FOODBORNE PATHOGENS AND DISEASE
Volume 00, Number 00, 2026

DOI: 10.1177/15353141251408323

Listeria monocytogenes in Meat and Meat Products: Occurrence, Detection, Antibiotic Resistance, and Food Safety Implications

Sawsan A. Al-Hilifi,[1] Saher Sobeih George,[1] Shahd Abdul Karim,[1] Mamta Thakur,[2] Anka Trajkovska Petkoska,[3,4] Ammar Al-Farga,[5] Saeed Paidari,[6] Mohamed A. Fahmy,[7] and Sameh A. Korma[8,9]

Abstract

Listeria monocytogenes is a significant foodborne pathogen that poses serious risks to public health and the food industry. In humans, infections can lead to severe clinical outcomes, including gastroenteritis, septicemia, meningitis, encephalitis, and pregnancy-related complications such as stillbirths and spontaneous miscarriages. Contamination of meat and meat products has been associated with numerous outbreaks and sporadic cases worldwide. The detection and identification of *L. monocytogenes* involve traditional microbiological and biochemical methods, as well as advanced molecular techniques, including the polymerase chain reaction and matrix-assisted laser desorption/ionization time-of-flight mass spectrometry. This review provides a comprehensive overview of the microbiological characteristics, global prevalence, and antibiotic resistance profiles of *L. monocytogenes*. The emergence of multidrug-resistant strains underscores the importance of ongoing surveillance, effective antimicrobial stewardship, and rigorous adherence to food safety measures. Integrated efforts across the meat production and processing chain, combined with rapid diagnostic tools and public health interventions, are crucial to reducing the risk of listeriosis and ensuring the safety of meat products globally.

Keywords: *Listeria monocytogenes*, meat, contamination, infections, polymerase chain reaction, antibiotic resistance

Introduction

Meat is a nutrient-dense food that provides high-quality proteins, essential amino acids, fats, vitamins, and minerals. Its chemical composition varies by source and is commonly classified as white or red meat based on the myoglobin content of the muscle fibers. Red meat, which is rich in myoglobin, acquires a bright red color when myoglobin is exposed to oxygen and converted into oxymyoglobin. White meat, such as chicken, turkey, duck, pigeon, and fish, contains lower levels of myoglobin (Aalto-Araneda et al., 2019; Befa Kinki et al., 2024; Bonos et al., 2022). Meat contains varying amounts of protein, fat, and moisture, depending on the type of meat. Red meat is generally richer in myoglobin, fat-soluble vitamins, and iron compared with white meat. These components contribute to both the nutritional value and palatability of meat (Bonos et al., 2022; Gál et al., 2022; Pleadin et al., 2021; Wang et al., 2024). In addition to fats, meat contains proteins necessary for muscle development and tissue repair. It provides essential amino acids, which are vital for overall health (Budiarto et al., 2024; Wu et al., 2024). Iron content is higher in red meat compared with white meat (Cosgrove et al., 2005). Meat contains almost no carbohydrates, whereas the ash and moisture contents are approximately 1.1% and 69%, respectively (Romão et al., 2023). Being nutrient-dense and high in moisture, meat is easily susceptible to microbial attack, which can lead to the production of toxic substances and contamination of meat or

[1]Department of Food Science, College of Agriculture, University of Basrah, Basrah, Iraq.
[2]Department of Food Technology, School of Sciences, ITM University, Gwalior, India.
[3]Faculty of Technology and Technical Social Sciences, St. Kliment Ohridski University—Bitola, Veles, North Macedonia.
[4]Department of Materials Science and Engineering, Korea University, Seoul, Korea.
[5]Department of Biological Sciences, College of Science, University of Jeddah, Jeddah, Saudi Arabia.
[6]Department of Food Science and Technology, Isfahan (Khorasgan) Branch, Islamic Azad University, Isfahan, Iran.
[7]Department of Agricultural Microbiology, Faculty of Agriculture, Zagazig University, Zagazig, Egypt.
[8]School of Food Science and Engineering, South China University of Technology, Guangzhou, China.
[9]Department of Food Science, Faculty of Agriculture, Zagazig University, Zagazig, Egypt.

meat products (Abebe Bersisa et al., 2019; Smith et al., 2024; Zhang et al., 2024b). Foodborne pathogens in meat pose significant risks to public health. The World Health Organization (WHO, 2007–2015) estimates that foodborne diseases cause approximately 420,000 deaths annually, accounting for one-third of fatalities in children under 5 years of age (WHO, 2015). Bacteria, viruses, and parasites are the most common causes of foodborne illnesses, with *Listeria monocytogenes* being a notable pathogen due to its ability to contaminate meat, poultry, ready-to-eat foods, and dairy products (Hadi and Medicine, 2020; Moura et al., 2024; Shamloo et al., 2019). In addition to *Staphylococcus aureus*, *Salmonella* spp., and *Escherichia coli* O157:H7, *Listeria*-contaminated meat is a common cause of foodborne illnesses. Even small numbers of such pathogenic bacteria may cause cases of food poisoning, with the primary sources being animals immediately after slaughter, contaminated hands of workers, or the surrounding environment. There are more than 17 known species of the facultative anaerobic, Gram-positive *Listeria* (Osek et al., 2022; Zakaria and Sabala, 2024). *Listeria* is abundant in nature and has been isolated from humans, various animals, seaweeds, and a wide range of foods (Jamshidi and Zeinali, 2019; Orsi and Wiedmann, 2016). Pathogenic strains such as *L. monocytogenes* and *L. ivanovii* affect both humans and animals (Troxler et al., 2000). Common *Listeria* species are widely distributed pathogens that are frequently isolated from food (Kaszoni-Rückerl et al., 2020). When sanitary measures are inadequate, *L. monocytogenes* can naturally spread and persist in the environment and food processing areas. It is known to colonize a variety of foods, primarily those of animal origin and, less frequently, plant-based foods (Barbuddhe et al., 2021; Vitas and Garcia-Jalon, 2004). Cross-contamination can promote the growth of *Listeria* spp., especially in facilities where good manufacturing practices (GMPs) are not implemented (Aalto-Araneda et al., 2019). Listeriosis, resulting from the consumption of contaminated meat and meat products, can cause severe clinical outcomes in humans, including gastroenteritis, septicemia, meningitis, encephalitis, and pregnancy-related complications such as spontaneous miscarriages and stillbirths (Bustamante et al., 2020; Fagerlund et al., 2020; Liu et al., 2024). *L. monocytogenes* remains a focus pathogen in the food industry due to the high incidence and mortality of listeriosis, posing risks to public health and the economy. The food safety implications of *L. monocytogenes* contamination are substantial. Outbreaks often lead to large-scale product recalls, trade restrictions, and financial losses for the meat industry. Regulatory agencies such as the European Food Safety Authority and the U.S. Food and Drug Administration (FDA) require *L. monocytogenes* to be absent in 25 g of ready-to-eat meat products (FDA, 2022). In the European Union, Regulation 2073/2005 and its 2024 update mandate the absence of the pathogen in foods for infants or for special medical purposes, and ≤100 CFU/g in other ready-to-eat products at the end of shelf life (European Commission, 2005/2024) (EC, 2005). These measures reflect strict control policies designed to protect public health and prevent contamination in high-risk foods. These factors underscore the urgent need for comprehensive monitoring and prevention measures to safeguard consumer health and ensure food security. Therefore, understanding the occurrence, detection, and antibiotic resistance of *L. monocytogenes* is crucial to ensuring food safety (Paul, 2020; Shamloo et al., 2019). Detection methods range from conventional microbiological and biochemical techniques to advanced molecular approaches, including polymerase chain reaction (PCR) and matrix-assisted laser desorption/ionization time-of-flight mass spectrometry (MALDI-TOF-MS). This review provides a comprehensive overview of the occurrence, detection, antibiotic resistance, and food safety implications of *L. monocytogenes* in meat and meat products. The emergence of multidrug-resistant strains underscores the need for continuous surveillance, effective antimicrobial stewardship, and strict implementation of food safety measures. Integrated efforts across the meat production and processing chain, combined with rapid diagnostic tools and public health interventions, are crucial to reducing the risk of listeriosis and ensuring the global safety of meat products.

