiktorczyk-Kapischke et al., 2021). Biofilm formation plays a crucial role in the survival of *L. monocytogenes* within the food industry. Strains that persist in industrial settings tend to form thicker biofilms than those found sporadically (Mazaheri et al., 2021). Within biofilms, *L. monocytogenes* cells exhibit distinct traits compared to free-floating (planktonic) cells. Adherent cells undergo morphological changes, shifting from rod-shaped to coccoid forms as the population ages, and they grow more slowly (Trémoulet et al., 2002; Angelo et al., 2016). These embedded cells also show greater resistance to antibiotics and sanitizers, making their removal more difficult (Wiktorczyk-Kapischke et al., 2021).

Although different isolates show varying capacities to form biofilms, no direct link has been established with specific serovars or other factors (Borucki et al., 2004). Environmental conditions such as temperature, incubation time, adhesion surface, and the design of the experiment can significantly influence biofilm formation (Maury et al., 2016; Lee et al., 2017). Researchers have also examined the fatty acid profiles of biofilm-forming *L. monocytogenes* cells and observed elevated levels of specific fatty acids - iso-C14:0, anteiso-C15:0, and iso-C16:0 in strains with stronger biofilm-forming abilities. This suggests a potential link between fatty acid composition and biofilm development (Perez et al., 2012).

Specific regulation of *L. monocytogenes* biofilm formation

Adhesion is the critical first step in biofilm formation, setting the foundation for a sessile lifestyle. During this phase, various bacterial surface structures function as adhesins. Common bacterial appendages involved in adhesion include capsules, fimbriae, pili, and flagella. Capsules help protect bacteria from host immune responses; for example, capsular polysaccharides in *K. pneumoniae* enhance adhesion (Rajagopal and Walker, 2017). Fimbriae and pili, which are filamentous structures present in many pathogens, contribute to adhesion, colonization, and invasion of host tissues. Fimbriae have been implicated in biofilm formation and maturation in several species, including *E. coli* (Avalos Vizcarra et al., 2016), *Proteus mirabilis* and *K. pneumoniae* (Santos et al., 2019).

In *L. monocytogenes*, flagellar motility plays a pivotal role in biofilm formation. Genes such as *fliQ, flaA, fli1, motA,* and *lrmg_00396* have been identified as essential for biofilm development, particularly for early surface adhesion, through transposon mutagenesis studies (Osek et al., 2022). Flagella provide swimming ability, allowing bacteria to move toward favorable environments

(e.g., nutrients) and away from harmful stimuli (disinfectants), thereby maintaining a dynamic balance between motility and adhesion.

Importance of Cyclic-di-GMP on *L. monocytogenes* biofilm formation

Cyclic-di-GMP (c-di-GMP), also known as bis-(3′,5′)-cyclic diguanosine monophosphate, was first identified in *Acetobacter xylinum* in 1987 as an allosteric activator of cellulose synthase (Ross et al., 1987). Since then, it has been recognized as a key second messenger that regulates a wide array of bacterial processes through diverse signaling pathways (Hengge et al., 2016). Its significance lies in its ability to modulate various cellular behaviors, including biofilm formation, motility, and virulence.

The production and degradation of c-di-GMP are primarily mediated by proteins containing GGDEF (diguanylate cyclase) and EAL (phosphodiesterase) domains, which often function together. Additionally, its regulation is influenced by sensor kinases in bacterial two-component systems, allowing bacteria to respond rapidly to environmental changes (Ryjenkov et al., 2005). These domains and regulatory systems collectively control c-di-GMP levels and their downstream effects on bacterial physiology (see Figure 2).

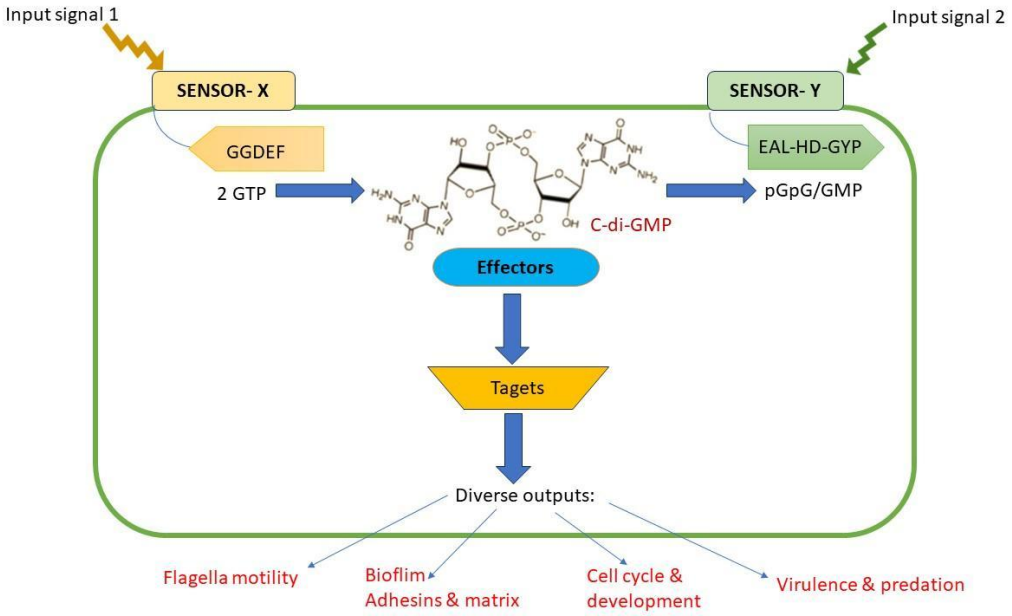

Figure. 2. The general scheme of production, degradation, mechanism of action and physiological target functions of the second messenger c-di-GMP.