Review Methodology

This narrative review was designed and conducted in accordance with the Scale for the Assessment of Narrative Review Articles (SANRA) guidelines to ensure scientific rigor, transparency, and clarity. The objective was to synthesize and critically discuss current knowledge on *L. monocytogenes*, including its biochemical characteristics, diagnostic and detection methods, antimicrobial mechanisms of action, and occurrence in meat and meat-derived products. A comprehensive literature search was conducted across four major scientific databases—PubMed, Scopus, Web of Science, and Google Scholar—to identify publications from January 2010 to October 2025. The search strategy combined controlled vocabulary and free-text terms, including *L. monocytogenes*, oxidase status, biochemical identification, diagnostic methods, antimicrobial resistance, meat contamination, detection techniques, and foodborne pathogens. Boolean operators (AND, OR) and truncations were applied to refine the results. Titles and abstracts were screened for relevance, followed by full-text evaluation of potentially eligible studies. Inclusion criteria comprised peer-reviewed original research and review articles published in English that provided biochemical, diagnostic, or antimicrobial data relevant to *L. monocytogenes*. Exclusion criteria included non-peer-reviewed sources, conference abstracts, duplicate records, and studies lacking sufficient methodological detail. Although a Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) flow diagram was not applicable to this type of review, the screening and selection process was conducted transparently and systematically in alignment with the SANRA framework. The structure, argumentation, and synthesis of findings adhere to SANRA's six key criteria: justification of the review's rationale, comprehensive literature coverage, logical structuring, consistency between evidence and conclusions, linguistic clarity, and scientific contribution.

Characteristics of *L. monocytogenes*

L. monocytogenes emerged as a major foodborne pathogen in the early 1980s and is considered one of the most critical threats to food safety (Jamshidi and Zeinali, 2019; Osek et al., 2022). The bacterium was initially named *Listerella* in 1940. It is a Gram-positive, bacillus-shaped, nonspore-forming bacterium exhibiting psychrotrophic properties and facultative anaerobic metabolism (Lourenco et al., 2022). According to Painter and Slutsker (2007), it ferments sugars

such as rhamnose, produces lactic acid, and exhibits complete β-hemolysis. *L. monocytogenes* can grow across a wide temperature range (0–45°C), with optimal growth between 30°C and 37°C. Its pH growth range is 4.1–9.6 (Khan et al., 2016), although survival at pH values below 4 has also been reported. The bacterium can grow under both aerobic and anaerobic conditions, with anaerobic environments being more favorable (Lado and Yousef, 2007; Osek et al., 2022). Additionally, *L. monocytogenes* is catalase-positive and motile at temperatures ranging from 24°C to 28°C due to its peritrichous flagella; however, it becomes nonmotile at temperatures above 30°C (Indrawattana et al., 2011; Mohammad et al., 2024).

In humans, *L. monocytogenes* causes serious diseases, including abortion, recurrent infections in pregnant women, meningitis, and hemolysis in newborns. Clinical manifestations may resemble influenza or remain asymptomatic (Frece et al., 2010). Immunocompromised individuals, such as patients with cancer or those with acquired immunodeficiency syndrome, are particularly susceptible to listeriosis (Massawe et al., 2017). Natural reservoirs of *L. monocytogenes* include soil, swamps, plants, and animal feces, and it is often associated with lactic acid bacteria such as *Brochothrix* (Jamshidi and Zeinali, 2019). The bacterium has been detected in vegetables and fruits like cucumber, lettuce, potato, and parsley (Hamidiyan et al., 2018; Szymczak et al., 2014); in milk and milk products (Ribeiro et al., 2023), in fresh and frozen meat and poultry (Mustafa and Al-Nazal, 2019); as well as in seafood and seafood products (Madharsha et al., 2018). Due to its presence in diverse food and environmental sources, the proper isolation and accurate diagnosis of *L. monocytogenes* are essential (Fig. 1). Transmission to humans primarily occurs through the ingestion of contaminated food. At the cellular level, *L. monocytogenes* exhibits a unique intracellular lifestyle. After ingestion, the bacterium enters phagosomes of phagocytic cells and subsequently escapes into the cytoplasm. In non-phagocytic host cells, invasion requires bacterial surface proteins known as internalins. Internalin A binds to E-cadherin on epithelial cells, while internalin B facilitates the invasion of hepatocytes. Additional internalins, such as internalin C and internalin J, contribute to intestinal invasion and systemic infection. Once inside host cells, *L. monocytogenes* secretes listeriolysin O, a pore-forming toxin essential for phagosomal escape, intracellular survival, and cell-to-cell spread (Dhama et al., 2015; Jadhav et al., 2012).

Prevalence of *L. monocytogenes* and Other *Listeria* Species in Meat and Meat Products

L. monocytogenes is a monophyletic species that was initially classified within the family *Corynebacteriaceae* (Stuart and Welshimer, 1974). Currently, *L. monocytogenes* belongs to the family *Listeriaceae*, which includes 20 recognized species of the genus *Listeria*. Among these, only *L. monocytogenes* and *L. ivanovii* are pathogenic, with *L. monocytogenes* being the primary species associated with human disease (Hassan and Ali, 2024). The species *L. denitrificans*

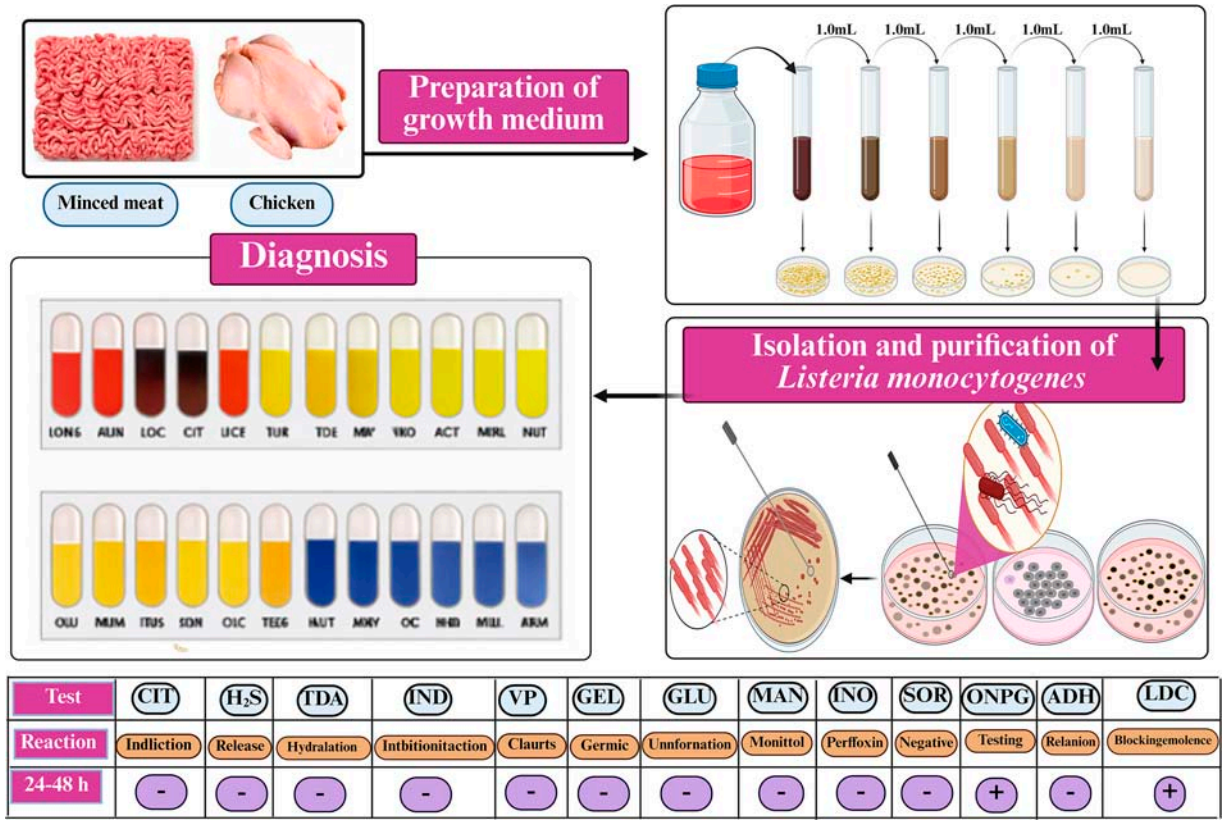

FIG. 1. Overview of the workflow for isolating and identifying *Listeria monocytogenes*, including preparation of growth medium, sample isolation, colony purification, and biochemical confirmation using the API *Listeria* test. API, analytical profile index.

was once classified in the genus *Listeria*; however, this classification was not retained because earlier analyses provided weak evidence for its relationship to other *Listeria* species.

Using numerical taxonomy based on Adansonian principles, Sneath and Cowan (1958) grouped *L. monocytogenes* with *Streptococcus, Micrococcus*, *Staphylococcus*, *Enterococcus*, *Erysipelothrix*, and *Corynebacterium pyogenes*. Similarly, da Silva and Holt (1965) demonstrated, through phenotypic classification dendrograms, that *Kurthia* (family *Brevibacteriaceae*) and *Listeria* occupy comparable phenon levels with *Corynebacterium* strains. Furthermore, Jones et al. (1966) observed considerable differences in serology and susceptibility to specific inhibitors. Still, they concluded that *L. monocytogenes* and *Erysipelothrix* share a close relationship, as evidenced by similarities in morphology, growth requirements, and pathogenic potential. According to the List of Prokaryotic Names with Standing in Nomenclature, *L. monocytogenes* remains the most significant pathogenic species, particularly for humans (Nwaiwu, 2020). *L. monocytogenes* is the most prevalent, frequently isolated from meat, poultry, seafood, dairy, and fresh produce (Cavalcanti et al., 2022; Matle et al., 2019; Oravcová et al., 2008; Santorum et al., 2012). Other species, such as *L. innocua*, *L. grayi*, and *L. welshimeri*, are commonly found in milk, cereals, and raw meat (Calderón-Miranda et al., 1999; Getaneh et al., 2025; Meshref et al., 2015), whereas environmental and recently described taxa (e.g., *L. marthii*, *L. riparia*, *L. thailandensis*) are primarily associated with soil, water, or food-processing environments (Graves et al., 2010; Leclercq et al., 2010; Núñez-Montero et al., 2018). Pathogenic species such as *L. ivanovii* and *L. seeligeri* have also been reported in meat, seafood, and ready-to-eat foods (Mpundu, 2023; Rossi et al., 2022). Overall, while multiple *Listeria* species can contaminate a wide range of foods, *L. monocytogenes* remains the primary threat to meat safety and public health. *L. monocytogenes* and other *Listeria* species isolated from meat, meat products, and other food sources are summarized in Table 1.

Global Prevalence (%) of *L. monocytogenes* in Meat and Meat Products

Animal-derived foods, particularly raw or partially cooked meat and meat products, are among the most significant sources of *L. monocytogenes*. Contaminated ready-to-eat or cooked meat products may also harbor this pathogen due to cross-contamination during handling, processing, packaging, or transportation. Although listeriosis is relatively rare, it is a life-threatening disease with considerable public health and economic implications. *L. monocytogenes* can survive and even grow at refrigeration temperatures, facilitating its persistence throughout the meat supply chain (Lomonaco et al., 2015; Ravindhiran et al., 2023). While the bacterium has been detected in other foods, such as dairy products, fresh produce, and seafood, meat and meat products remain the primary vehicles for human infection. Global prevalence data show considerable variability across regions and product types (Table 2). High contamination rates are observed in ready-to-eat and processed meat products, such as 59% in Brazil and 57% in Italy, as well as in chicken wing meat in Turkey (45%) (Cavalcanti et al., 2022; Elmali et al., 2015; Panebianco et al., 2022). Moderate prevalence is reported in India (40% in fresh milk and ice cream) and Malaysia (26.39% in chicken internal organs) (Goudar et al., 2021; Kuan et al., 2013), whereas lower rates are found in Morocco (2.4%) and Algeria (2.6%) (Bouayad and Hamdi, 2012; Ennaji et al., 2008).

Table 2 presents the global prevalence of *L. monocytogenes* in various food products, including meat and other foods, across different countries. The data reveal substantial variability, with higher contamination rates typically observed in ready-to-eat and processed meat products compared with raw meats. These trends highlight critical control points in hygiene and monitoring, emphasizing the importance of targeted surveillance, preventive measures, and region-specific risk assessment. The prevalence trends highlight the need for continuous monitoring and effective implementation of food safety systems. Specific interventions include the strict separation of raw and cooked products, regular sanitization of equipment and surfaces using approved disinfectants, continuous temperature monitoring during storage and transportation, employee training on proper handling and hand hygiene practices, and routine environmental monitoring for *L. monocytogenes*. Integration of these practices within hazard analysis and critical control points (HACCP) and GMP frameworks ensures proactive contamination control, facilitates rapid outbreak response, and mitigates public health risks associated with *L. monocytogenes* in meat and meat products (Lomonaco et al., 2015; Panebianco et al., 2022; Ravindhiran et al., 2023).

Occurrence and Key Contamination Points of *L. monocytogenes* in the Meat and Meat Products Chain

L. monocytogenes is widely distributed in the environment, having been isolated from agricultural soils and vegetation (Rodrigues et al., 2017), food-processing facilities (Martín et al., 2014), and retail outlets (Henri et al., 2016). Consequently, multiple contamination routes exist through which the pathogen can enter the meat production continuum, ultimately posing a risk to consumers. Contamination of meat and meat products is a complex, multistep process that links primary production on farms and feedlots with processing facilities, retail outlets, and distribution networks (Fig. 2).

L. monocytogenes *at the farm level*

On farms and feedlots, *L. monocytogenes* is primarily associated with soil, where it persists as a natural inhabitant, usually at low levels but capable of surviving for months or even proliferating under favorable conditions (O'Connor et al., 2010). Prevalence surveys have reported *L. monocytogenes* in 8.7–51.4% of agricultural soils and 15.2–43.2% of nonagricultural soils (Sauders et al., 2012), confirming that soil is a significant reservoir for animal exposure. Contaminated soil dust may further facilitate the airborne dissemination of contaminants to animals and, indirectly, to humans (Korthals et al., 2008). Listeriosis in animals has frequently been linked to the ingestion of contaminated silage (Harakeh et al., 2009). Poorly fermented or inadequately stored silage provides favorable conditions for bacterial growth (Zhu et al., 2017). Infected feces and contaminated feed may serve as vehicles for pathogen recycling within the environment