GGDEF domain proteins possess diguanylate cyclase (DGC) activity, enabling them to synthesize c-di-GMP. On the other hand, EAL and HD-GYP domain proteins, which belong to distinct families of c-di-GMP-specific phosphodiesterases (PDEs), facilitate the degradation of c-di-GMP. In bacteria, the expression of these domains and the resulting c-di-GMP signaling pathway are integral to normal cellular processes. These domains are often associated with the bacterial

membrane. Environmental and intracellular signals, such as light (Tschowri et al., 2012), oxygen (Schmidt et al., 2016), membrane-derived signals, and various small ligands (Furukawa et al., 2012), serve as sensory cues. They modulate the levels of c-di-GMP, which, in turn, governs bacterial lifestyles, including biofilm formation and the production of exopolysaccharides in diverse proteobacterial organisms (Ryjenkov et al., 2005). This dynamic regulation of c-di-GMP plays a crucial role in shaping bacterial behaviors and adaptive responses in different environments. The involvement of this signaling pathway in exopolysaccharide production and biofilm regulation has been demonstrated in various bacterial species. In *Acetobacter xylinum, Vibrio cholerae, Pseudomonas aeruginosa, Pseudomonas fluorescens, Salmonella enterica, Agrobacterium tumefaciens* and *Escherichia coli*, the function of this pathway in exopolysaccharide development and biofilm regulation has been elucidated (D'Argenio et al., 2002; Branchu et al., 2013; Lindenberg et al., 2013; Richter et al., 2014). In *Listeria monocytogenes*, c-di-GMP-induced exopolysaccharide production was found to result in cell aggregation and increased bacterial resistance to disinfectants and desiccation stress. However, it did not promote biofilm formation on abiotic surfaces (Chen et al.,2014). These studies highlight the diverse effects of c-di-GMP-regulated exopolysaccharides in different bacterial species, influencing cellular behaviors, environmental adaptation, and bacterial survival strategies.

Persistence and biofilms of *L. monocytogenes*

Several studies have explored the relationship between bacterial lineage and biofilm formation. While some report that Lineage I strain forms stronger biofilms than Lineage II (Reis-Teixeira et al., 2017), others suggest the opposite, with Lineage II strains exhibiting greater biofilm-forming capacity (Byun et al., 2022). Persistence has also been linked to biofilm formation. Persistent strains that repeatedly are isolated from food-processing environments over time tend to form more robust biofilms than sporadic strains, which appear infrequently (Alexander et al., 2019). In the early stages of biofilm development, persistent strains show a higher initial attachment to food-contact surfaces compared to non-persistent strains; however, this difference diminishes after 72 hours. Contrarily, other studies have shown no significant difference in adhesion between persistent and non-persistent strains (Szlavik et al., 2012).

Genotypic analyses using PFGE and AFLP have failed to identify specific lineages associated with persistence, suggesting that persistence may depend more on environmental conditions and adaptation than on genotype (Unrath et al., 2021). Additionally, epidemic strains commonly linked to outbreaks adhere more strongly to surfaces and form denser biofilms within 24 hours than sporadic strains, indicating distinct behaviors between these groups (Lee et al., 2019).

Extracellular and biofilm-associated surface proteins

Biofilms are aggregates of sessile bacterial cells embedded in an extracellular matrix (ECM), which functions to anchor the bacteria both to each other and to biotic or abiotic surfaces (Bonsaglia et al., 2014; Xu et al., 2021). The composition of the ECM varies depending on the bacterial species and growth conditions, and typically includes exopolysaccharides, nucleic acids, lipids, and proteins (Flemming &Wingender, 2001). Among the proteins found in the ECM is a high-molecular-weight adhesin known as HMW1, which plays a key role in bacterial adhesion. Its extracellular localization supports its function in facilitating attachment. Additionally, several biofilm-specific proteins have been identified that contribute to the attachment and maturation stages of biofilm formation (Yang et al., 2024). Regulatory mechanisms governing the transition to a biofilm phenotype and the expression of these proteins have also been studied (Yao et al., 2018).

In *L. monocytogenes*, initial surface attachment is critically dependent on surface-associated and extracellular proteins (Nguyen et al.,2014). The bacterium possesses an extensive repertoire of over 130 surface proteins, which enhances its adaptability to diverse environmental conditions. Among these, Internalin A (InlA), a cell-wall-anchored protein, plays a crucial role in adhesion to and invasion of host cells by specifically binding to E-cadherin (Yujuan et al., 2024).

Protein (Bap)

Biofilm-associated protein (Bap) belongs to a family of surface proteins that are integral to biofilm formation. All Bap-related proteins share conserved structural features, including high molecular weight and a core domain composed of repetitive sequences, which facilitate the development of biofilm architecture. These proteins not only contribute to bacterial adhesion and biofilm maturation but also play significant roles in the pathogenesis of various bacterial species. Notably, Bap-like proteins are frequently encoded within mobile genetic elements, enhancing their dissemination across bacterial populations (Lasa and Penadés, 2006).