TABLE 1. REPORTED FOOD MATRICES ASSOCIATED WITH THE ISOLATION OF *LISTERIA MONOCYTOGENES* AND OTHER *LISTERIA* SPECIES

Listeria *species*	*Foods*	*References*
L. innocua	Skim milk	(Calderón-Miranda et al., 1999)
	Cereal	(Yong et al., 2024)
	Fish, meat, pork pies, crab meat, and pâté	(Nayak et al., 2015)
	Raw meat	(Getaneh et al., 2025)
L. monocytogenes	Strawberries, potatoes, and parsley	(Oravcová et al., 2008; Szymczak et al., 2014)
	Non-smoked steamed cheese, frozen fish, frozen burger, and frozen chicken	(Al-Ghanim and Abbas, 2021)
	Petrovská klobása sausage	(Janković et al., 2017)
	Raw milk, beef, and Turkey ready-to-eat meat	(Santorum et al., 2012)
	Seafood products	(Fallah et al., 2013)
	Austrian cooked-cured meat products	(Awaiwanont et al., 2015)
	Ready-to-eat dairy and meat foods, retail meat and dairy products	(Bouayad and Hamdi, 2012)
	Raw meat, meat products, and poultry	(Burnett et al., 2022; Cavalcanti et al., 2022; Ennaji et al., 2008; Getaneh et al., 2025; Matle et al., 2019; Panebianco et al., 2022)
	Ready-to-eat meat	(Zhang et al., 2021b)
	Chicken internal organs (heart, liver, and gizzards)	(Kuan et al., 2013)
	Fresh milk and ice cream	(Goudar et al., 2021)
	Poultry and pork	(Filipello et al., 2020)
	Minced meat, chicken liver, sausages, chicken meat, and frozen fish	(Mustafa and Al-Nazal, 2019)
	Meat products, lettuce, spices, and cucumbers	(Hamidiyan et al., 2018)
	Food samples from supermarkets and street vendors, ready-to-eat food	(El-Shenawy et al., 2011; Obi et al., 2012)
	Fresh chicken meat	(Zeinali et al., 2017)
	Chicken wing meat	(Elmali et al., 2015)
L. rocourtiae	Lettuce	(Leclercq et al., 2010)
L. marthii	Soil, standing water, and flowing water samples	(Graves et al., 2010)
L. murrayi	Raw beef	(Gebretsadik et al., 2011)
L. grayi	Raw meat	(Getaneh et al., 2025)
	Milk and burger	(Meshref et al., 2015)
L. welshimer	Raw meat	(Getaneh et al., 2025)
L. weihenstephanensis	*Lemna trisulca*	(Lang Halter et al., 2013)
L. fleischmannii	Cheese	(Bertsch et al., 2013)
L. riparia	Water	(den Bakker et al., 2014)
L. grandensis		
L. floridensis		
L. cornellensis		
L. aquatic		
L. seeligeri	Buffalo milk and meat	(Nayak et al., 2015)
	Poultry, beef, ready-to-eat deli meats, lettuce, and environmental samples	(Mpundu, 2023)
	Raw meat	(Getaneh et al., 2025)
L. newyorkensis	Seafood and dairy	(Weller et al., 2015)
L. booriae		
L. goaensis	Mangrove swamps	(Doijad et al., 2018)
L. costaricensis	Food processing drainage system	(Núñez-Montero et al., 2018)
L. thailandensis	Fried chicken	(Leclercq et al., 2019)
L. ivanovii	Conserved fish and seafood	(Rossi et al., 2022)
	Cheese and burger	(Meshref et al., 2015)

(Deniz et al., 2025), while asymptomatic shedding of *L. monocytogenes* by livestock further increases the risk of silent transmission through the food chain (Leong et al., 2016). Additional farm-level risk factors include inadequate husbandry practices and contaminated drinking water or wastewater, which may harbor high levels of the pathogen (Linke et al., 2014). Control at this stage is critical for reducing downstream contamination risks. Recommended preharvest strategies include optimizing diet, implementing biosecurity measures, providing clean feed and water, and effective waste management (Buncic et al., 2014; Nørrung and Buncic, 2008; Sofos and Geornaras, 2010). However, their implementation is often limited by economic constraints, resource availability, and the level of farmer awareness.

Table 2. Regional Prevalence (%) of *Listeria monocytogenes* in Meat, Meat Products, and Various Food Matrices Based on Reported Sampling Frames

Regions	*Foods*	*Sampling frame*	L. monocytogenes *(%)*	n/N *(if available)*	*References*
China	Ready-to-eat meat	49/400	12.2	Retail outlets and processing plants	(Zhang et al., 2021b)
Brazil	Meat products	59/100	59	Processing facilities and retail markets	(Cavalcanti et al., 2022)
Jamaica	Meat	24/100	24	Local markets and abattoirs	(Burnett et al., 2022)
Morocco	Raw meat, meat products, and poultry	NA	2.4	Butcher shops and retail outlets	(Ennaji et al., 2008)
Malaysia	Chicken internal organs (heart, liver, and gizzards)	NA	26.39	Wet markets	(Kuan et al., 2013)
South Africa	Meat and meat products	14/95	14.7	Retail stores	(Matle et al., 2019)
Turkey	Chicken wing meat	45/100	45	Poultry processing plants	(Elmali et al., 2015)
Northeast Iran	Fresh chicken meat	18/100	18	Local markets	(Zeinali et al., 2017)
Poland	Strawberries	NA	10	Retail markets	(Szymczak et al., 2014)
	Potatoes	NA	15	Farm and retail samples	
	Parsley	NA	5	Local markets	
Egypt	Street vendors sold ready-to-eat food	14/100	14	Street vendors	(El-Shenawy et al., 2011)
Botswana	Food samples from supermarkets and street vendors	4/100	4.3	Mixed retail and street sources	(Obi et al., 2012)
Iran	Cucumbers	14/100	14	Local markets	(Hamidiyan et al., 2018)
	Spices	12/100	12	Retail spice shops	
	Lettuce	10/100	10	Wet markets	
	Meat products	6/100	6	Retail markets	
Iraq	Minced meat	5/100	5	Butcher shops	(Mustafa and Al-Nazal, 2019)
	Chicken liver	5/100	5	Retail markets	
	Sausages	10/100	10	Local stores	
	Chicken meat	5/100	5	Retail markets	
	Frozen fish	10/100	10	Local supermarkets	
Italy	Poultry and pork	15/100	15	Slaughterhouses and retail	(Filipello et al., 2020)
	Meat	57/100	57	Processing facilities	(Panebianco et al., 2022)
India	Fresh milk and ice cream	40/100	40	Retail and dairy plants	(Goudar et al., 2021)
Ethiopia	Retail meat and dairy products	4/100	4.1	Local markets	(Bouayad and Hamdi, 2012)
Algeria	Ready-to-eat dairy and meat foods	3/115	2.6	Street vendors and markets	(Bouayad and Hamdi, 2012)
Southwest Ethiopia	Raw meat from abattoirs and butcher shops	7/100	7	Abattoirs and butcheries	(Getaneh et al., 2025)

Sampling frames were derived from each study's description (e.g., retail markets, abattoirs, or processing facilities). Prevalence values represent the proportion of positive samples among the total tested (n/N) when available. Confidence intervals (CIs) were inconsistently reported; therefore, direct cross-country comparisons should be interpreted cautiously due to methodological heterogeneity.

NA, data not available in the cited source.

L. monocytogenes *at the food-processing level*

Food-processing facilities, including abattoirs, meat-processing plants, and butcheries, represent critical points of contamination (Carpentier and Cerf, 2011; Rajalingam and Van Haute, 2025). Animals arriving for slaughter can serve as carriers, and molecular studies, such as pulsed-field gel electrophoresis typing, have confirmed the transmission of identical strains from farm environments to carcasses (Deniz et al., 2025). Other significant sources of contamination include raw materials, workers, equipment, and environmental surfaces such as drains, floors, and conveyors (El-Shenawy et al., 2011; Gil et al., 2024). Most studies on *L. monocytogenes* have focused on meat and meat products, as well as ready-to-eat foods. However, few studies have addressed the environment and processing equipment, which are also critical vectors for the transmission of this bacterium and should be emphasized rather than neglected (Adebesin et al., 2024). The persistence of *L. monocytogenes* in processing environments is primarily attributed to its remarkable tolerance to stress conditions, including low temperatures, pH, and osmotic pressure, as well as its resistance to disinfectants and ability to form biofilms (Carpentier and Cerf, 2011). Unlike many bacteria, *L. monocytogenes* can proliferate during cold storage due to the activity of cold-shock proteins and the stress response regulator sigma

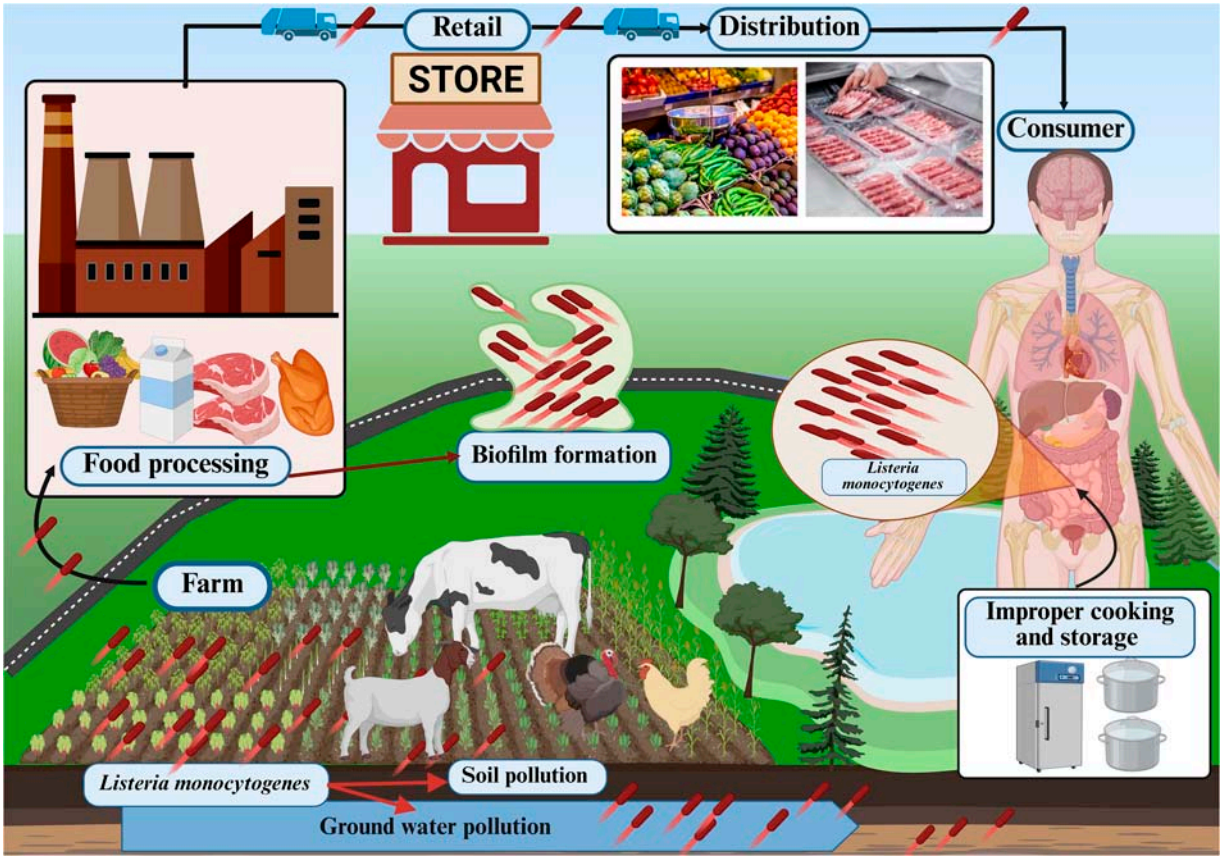

FIG. 2. Transmission pathways and key contamination points of *Listeria monocytogenes* from environmental sources (soil and groundwater) through farm, food processing, storage, distribution, and retail, to consumers, including risks from improper cooking and storage.

B (Leong et al., 2016). Insufficient sanitation, inaccessible harborages, and biofilm formation on surfaces such as stainless steel, polyethylene, glass, and polyvinyl chloride further enhance its persistence (Fouladynezhad et al., 2013).

L. monocytogenes *at the retail level*

At retail, the detection of *L. monocytogenes* does not always indicate contamination at that point, as the pathogen may have originated earlier in the production chain (Sauders et al., 2009). Nevertheless, cross-contamination in retail outlets is a common occurrence, with food-contact surfaces, utensils, slicing equipment, and handlers serving as key vectors. Meat that is sliced, repackaged, or otherwise manipulated at retail often shows higher contamination levels compared with vacuum-packed or factory-sealed products (Gombas et al., 2003). Recent studies have highlighted the persistence of *L. monocytogenes* at the retail level in various food categories, including meat, dairy, and fresh produce, underscoring its ability to survive under diverse storage and handling conditions (Burnett et al., 2020; Tirloni et al., 2024; Zhang et al., 2024a). These findings highlight that retail environments not only represent a point of potential contamination but also serve as a reservoir where the pathogen can persist and spread across different product types. Preventive strategies at this stage are centered on rigorous hygiene practices, including proper sanitation of surfaces and utensils, strict personal hygiene among workers, and maintenance of storage temperatures that limit pathogen growth. Since retail represents a direct interface with consumers, these control measures are especially critical for preventing human exposure.

L. monocytogenes *at the distribution level of meat and meat products*

During distribution, *L. monocytogenes* contamination has been reported in a wide range of meat products from both domestic livestock and game animals (Kramarenko et al., 2013; Lambertz et al., 2012). The contamination rates of this pathogen have been documented as 5–92% in meat and meat products, 12–60% in poultry, and 4–18% in seafood (Atasever, 2025; Sharma et al., 2024). Prevalence rates vary widely depending on region, product type, and processing conditions. In Spain, contamination was reported in 34.9% of minced pork and beef and 36.1% of poultry products (Vitas and Garcia-Jalon, 2004). In Sweden, heat-treated ready-to-eat products showed prevalence rates of 61% in ham, 12% in turkey, 9% in roast beef, and 7% in sausage (Lambertz et al., 2012). In Estonia, prevalence reached 18.7% in raw meat and 2% in ready-to-eat products (Kramarenko et al., 2013), while in Ireland, 4.2% of poultry-based ready-to-eat meat products tested positive (Leong et al., 2016). Other studies from India, Japan, and South Africa also report variable prevalence rates (Matle et al., 2019). Studies have shown that the consumption of foods

contaminated with *L. monocytogenes*, such as turkey sausage, can lead to listeriosis (Zhang et al., 2021a). The majority of meat products have been implicated in outbreaks or sporadic cases of the disease (Burnett et al., 2020). Additionally, processed and vacuum-packed meat products sold in markets without proper temperature control, particularly when exposed to seasonal fluctuations, represent a potential source of infection. Reports indicate that *L. monocytogenes* is a primary contributor to meat contamination at points of sale. Its prevalence in meat varies across countries, as documented in several studies (Maćkiw et al., 2020; Meza-Bone et al., 2023; Parra-Flores et al., 2021; Rincón-Gamboa et al., 2024). These findings highlight the widespread occurrence of this pathogen across the meat value chain and emphasize the importance of identifying critical control points to limit consumer exposure. The transmission pathways and key contamination hotspots, spanning from farm environments to consumer-ready products, are summarized in Figure 2.