In *Listeria monocytogenes*, a recent in silico genome analysis identified an open reading frame (lmo0435) encoding a protein structurally similar to Bap, which has been designated BapL. This protein has been implicated in bacterial attachment to abiotic surfaces. Functional studies comparing an lmo0435 knockout mutant of *L. monocytogenes* strain 10403S to its isogenic wild-type strain demonstrated a marked reduction in attachment ability in the mutant, confirming the role of BapL in adhesion (Jordan et al., 2008). However, unlike other Bap homologs, BapL does not appear to be essential for virulence. Nonetheless, it remains a significant factor in the adhesion and colonization process *of L. monocytogenes.*

Biofilm formation and associated genes in *L. Monocytogenes*

Biofilm formation in *L. monocytogenes* is a complex and multifactorial process involving a wide

array of regulatory and structural genes associated with virulence, motility, stress response, and metabolic adaptation. Mutagenesis studies have identified several critical genes influencing biofilm development, particularly those involved in cell wall biosynthesis, motility, and metabolic functions (Chang et al., 2013). Extracellular appendages, especially flagella, have been shown to facilitate initial attachment to surfaces, a key step in biofilm initiation for both Gram-positive and Gram-negative bacteria (Rabin et al., 2015). To elucidate this process further, targeted mutational analyses of flagellar synthesis genes (e.g., *flaA, fliF, fliI, flgL, fliP*, and *fliD*) and motility-related genes (*motA*, *motB*) revealed that mutations significantly impaired surface adhesion and subsequent biofilm development (Fan et al., 2020; Luo et al., 2019).

In addition to structural genes, quorum-sensing (QS) systems also play a regulatory role in biofilm formation by controlling gene expression in response to bacterial population density. In *L. monocytogenes*, the QS system resembles the agr system of *S. aureus*, comprising the genes *agrD, agrB, agrC,* and *agrA* (Autret et al., 2003). Mutations in *agrA* and *agrD* have been shown to reduce biofilm formation under both static and dynamic conditions, highlighting their involvement in intercellular communication and surface colonization. Furthermore, the *luxS* gene, responsible for the synthesis of autoinducer-2 (AI-2) molecules, has also been implicated in QS-mediated regulation of biofilm architecture (Zetzmann et al., 2019).

The central virulence regulator *prfA* indirectly contributes to biofilm formation by influencing stress response and virulence-related gene expression. While *prfA*-deficient mutants retain motility and surface attachment abilities, they exhibit significantly impaired biofilm maturation (Palaiodimou et al., 2021). Interestingly, isolates harboring truncated *inlA* genes encoding the internalin A protein demonstrate enhanced biofilm-forming ability but reduced virulence, suggesting a possible trade-off between pathogenic potential and biofilm development (Janež et al., 2021).

Table 4 provides a concise overview of key genes involved in *L. monocytogenes* biofilm formation, detailing their functional roles and contributions to various stages of biofilm development. This tabulated summary enhances understanding of the genetic determinants underpinning biofilm regulation and persistence.

Table 4. Key biofilm-associated genes in Listeria monocytogenes and their roles in the regulation and development of biofilm formation.

Gene	Function	Role in Biofilm Formation	Reference
prfA	Transcriptional activator of virulence genes	Indirectly promotes biofilm via the regulation of stress and virulence genes	(Rieu et al., 2007)

sigB	Alternative sigma factor (σ^B)	Regulates stress response genes essential for biofilm initiation and persistence	(Gueriri et al., 2008)
flaA	Flagellin structural gene	Involved in initial surface attachment through flagella-mediated motility	(Lemon et al., 2007)
luxS	AI-2 quorum-sensing system	Modulates intercellular signaling, impacting biofilm structure and density	(Sela et al.,2006)
agrA	Agr quorum-sensing system	Negative regulation of biofilm formation and motility	(Marion et al.,2016)
bapL	Biofilm-associated protein-like gene	Involved in surface adhesion and microcolony formation	(Jordan et al., 2008)
inlA/inlB	Internalins	May contribute to initial adhesion during biofilm development	(Chen et al., 2009)
actA	Actin-assembly inducing protein	Important in cell aggregation and maturation of biofilm	(Travier et al., 2013)
lmo0673	Transcriptional regulator	Contributes to biofilm formation under nutrient-limited conditions	(Lemon et al., 2010
lmo2504	Putative membrane protein	Related to biofilm formation on abiotic surfaces	(Piercey et al., 2016))

RpoS activity

Sigma factors are essential bacterial proteins that facilitate the initiation of transcription by forming complexes with RNA polymerase (RNAP) and directing it to specific promoter regions. These transcriptional regulators enable the selective expression of gene sets in response to environmental or physiological cues. In *E. coli*, a well-studied bacterial model, there are seven distinct sigma factors, each governing the transcription of specific regulons (Gottesman, 2019). The primary sigma factor, σ^70 (also known as σ^D), is referred to as the "housekeeping" sigma factor. It is crucial for cell viability and governs the expression of genes involved in fundamental cellular processes, including growth and replication. In contrast, σ^38, also known as RpoS or σ^S, is the master regulator of the general stress response. RpoS controls the expression of a broad array of genes required for survival under adverse conditions, such as cold shock, entry into the stationary phase, oxidative stress, acid stress, and osmotic stress (Schellhorn, 2020).

The genes within the RpoS regulon are typically repressed under normal conditions and are only activated when specific stress signals are encountered. Thus, RpoS expression and activity are tightly regulated at multiple levels, including transcriptional, translational, post-translational, and proteolytic pathways to ensure that the stress response is activated only when necessary (Hengge, 2016; Gottesman, 2019).

Bio-preservation: application of bacteriocin

Biopreservation is characterized as the use of non-pathogenic microorganisms or their metabolites to improve microbiological protection and prolong the shelf life of foods (Abouloifa et al., 2022). Bio-preservation refers to the use of natural microflora and/or their antibacterial products to prolong the storage life and increase the protection of foods. It is known as the use of natural or regulated microbiota and/or their antimicrobial compounds to extend shelf life and food safety (Soltani et al., 2021). Fermentation, a process focused on the growth of microorganisms in foods, whether natural or added, is one of the most common types of food biopreservation. To ensure antifungal activity and improve organoleptic qualities, it uses the breakdown of complex compounds, the processing of acids and alcohols, the synthesis of Vitamin-B12, riboflavin, and Vitamin-C precursors, as well as the improvement of organoleptic qualities such as the production of flavor and aroma compounds. In the processing of fish, biopreservation is achieved by adding antimicrobials.

Bacteriocin production from *Lactobacillus* sp.

Bacteriocins are cationic, ribosomally synthesized antimicrobial peptides that exert their activity by disrupting the integrity of target cell membranes, typically through pore formation, ultimately leading to cell death. Lactobacillus and other lactic acid bacteria (LAB) are prolific producers of bacteriocins, which exhibit several advantageous characteristics, including a broad spectrum of antimicrobial activity, stability under varying pH and thermal conditions, and non-toxic effects on host tissues (García-Vela et al., 2023). A distinctive feature of LAB-derived bacteriocins is their resistance to digestive enzymes such as pancreatic proteases, trypsin, and chymotrypsin. This resistance allows them to act without disturbing the gut microbiota, making them safe for both therapeutic and food preservation applications (Silva et al., 2018; Darbandi et al., 2022). Although it is estimated that a significant percentage of bacterial species produce at least one type of bacteriocin, the majority remain undiscovered due to limited investigation and characterization.

Bacteriocins differ from conventional antibiotics in two fundamental ways: they are ribosomally synthesized, and they generally exhibit a narrow spectrum of activity. These peptides can be categorized based on molecular weight, target organisms, mechanisms of action, release systems, and immunity proteins. Notably, bacteriocins produced by Gram-positive and Gram-negative bacteria differ significantly in their structure and mode of action. Given their safety and specificity, bacteriocins are considered promising alternatives to traditional antibiotics. Their antimicrobial mechanisms include inhibition of cell wall biosynthesis, interference with nucleic acid (DNase or RNase) activity, or pore formation in the cytoplasmic membrane. LAB, particularly *Lactobacillus* spp., have a long history of use in the food industry, making them ideal candidates for bacteriocin

production in biocontrol applications. In food biopreservation, bacteriocins can be applied either by direct inoculation with bacteriocin-producing strains or through the addition of purified or semi-purified bacteriocins. These approaches can elicit either a bactericidal effect (with or without cell lysis) or a bacteriostatic effect, preventing microbial proliferation. Most LAB-derived bacteriocins, especially those targeting Gram-positive bacteria, primarily act by compromising the bacterial cell membrane (da Silva et al., 2014).

Classification of bacteriocins

Bacteriocins have been classified into various groups, taking into account different factors including the type of producing organism, physical characteristics, molecular sizes, chemical structures, and other relevant properties. Their mechanism of action is their mode of action. However, there is a lack of a clear classification for bacteriocins, and they were not extensively utilized in the initial stages. Ng et al., (2020) categorized them into four distinct groups. Class I is made up of low molecular weight lantibiotics and are a type of lantibiotic. Lanthionine and its derivatives make up this protein, which has a molecular weight of around 5kDa. The class II peptides are small thermostable peptides that lack lanthionine derivatives and have a molecular weight of about 10 kDa. Class II is further subdivided into three subclasses: IIa, IIb and IIc. Class III consists of thermostable high molecular weight compounds >30 kDa, while class IV consists of massive peptides paired with carbohydrates or lipids (Balciunas et al., 2013).

The intricate structures observed in class IV bacteriocins are merely byproducts of incomplete purification and should not be classified as a separate class of bacteriocins (Cleveland et al.2001; Kumariya et al., 2019). Cotter et al. introduced a new model in 2005. The classification is divided into two classes: class I consists of lantibiotics, while class II consists of peptides lacking lanthionine. Bacteriolysins are high molecular weight thermolabile peptides that have been classified separately (Cotter et al., 2005). Table 5 shows the new classification consisted of three major groups that were separated based on their genetic and biochemical characteristic (Drider et al., 2016).