Detection of *L. monocytogenes*

The genus *Listeria* consists of Gram-positive bacilli that are motile at 25°C and do not form spores. On blood agar containing 5% sheep or human blood, *L. monocytogenes* typically produces small colonies surrounded by a narrow zone of β-hemolysis due to its ability to lyse red blood cells. Selective media, such as polymyxin, acriflavine, lithium chloride, cephaloridine, aesculin, mannitol (PALCAM) agar (which comes from its main selective ingredients: polymyxin, acriflavine, lithium chloride, ceftazidime, aesculin, and mannitol) and Oxford agar, are commonly used to isolate and purify *Listeria* from food samples. In diagnostic tests, *L. monocytogenes* is catalase-positive and oxidase-negative, which are imperative biochemical markers (Kureljušić et al., 2017; Legba et al., 2020; Toplu and Tuncer, 2023). The bacterium can survive under a wide range of environmental conditions. It grows at temperatures between 2°C and 45°C, can multiply at refrigeration temperatures (4°C), and withstands desiccation for extended periods. Although *L. monocytogenes* is sensitive to heat, it may survive mild heat treatments. For example, it can survive 60°C for 10 min, but standard high-temperature short-time pasteurization (72°C for 15 s) is generally effective in inactivating it (Mustafa and Al-Nazal, 2019). Its ability to persist in diverse environments and under stress conditions makes it a pathogen of significant concern in the food industry. A variety of conventional and molecular methods have been developed to detect *L. monocytogenes* in food. Conventional culture and biochemical tests remain widely used (Table 3). For instance, colonies on selective media such as PALCAM can be further characterized using catalase tests, oxidase tests, Gram staining, and the Christie–Atkins–Munch–Peterson (CAMP) test (Madharsha et al., 2018; Rapeanu et al., 2017; Wang et al., 2019). These methods allow preliminary identification and confirmation of the bacterium in a range of food matrices. Molecular methods have greatly improved the sensitivity and specificity of detection. PCR techniques have been successfully applied to confirm *L. monocytogenes* in strawberries, parsley, and potatoes (Szymczak et al., 2014). More recently, Song et al. (2023) developed the Proofman-LMTIA (ladder-shape melting temperature isothermal amplification) assay for rapid detection in fresh pork. This method demonstrated high specificity and sensitivity, making it a reliable tool for rapid monitoring and supporting food safety regulations.

Various methods have been developed for the detection of *L. monocytogenes*, categorized into reference (conventional) methods and alternative rapid methods. Reference methods, including ISO 11290-1 and the FDA Bacteriological Analytical Manual protocols, are widely used in previous studies and involve comprehensive enrichment and confirmation steps to ensure high reliability. In contrast, rapid methods such as PCR-based assays and lateral flow immunoassays provide shorter detection times. However, they often require a brief pre-enrichment step and subsequent confirmation to maintain accuracy. Each method is characterized by its analytical unit, enrichment procedure, and confirmation pathway, which vary depending on the type of sample (e.g., solid vs. liquid food). Table 4 summarizes the key features of commonly used reference and rapid detection methods as reported in the literature.

Table 3. Overview of Conventional, Molecular, and Rapid Detection Methods for *Listeria monocytogenes* in Food Samples, Including Principles and Applications

Detection method	*Principle/technique*	*Sample/application*	*References*	*Notes*
Culture/selective media	Isolation on PALCAM or Oxford agar; β-hemolysis on blood agar	Fish, meat, dairy, and vegetables	(Kureljušić et al., 2017; Madharsha et al., 2018)	Produces typical colonies; allows subsequent biochemical testing
Biochemical tests	Catalase test (positive), oxidase test (negative), CAMP test	Lettuce, other food matrices	(Rapeanu et al., 2017; Wang et al., 2019)	Traditional confirmation methods
Gram staining	Visual identification of Gram-positive bacilli	Lettuce, vegetables	(Rapeanu et al., 2017; Wang et al., 2019)	Confirms morphology; simple and rapid
PCR/molecular detection	Amplification of specific *L. monocytogenes* genes	Strawberry, parsley, potato	(Szymczak et al., 2014)	High sensitivity and specificity
Proofman-LMTIA (rapid molecular assay)	Ladder-shaped melting temperature isothermal amplification	Fresh pork	(Song et al., 2023)	Rapid, reliable, high specificity; suitable for food safety monitoring

PALCAM, polymyxin, acriflavine, lithium chloride, cephaloridine, aesculin, mannitol (agar); CAMP, Christie–Atkins–Munch–Peterson (test); PCR, polymerase chain reaction; LMTIA, ladder-shape melting temperature isothermal amplification.

Table 4. Comparative Overview of Conventional and Emerging Rapid Methods for Detecting *Listeria monocytogenes* in Food Samples, Including Procedural Steps, Analytical Parameters, Performance Characteristics, Advantages, and Limitations

Method type	*Reference/ rapid*	*Sample size/ analytical volume*	*Pre-enrichment*	*Enrichment*	*Selective isolation*	*Confirmation*
ISO 11290-1	Reference	25 g solid/25 mL liquid	Optional pre-enrichment	Half-Fraser broth 24–48 h → Fraser broth 24–48 h	Plating on selective agar	Biochemical tests or PCR confirmation
FDA BAM	Reference	25 g/25 mL	Optional pre-enrichment	Buffered *Listeria* enrichment broth 24–48 h	Plating on selective agar	Biochemical/serological confirmation
PCR-based kit	Rapid	1 g/1 mL	Short pre-enrichment 18–24 h (optional)	Optional	Plating on selective agar	PCR detection
Lateral flow/immunoassay	Rapid	25 g	Short pre-enrichment 18–24 h	Optional	Direct detection possible	Device readout
ELISA-based detection	Rapid	25 g	Short pre-enrichment 18–24 h	Optional	Direct detection on the device	Immunoassay confirmation
Fluorescence immunoassay (MBs + Core-Shell QDs)	Rapid	1–10 mL	Not required	Not required	Direct detection using magnetic bead capture	Fluorescence signal confirmation

ISO, international organization for standardization; PCR, polymerase chain reaction; FDA BAM, food and drug administration bacteriological analytical manual; ELISA, enzyme-linked immunosorbent assay; MBs, magnetic beads; QDs, quantum dots; LOD, limit of detection; CFU, colony-forming unit.

Table 4. Extended

Method type	*Time to result*	*Advantages*	*Limitations*	*References*
ISO 11290-1	≈5–7 days	Highly reliable, standardized, widely accepted	Time-consuming, labor-intensive	(Jadhav et al., 2012)
FDA BAM	≈5–7 days	Standardized, validated by regulatory agencies	Time-consuming, requires skilled personnel	(Aladhadh, 2023; Law et al., 2014)
PCR-based kit	≈1–2 days	Fast, sensitive, and capable of detecting low bacterial loads	May require enrichment for very low bacterial concentration loads	(An et al., 2025; Law et al., 2014; Yordanova and Andonova, 2024)
Lateral flow/immunoassay	<1 day	Rapid, easy to use, minimal training required	Lower sensitivity, confirmation recommended	(Law et al., 2014; Zhang et al., 2025)
ELISA-based detection	≈1–2 days	Can detect antigens directly, semi-quantitatively	Potential for false positives, may require confirmation	(Law et al., 2014)
Fluorescence immunoassay (MBs + Core-Shell QDs)	35 min	Ultrasensitive (LOD 0.26 CFU/mL), rapid, high specificity (∼96%), high reproducibility, minimal background	Requires quantum dot reagents, specialized equipment, and stability under long-term storage needs validation	(Thi Le et al., 2025)

Nutritional Media for the Diagnosis of *L. monocytogenes*

Culture media are essential for the isolation and diagnosis of microorganisms, as they provide the nutrients and conditions required for growth and multiplication. Solid culture media usually contain agar, a gelatinous substance extracted from red algae, whereas media without agar remain in liquid form and are referred to as broths (Jamali et al., 2013). Several enrichment, selective, and differential media are routinely used for the detection of *L. monocytogenes*. Enrichment broths such as Half Fraser and Fraser broth promote the selective growth of *Listeria* species while suppressing background microorganisms. For isolation, selective agar media including Oxford agar and PALCAM agar are widely applied; *Listeria* colonies typically appear black or gray-green with dark centers due to esculin hydrolysis, which distinguishes them from non-*Listeria* colonies (Rapeanu et al., 2017). Other specialized media have also been developed. For example, Mustafa and Al-Nazal (2019) reported the use of *Listeria* selective agar base (TSBYE), composed of trypticase soy broth supplemented with yeast extract, to enhance recovery and purification of *Listeria*. In addition, blood agar supplemented with 5% sheep or human blood is frequently used to observe β-hemolysis, a differential feature characteristic of *L. monocytogenes* colonies. The main culture media applied for its diagnosis are summarized in Table 5. The careful selection of enrichment and selective media is critical for accurate detection of *L. monocytogenes*, as inappropriate media can either inhibit its growth or fail to distinguish it from other microorganisms, ultimately leading to false-negative or misleading results in food safety investigations.