Table 5. Classification, Characteristics and Mode of Action of Bacteriocins

Class	Subtype / Type	Bacteriocin	Producer Organism	Characteristics	Mode of Action	Class
Class I	Lantibiotics (lanthionine-containing peptides) Type A	Nisin	*Lactococcus lactis*	Small (<5 kDa), heat-stable peptides containing unusual amino acids like lanthionine	Pore formation via lipid II binding	(Parada., 2007)
		Epidermin	*Staphylococcus epidermidis*		Disrupts membrane potential via lipid II	(Alvarez-Sieiro et al., 2016)
	(Type B)	Mersacidin	*Bacillus subtilis*			(Mahrous et al., 2013)

Class II	IIa (Anti-Listeria)	Pediocin PA-1	*Pediococcus acidilactici*	Small, heat-stable peptides; strong anti-Listeria activity	Creates pores by binding to mannose phosphotransferase system	(Zacharof, and Lovitt., 2012)
	IIb (Two-peptide)	Lactococcin G	*Leuconostoc gelidum*	Requires two complementary peptides	Synergistic pore formation	(Nissen-Meyer & Nes, 1996)
	IIc (Circular)	Enterocin AS-48	*Enterococcus faecalis*	Head-to-tail cyclized peptide; very stable	Membrane insertion and disruption	(Abengóza et al., 2017)
	IId (Linear, single peptide)	Lactococcin A	*Lactococcus lactis subsp*	Linear, non-pediocin-like; single peptides	Pore formation	(Heng et al., 2006)
Class III	Large, thermolabile bacteriocins	Helveticin J	*Lactobacillus helveticus*	Large (>30 kDa), heat-labile proteins	Enzyme-like degradation of cell wall	(Perez, 2014) Sun et al., 2018)
Class IV (Complex bacteriocins)	Lipoprotein or glyco-bacteriocins)	Lactococcin DR1	*Lactococcus lactis*	Contains lipid or carbohydrate moieties	Enhanced membrane-targeting capabilities.	(Bédard & Biron., 2018)

Mechanism of action of bacteriocins

Bacteriocins' mechanism of action is determined by their primary structure. Others can function on the cytoplasmic membrane, releasing compounds that are essential to susceptible bacteria (cell lysis); and can penetrate the cytoplasm, affecting gene expression and protein synthesis synopsis (Figure 3).

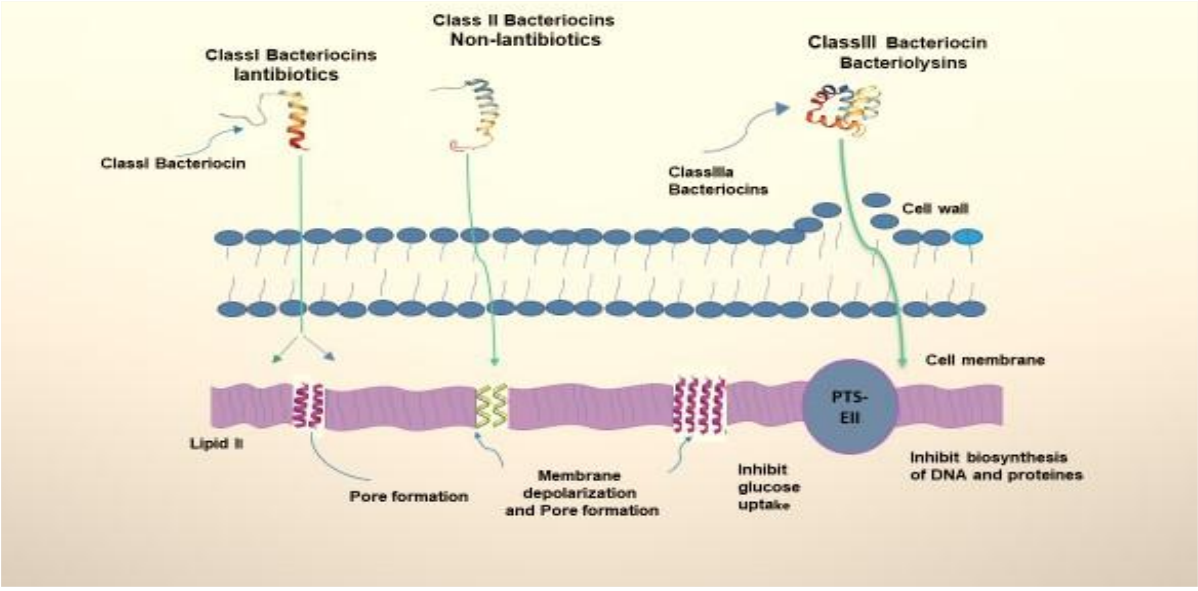

Figure 3. Mode of action of bacteriocins. Bacteriocins generate pores in the bacterial cell membrane by acting directly on the membrane or through a particular receptor on the target cell, resulting in cell death.

Bacteriocins belonging to the antibiotic class (Class I) exhibit a two-fold mechanism of action. Their primary function is to inhibit bacterial replication. This is accomplished by binding to lipid II, a hydrophobic peptidoglycan messenger, which initiates the synthesis of the cell wall. By disrupting the flow of monomers from the cytoplasm to the cell wall, these bacteriocins severely impair cell viability. Additionally, lantibiotics can utilize lipid II as a docking molecule, initiating a process that involves the insertion of the bacteriocin into the bacterial membrane and the subsequent formation of pores (Zhu et al., 2022). Bacteriocins classified as non-lantibiotics (Class II), including pediocin-like and one-peptide nonpediocin-like bacteriocins (Class IIa and Class IId), bind to the MptC and MptD subunits of the mannose transporter, known as permease phosphotransferase (Man-PTS). Once these bacteriocins are integrated into the membrane of the target cell, they induce the irreversible opening of an inherent channel. This channel permits the diffusion of ions across the membrane, ultimately resulting in the demise of the targeted cell (Todorov et al., 2022). Class IIb bacteriocins are a type of unmodified two-peptide bacteriocins that have the ability to permeabilize and create pores in the membranes of susceptible bacteria. These pores exhibit specificity towards monovalent cations, including Na+, K+, Li+, Cs+, and Rb+, as observed in lactococcin G, which is a notable example (Alexis et al., 2020). On the other hand, circular bacteriocins (Class IIc) have a positive net charge and can interact directly with the negatively charged bacterial membrane without the need for receptor molecules. Consequently, the formation of pores in the bacterial cell membrane occurs, leading to the escape of ions and the dissipation of the membrane potential, ultimately resulting in cell death (Perez et al., 2014). Bacteriolysins, classified as class IIIa bacteriocins, induce cell lysis by catalyzing the hydrolysis of the cell wall (Sun et al., 2018). Bacteriocins classified as class IIIb, which do not possess bacteriolytic properties, operate by disrupting the uptake of glucose by the target bacteria, leading to starvation and the disruption of membrane potential. Another mechanism involves inhibiting the synthesis of DNA and proteins in the targeted bacteria (Alexis et al., 2020).

Range of activity

Bacteriocins exhibit a diverse array of characteristics, including their antimicrobial range, producing organisms, molecular weight, stability, physical-chemical properties, and mode of action, making them a heterogeneous group. The classic type of bacteriocins displays activity primarily against closely related species, while the less common second type demonstrates a broader spectrum of activity against a wide range of Gram-positive microorganisms. For instance, nisin, produced by specific strains of *L. lactis* subsp. lactis (Martín et al., 2022), exemplifies this second type. Another example is pediocin, produced by *P. pentosaceus*. Nisin, an enzyme released by *Lactobacillus lactis* subsp. lactis, exhibits bactericidal effects specifically against Gram-

positive bacteria. Its effectiveness is observed at high concentrations or when the target cells have been pre-treated with EDTA (Roy et al., 2016). Nisin serves as a protective agent against food-borne pathogens like *L. monocytogenes* and other Gram-positive spoilage microbes (Barbosa et al., 2021). In Spain, nisin is referred to as E-234 and is recognized as a natural ingredient preservative. Alongside nisin, several other bacteriocins have been discovered, presenting potential challenges during the approval process for their use in food (Modugno et al.,2019).
Bacteriocins have limited effectiveness against Gram-negative bacteria due to the protective nature of their outer membrane, which acts as a barrier to antibacterial agents. However, there are exceptions. Yi etal. (2022) noted that bacteriocins ST28MS and ST26MS, produced by *L. plantarum* isolated from molasses, exhibited inhibitory effects on *E. coli, A. baumannii* and certain Gram-positive bacteria (Lade et al., 2006) found *that L. plantarum* and *L. lactis* from vegetable waste produced a bacteriocin that inhibited *E. coli*.

P. acidilactici QC38 inhibits *L. monocytogenes, L. innocua, S. typhimurium, E. coli, V. cholerae* NO 01 and *V. cholerae* O1 Ogawa (Morales-Estrada et al., 2016). The inhibitory activity of *Pediococcus* spp. against *Listeria* species was reported by Cavicchioli et al. (2017), indicating that bacteriocins produced by *E. hirae* ST57ACC and *P. pentosaceus* ST65ACC inhibited 100% of *L. monocytogenes strains* and two *L. innocua* strains. Nisin, produced by *L. lactis* subsp. *lactis*, has been reported to inhibit Gram-positive bacteria, *Clostridium*, and *Bacillus* spores. Considering its antimicrobial activity against *Listeria* spp., pediocin (*P. acidilactici*) has been shown to mitigate spoilage microorganisms during meat storage and efficiently inhibit *L. monocytogenes* in beef, turkey, and sliced jambon (da Costa et al., 2019). Similar to pediocin, the semi-purified bacteriocin BacTN635 (produced by *L. plantarum* sp. TN635) is strongly active against spoilage microorganisms in chicken breast and beef. The combined application of various bacteriocins, including subclass IIa bacteriocins, *L. fermentum* ACA-DC179, and bioprotective cultures of *E. faecium* PCD71, effectively inhibits *L. monocytogenes* in various meat products. Broad-spectrum antimicrobial enterocins against foodborne pathogens (*Clostridium* spp. and *Listeria* spp.) have also been noted (Silva et al.,2018). Purified bifidocin A displays a broad range of antimicrobial activity against spoilage and foodborne pathogens such as *S. aureus, L. monocytogenes, E. coli,* and some types of yeasts (Liu et al., 2015).

Bacteriocins and food preservation

Antimicrobial proteins derived from various bacterial sources, particularly bacteriocins, have gained attention for their application as natural bio-preservatives in diverse food products (Mohamed et al., 2016). Bacteriocins offer a promising complement to existing food preservation strategies due to their targeted antimicrobial activity and safety. Among these, bacteriocins produced by lactic acid bacteria (LAB) have been extensively investigated, especially in relation to meat products where LAB are frequently found. Although numerous bacteriocins have been isolated from LAB associated with food systems, their effectiveness can vary depending on the food matrix and application method. Nonetheless, when applied under optimal conditions, several bacteriocins demonstrate significant potential for industrial use. A well-documented example is the application of nisin in meat systems, which has shown consistent efficacy (Tanushree et al., 2021).