Biochemical Tests for *L. monocytogenes*

Biochemical tests are widely used to diagnose and differentiate bacterial species, as the biochemical activity of microorganisms varies according to the enzymes they produce (Abdul Karim et al., 2024; Sasakawa, 2009). Some bacteria produce a wide range of enzymes, while others synthesize only a few or none at all, resulting in distinct biochemical profiles. These differences are essential for classifying microorganisms and accurately identifying pathogenic bacteria. For *L. monocytogenes*, biochemical characterization represents a critical step for accurate diagnosis and confirmation, as it enables differentiation of this pathogen from other *Listeria* species and closely related Gram-positive bacteria. According to Bergey's Manual of Systematics of Archaea and Bacteria (Zuerner, 2015), *L. monocytogenes* appears as short, Gram-positive rods occurring singly or in short chains, nonspore-forming, and facultatively anaerobic. It is catalase-positive and oxidase-negative, exhibiting characteristic tumbling motility at 20–25°C and growing over a broad temperature range (0–45°C, optimum 30–37°C). Biochemically, *L. monocytogenes* is glucose- and maltose-positive, methyl red- and Voges–Proskauer-positive, and capable of hydrolyzing esculin. In contrast, it is negative for urease production, indole formation, citrate utilization (CIT), and mannitol fermentation. These collective biochemical and physiological traits are fundamental for distinguishing *L. monocytogenes* from other Gram-positive bacteria and related *Listeria* species. The typical biochemical reactions of *L. monocytogenes* are summarized in Table 6. Although biochemical tests remain a cornerstone for the identification and differentiation of *L. monocytogenes*, their use in combination with molecular methods provides greater accuracy and reliability, ensuring robust confirmation of the pathogen in food safety investigations. Importantly, certain biochemical traits can also help differentiate *L. monocytogenes* from other *Listeria* species; for example, *L. innocua* is nonhemolytic and usually negative in the CAMP test, while *L. ivanovii* is CAMP-positive with *Rhodococcus equi* but not with *S. aureus*. These distinctions highlight the diagnostic value of biochemical testing before molecular confirmation.

Modern Methods Used in Diagnosing *L. monocytogenes*

Understanding *L. monocytogenes* adaptations to environmental stressors is crucial for developing effective and affordable technologies to combat pathogens in the food industry, ensuring the safety of food production (Rohilla et al., 2024). Modern diagnostic approaches not only assess bacterial growth on various substrates but also perform simultaneous biochemical profiling using systems such as Enterotube, API 20 A, and API 20E. These methods are rapid, cost-effective, and provide accurate identification. Although traditional microbiology methods have been used for decades, several recent innovations are poised to transform microbial diagnostics fundamentally. For instance, MALDI-TOF-MS has rapidly replaced conventional

Table 5. Commonly Used Culture Media for the Isolation and Identification of *Listeria monocytogenes*, Including Medium Type, Purpose, and Characteristics

Type of medium	*Medium name*	*Purpose/characteristics*	*References*
Enrichment broths	Half Fraser broth/Fraser broth	Selective enrichment; supports the growth of *Listeria* species while inhibiting competing flora	(Jamali et al., 2013)
Selective agar media	Oxford agar	Selective isolation; colonies appear black due to esculin hydrolysis	(Rapeanu et al., 2017)
	PALCAM agar	Selective isolation; colonies are gray-green with black centers, suppressing non-*Listeria* bacteria	(Rapeanu et al., 2017)
Specialized media	*Listeria* selective agar base (trypticase soy broth with yeast extract)	Enhances recovery and purification of *Listeria* spp.	(Mustafa and Al-Nazal, 2019)
Differential media	Blood agar (5% sheep/human blood)	Demonstrates β-hemolysis, characteristic of *L. monocytogenes*	(Jamali et al., 2013)

PALCAM, polymyxin, acriflavine, lithium chloride, cephaloridine, aesculin, mannitol (agar).

Table 6. Biochemical Characteristics and Test Results of *Listeria monocytogenes* Isolates

Test type	*Results*	*References*
Gram stain	Positive	(Abdul Karim et al., 2024)
Catalase		
Glucose		
Mannitol	Negative	(Abdul Karim et al., 2024; Zuerner, 2015)
Oxidase		
Simmons citrate		
Urease		
Esculin hydrolysis	Positive	(Sasakawa, 2009)
Methyl red		
Voges–Proskauer		
Maltose		
Indole	Negative	(Sasakawa, 2009)

bacterial identification techniques in many laboratories, improving turnaround times, accuracy, and cost-efficiency compared with older methods (Peri et al., 2021). Automated blood culture systems, such as BACTEC™ FX and BacT/ALERT®, employ various media and sensors to monitor bacterial growth and antimicrobial susceptibility, enhancing detection efficiency (Park et al., 2017). Additionally, rapid tests designed as point-of-use or point-of-care devices offer fast, precise detection without complex sampling or preparation protocols, representing a practical alternative to traditional culture-based methods (Canciu et al., 2021). These modern approaches outperform conventional methods in both speed and reliability, particularly for ensuring the microbiological quality of food production environments. An example of the power of modern genomic tools is the whole genome sequencing analysis of 252 *L. monocytogenes* ST9 isolates obtained from four Norwegian meat production facilities between 2017 and 2019, which allowed precise identification, tracking, and epidemiological investigation of strains (Fagerlund et al., 2020). Table 7 summarizes the primary modern diagnostic methods for *L. monocytogenes*, along with their principles, advantages, and limitations.

PCR method

PCR is widely used for the rapid and specific detection of *L. monocytogenes*. One advanced approach is Multiplex PCR PreMix technology, which utilizes a preprepared mixture containing PCR buffer, dNTPs, pfu polymerase, pyrophosphatase, and pyrophosphate. This enables simultaneous amplification of multiple target genes from bacterial isolates. DNA fragment sizes are determined using standard markers such as the 100 bp and 1 kb DNA ladders. For multiplex PCR, a master reaction mixture without DNA is prepared, and DNA samples from bacterial isolates are added individually. Typically, 10 bacterial DNA samples and 1 negative control per bacterial type are included, resulting in a total of 11 reactions. The mixture is distributed into 0.2 mL tubes, with 23 μL of master mix and 2 μL of DNA per tube,

Table 7. Modern Diagnostic Methods for Detecting *Listeria monocytogenes*, Including Their Principles, Advantages, and Limitations

Method	*Principles*	*Advantages*	*Limitations*	*References*
PCR	Amplification of target DNA sequences	Rapid, sensitive, specific, detects low bacterial counts	Requires specialized equipment, DNA extraction, potential inhibitors in complex food matrices	(Rohilla et al., 2024)
API 20E/API 20A	Biochemical profiling using standardized panels	Quick, cost-effective, easy to use, simultaneous multiple tests	Limited to bacteria that can grow in panel conditions, may misidentify atypical strains	(Canciu et al., 2021)
MALDI-TOF-MS	Protein fingerprinting using mass spectrometry	Extremely rapid, highly accurate, minimal sample preparation, distinguishes closely related species	Expensive instrumentation, requires reference spectra databases	(Peri et al., 2021)
Automated blood culture systems (BACTEC™ FX, BacT/ALERT®)	Growth monitoring using sensors and selective media	Continuous monitoring, detects growth and antimicrobial susceptibility, reduced human error	Expensive, specialized systems, limited direct application to food samples	(Park et al., 2017)
Whole genome sequencing	Sequencing entire bacterial genome	High-resolution strain typing, epidemiological tracking, identifies virulence and resistance genes	Costly, bioinformatics expertise required, slower than rapid tests	(Fagerlund et al., 2020)
Point-of-care/point-of-use rapid tests	Immunological or nucleic acid-based detection	Quick, simple, minimal training required, suitable for field or food industry use	May be less sensitive than laboratory-based methods, limited multiplexing	(Canciu et al., 2021)

PCR, polymerase chain reaction; API, analytical profile index; MALDI-TOF-MS, matrix-assisted laser desorption/ionization time-of-flight mass spectrometry.

making a final volume of 25 μL. The tubes are then subjected to thermal cycling, and amplified products are analyzed on 1.5% agarose gels to detect specific genes (Du et al., 2020; Gouws and Liedemann, 2005). Detection of *L. monocytogenes* in meat typically involves the isolation of chromosomal DNA followed by amplification using PCR with specific primers targeting virulence-associated genes such as *hly*. The PCR products are then analyzed using gel electrophoresis to confirm the presence of the pathogen (Frece et al., 2005; Markov et al., 2009). This molecular approach provides a rapid and sensitive method for identifying *L. monocytogenes* in food samples and is widely used in both research and routine food safety monitoring. Agarose gel electrophoresis of PCR products from milk and dairy samples presumptively positive for *L. monocytogenes* using PALCAM agar or API *Listeria* tests (Supplementary Figs. S1 and Figs. S2) (Frece et al., 2010).