Traditionally, nitrites have been used to suppress *Clostridium* spp. in cured meats. However, health concerns related to nitrite usage have driven the search for alternative preservation methods. Bacteriocins offer a viable solution in this context, with studies showing that nisin alone or in combination with reduced levels of nitrites can effectively inhibit Clostridium growth. Numerous studies have demonstrated the practical application of bacteriocins in real food systems, particularly in controlling *L. monocytogenes*, a significant pathogen in ready-to-eat (RTE) foods. For example, the efficacy of sakacin A, produced by *Aureobasidium pullulans*, in RTE turkey breast has been examined (Trinetta et al., 2010). Direct application of the bacteriocin reduced *L. monocytogenes* by over 2 log CFU/g, while embedding sakacin A into pullulan based antimicrobial films resulted in an even greater reduction of approximately 3 log CFU/g.

Nisin, one of the most extensively studied bacteriocins, has been applied in RTE turkey ham at concentrations ranging from 0.2% to 0.5%, showing a clear dose dependent reduction in *L. monocytogenes* compared to untreated controls (Ruiz et al.2010). Leucocin A, produced by *Leuconostoc gelidum*, has also been used in products like wiener sausages, yielding a 1 log CFU/g reduction of *L. monocytogenes* after 16 days of refrigeration (Balay et al., 2017).

In dairy applications, nisin is frequently used for cheese preservation, particularly in fresh cheeses (Falardeau et al., 2021). Its effectiveness can be further enhanced when used in combination with other bacteriocins. For instance, co-application with bovicin HC5 in fresh cheese resulted in a 4 log CFU/g reduction of *L. monocytogenes* after nine days of cold storage (de Pimentel-Filho et al., 2014). In ripened cheeses, inoculating milk with a nisin-producing strain of Lactococcus lactis subsp. lactis resulted in an initial reduction of more than 2 log CFU/g (Dal Bello et al., 2012). However, a notable challenge remains the potential for pathogen regrowth during the ripening process (Falardeau et al., 2021). Other bacteriocins such as pediocins, enterocins and lactacins have shown some success, particularly when applied to the surfaces of fresh cheeses. However, their antimicrobial impact tends to diminish in aged dairy products (Ribeiro et al., 2017). Given this limitation, incorporating LAB strains that continuously produce bacteriocins in situ offers a promising strategy to enhance food safety, reduce reliance on synthetic preservatives, and support cleaner-label products (Possas et al., 2021).

Several successful industry-academic partnerships have demonstrated the practicality and impact of bacteriocins in real-world food systems. A prime example is nisin, a bacteriocin marketed as Nisaplin® by DuPont/Danisco. Its widespread use in cheese, canned foods and processed meats is the result of close collaboration between researchers and industry stakeholders, with a shared goal of controlling Listeria monocytogenes and other spoilage organisms.

Another notable case is the collaboration between Spanish food scientists and manufacturers on the incorporation of enterocin AS-48, produced by Enterococcus faecalis, into ready-to-eat food products. This initiative successfully demonstrated extended shelf life and reduced pathogenic load in commercial settings (Grande Burgos et al., 2014). In Europe, Plantaricin-producing strains of *L. plantarum* have been co-developed with local dairy producers for use in artisanal cheese fermentation. These collaborative efforts have resulted in improved microbial safety and longer shelf life without compromising sensory quality (Mills et al., 2017). Such examples underscore the importance of interdisciplinary collaboration in translating bacteriocin research into scalable, regulatory-compliant, and economically viable food preservation strategies. These partnerships not only help bridge the gap between lab and market but also support sustainable alternatives to synthetic additives.

Beyond *L. monocytogenes*, bacteriocins have also been explored for their broader role in extending the shelf life of fresh meat products. Bacteriocins such as leucocin A, enterocins, sakacins and carnobacteriocins A and B have demonstrated significant antimicrobial activity. Among these, pediocin PA-1, produced by *Pediococcus acidilactici*, is particularly effective, rapidly inhibiting pathogens including *Lactobacillus* spp. and *L. monocytogenes*. In one study, *L. monocytogenes* in raw chicken was successfully suppressed following treatment with pediocin PA-1. Additionally, bacteriocins from *P. acidilactici* have exhibited anti-biofilm properties, significantly reducing *Salmonella Typhimurium* contamination in food matrices and on processing surfaces (Seo and Kang, 2020).

A bacteriocin formulation derived from *Lactiplantibacillus plantarum* subsp., isolated from bacon, also demonstrated inhibitory effects against *L. monocytogenes*. Notably, when combined with nisin, this bacteriocin displayed a synergistic effect—achieving a 1000-fold reduction in *L. monocytogenes* at 4°C over a 13 day period, outperforming either agent alone. This combination holds significant promise for application in milk and dairy products, fruits, vegetables and fast foods (Owusu-Kwarteng et al., 2020).

Furthermore, Barman et al. (2018) developed a food-grade bacteriocin from *Lactococcus lactis* isolated from homemade buttermilk. The bacteriocin produced by this strain exhibited broad-spectrum antibacterial activity against both Gram-positive and Gram-negative foodborne pathogens, reinforcing its potential as a natural food preservative.

Limitations and challenges in the application of bacteriocins

Despite the promising potential of bacteriocins as natural bio-preservatives in the food industry, several limitations and challenges must be acknowledged. One primary concern is the regulatory approval process, which varies significantly across countries. While bacteriocins such as nisin have gained widespread acceptance and approval by the FDA and EFSA, many others lack the necessary regulatory status for use in commercial food systems. This poses a significant barrier to the broader adoption of newer bacteriocins (Garcia-Cano et al., 2019).

Bacteriocins produced by lactic acid bacteria (LAB) are widely regarded as safe and non-toxic compounds with antimicrobial properties. Numerous studies have reported that these bacteriocins show minimal toxicity at concentrations effective for inhibiting the growth of pathogenic or spoilage microorganisms. For instance, bacteriocins like nisin (Maher & McClean, 2006), colicins E1, E3, E7, and K (Murinda et al., 2003), plantaricin DM5 (Das & Goyal, 2014), and semi-purified bacteriocins from *Lactococcus lactis* subsp. lactis (Cavicchioli et al., 2017) demonstrated little to no cytotoxicity at their minimum inhibitory concentrations (MICs). However, nisin (Nutrition 21/USA) showed cytotoxic effects when applied at four times its MIC on HT29 cell lines and at

double the MIC on Caco-2 cells (Maher & McClean, 2006). Similarly, a semi-purified bacteriocin from Lactobacillus plantarum ST8SH exhibited significant cytotoxicity at 25 μg/mL, while no toxicity was observed at 5 μg/mL (Todorov et al., 2017). These findings highlight that the cytotoxic potential of LAB-derived bacteriocins is often concentration-dependent, an important factor to consider when determining their suitable application dosages.

In addition, optimizing bacteriocin production remains difficult due to slow synthesis rates and the need for specific growth conditions, including suitable nutrients, pH, and temperature (Banerjee et al., 2022). Some producing strains also fail to yield adequate amounts of active bacteriocins, limiting their protective role (Lahiri et al., 2022). Production and purification are often costly, and current methods can be inefficient (Bhattacharya et al., 2022). Additionally, bacteriocins are sensitive to harsh pH and temperature conditions and may bind poorly or distribute unevenly in food matrices, affecting their activity (Aljohani et al., 2023). Their performance also varies depending on the food system, as food composition influences their stability and efficacy (Lahiri et al., 2022).

Another concern is resistance development in target bacteria, often due to membrane modifications that reduce bacteriocin binding and effectiveness (Reuben &Torres, 2024). Their narrow antimicrobial spectrum further limits their use, especially against Gram-negative bacteria whose outer membranes act as barriers (Kirtonia et al., 2021). At low concentrations, bacteriocins target vegetative cells but not spores, and high doses may alter food taste or cause undesirable effects (Yu et al., 2023). Combining bacteriocins or using them with other antimicrobials can improve safety and efficacy (Kumariya et al., 2019). Genetic engineering also offers ways to enhance their properties, lower costs, and increase food application potential. Despite their promise, many bacteriocins remain unapproved due to regulatory barriers and concerns about cytotoxicity, including potential risks to mammalian cells. To gain approval, they must meet food safety standards and be produced by GRAS-certified strains (Lahiri et al.,2022).

Conclusion and future prospects

L. monocytogenes is a foodborne pathogen that can survive in the food chain and cause listeriosis, a serious illness. This bacterium's resilience is due to its ability to form biofilm communities of bacteria held together by a self-produced extracellular matrix. Contributing factors to its persistence include poor hygiene practices, ineffective sanitization, and genetic traits that provide resistance to extreme temperatures, pH variations, heavy metals, biocides, and biofilm formation. Despite extensive knowledge of its stress responses and tolerance mechanisms, *L. monocytogenes* continues to pose a significant threat in food production environments, representing a persistent hazard to consumers.

To address this issue, effective strategies are essential to reduce its presence in food industry settings and to develop safe and sustainable food preservation methods. This review highlights bacteriocins as promising antimicrobial agents for controlling biofilm formation by *L. monocytogenes*. Bacteriocins are ribosomally synthesized peptides that inhibit the growth of harmful bacteria. Their effectiveness depends on factors such as molecular structure, size, and antimicrobial spectrum. Importantly, bacteriocins are considered safe, health-beneficial, and environmentally friendly, making them valuable tools for improving food safety and preventing spoilage.

Despite the significant antimicrobial potential of bacteriocins produced by lactic acid bacteria (LAB), their widespread commercial application remains limited. Future research must address several key challenges to unlock the full potential of bacteriocins as natural food preservatives. Optimizing production and extraction processes is essential to increase bacteriocin yield and cost-efficiency while maintaining bioactivity. This can be achieved through improved fermentation strategies, metabolic engineering and the selection of high-yielding LAB strains. Furthermore, the development and application of novel bacteriocins with enhanced thermal stability, broader antimicrobial spectra especially against Gram-negative bacteria and increased resistance to food matrix interactions should be prioritized. Advances in biotechnology, such as genetic engineering and synthetic biology, can be leveraged to enhance bacteriocin expression, improve physicochemical properties, and overcome resistance mechanisms. Safety concerns continue to hinder regulatory approval; therefore, comprehensive toxicological evaluations and immunogenicity studies are required to support regulatory compliance and obtain GRAS (Generally Recognized as Safe) status for newly developed bacteriocins.

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