API Listeria *analytical profile index*

The API *Listeria* system (bioMérieux, Marcy-l'Étoile, France) is a rapid identification method for *Listeria* species based on the biochemical activities of bacterial isolates. The system contains a set of cupules, each with specific dehydrated substrates, which are inoculated with a bacterial suspension. During incubation, metabolic reactions produce visible color changes, either naturally or after adding specific reagents, depending on the test. Each reaction is interpreted using the API *Listeria* identification tables or a computerized system, converting observed biochemical reactions into numerical codes corresponding to specific *Listeria* species. Essential reagents used in the system include tryptophan deaminase (TDA) reagent, which tests TDA activity; indole reagents (Kovac's or James) for indole detection; Voges–Proskauer reagents (VP1 and VP2) for acetoin production; nitrate reagents (Nit1 and Nit2) for nitrite reduction; and oxidase reagent for cytochrome c oxidase activity. After incubation, the results of each biochemical test are read and compared with the reference tables. Positive and negative reactions are recorded, and the combination of results can be converted into numerical codes for bacterial identification. API *Listeria* test results for *L. monocytogenes*, highlighting its characteristic biochemical fingerprint (Supplementary Table S1) (Andareas et al., 2023). Positive reactions include *β*-galactosidase activity (ONPG test, yielding a yellow color), arginine dihydrolase activity (turning orangey-red), CIT (producing blue-green to blue), and acetoin production in the Voges–Proskauer test (VP, pink to red). *L. monocytogenes* also hydrolyzes gelatin (diffusion of black pigment) and ferments glucose (yellow), while showing variable carbohydrate fermentation patterns such as mannitol and rhamnose. In contrast, tests for urease (URE), TDA, indole production, and hydrogen sulfide production are typically negative, distinguishing *L. monocytogenes* from other bacteria. This specific biochemical profile, particularly the combination of positive VP and rhamnose fermentation with negative urease and indole reactions, is considered diagnostic for *L. monocytogenes* in laboratory settings. In addition, the API *Listeria* system allows differentiation of closely related *Listeria* species through specialized tests such as the D-arylamidase test, which is particularly useful for distinguishing *L. monocytogenes* from *L. innocua* (Supplementary Figs. S3 and Figs. S4) (Allerberger, 2003). Overall, the API *Listeria* system provides a reliable, standardized, and rapid approach for identifying *Listeria* species in clinical, food, and environmental samples, supporting both diagnostic and epidemiological investigations.

Analytical approach: MALDI-TOF-MS

Since 2010, MALDI-TOF-MS has been widely applied in health care and microbiological laboratories. Compared with traditional biochemical identification methods, MALDI-TOF-MS offers several advantages, including simplicity, speed, accuracy, and relatively low cost (Elbehiry et al., 2022). Many of the challenges associated with conventional identification of bacteria and fungi, such as long turnaround times and difficulty of interpretation, can be overcome with this method (Abdelhamed et al., 2022; Panebianco et al., 2022). The principle of MALDI-TOF-MS is based on the analysis of highly expressed cellular proteins, primarily ribosomal proteins, which reflect the genetic makeup of microorganisms. These proteins, typically ranging from 2000 to 20,000 Daltons, are ionized through the gain or loss of protons, generating charged particles that can be measured according to their mass-to-charge ratio (m/z) (Vrioni et al., 2018). For the process, a fresh colony is spotted onto a MALDI target plate and mixed with an energy-absorbing compound known as the matrix. After drying, the matrix and microbial proteins co-crystallize. When the sample is exposed to laser irradiation, the proteins are ionized and accelerated for m/z measurement. The resulting spectrum—unique to each microorganism—serves as a fingerprint that is compared with reference databases for species identification (Angeletti, 2017; Vrioni et al., 2018). MALDI-TOF-MS has established itself as a reliable and widely adopted technique for microbial identification in both clinical diagnostics and food safety testing (Elbehiry et al., 2022).

Antimicrobial Treatment and Antibiotic Resistance of *L. monocytogenes*

L. monocytogenes is a foodborne pathogen that can cause severe infections in humans, including septicemia and meningoencephalitis, and it also affects a wide range of animals, with mortality rates ranging from 21% to 44.4% (Matle et al., 2020; Michelet et al., 1994). According to Andriyanov et al. (2021), *L. monocytogenes* poses a major health hazard, particularly for elderly individuals with weakened immune systems, pregnant women, and newborns, who are the most vulnerable populations. Although no universally established treatment for listeriosis exists, several antibiotics are commonly employed. Ampicillin or penicillin, either alone or in combination with gentamicin, are considered first-line therapies (Andriyanov et al., 2021; Noll et al., 2018). Alternative options include amoxicillin, trimethoprim/sulfamethoxazole, fluoroquinolones, vancomycin, and erythromycin. Antibiotic resistance has been increasingly reported in *L. monocytogenes*. Clindamycin shows the highest resistance rates, followed by tetracycline and erythromycin (Mpundu et al., 2022). The first antibiotic-resistant strain of *L. monocytogenes* was reported in 1988 from a meningitis patient in France (Noll et al., 2018). Since then, resistant strains have been isolated from food, clinical cases, and

environmental sources. Resistance patterns vary depending on the source, geographical origin, and year of isolation. However, recent studies indicate a concerning increase in acquired resistance, underscoring the need for ongoing surveillance. The emergence and spread of antibiotic-resistant *L. monocytogenes* strains represent a serious threat to both public health and food safety (Andriyanov et al., 2021).

Antibiotic statistics of L. monocytogenes *from 1950 to 2021*

A total of 117 *L. monocytogenes* strains were isolated in the European part of Russia and studied between 1950 and 1980. In 2021, an additional 27 strains were analyzed from human, animal, and food sources. The distribution of strains across these sources was uneven both before and after the year 2000, reflecting historical changes in the epidemiology of *L. monocytogenes*, a pathogen of significant public health concern. Although clinical cases of listeriosis in humans were officially documented in Russia only after 2002, earlier reports indicate that the disease primarily affected animals before 1980. Following this period, changes in agricultural practices and the introduction of food safety legislation helped regulate the presence of *L. monocytogenes* in food products. In addition, the widespread use of antibiotics to control bacterial infections contributed to a marked reduction in the role of *L. monocytogenes* as an animal pathogen. Genetic characterization using multilocus sequence typing revealed that all analyzed strains belonged to phylogenetic lineages I and II, with no representatives of lineages III or IV. This pattern is consistent with global trends, as lineages I and II are most frequently associated with both human and animal infections. In contrast, lineages III and IV are rarely encountered and typically confined to specific ecological niches. Among the Russian isolates, lineage II predominated (97 strains), followed by lineage I (23 strains), confirming previous reports on the distribution of *L. monocytogenes* lineages in the European part of Russia (Andriyanov et al., 2021). The antibiotic resistance index of *L. monocytogenes* was evaluated according to isolation period, strain source, and phylogenetic lineage (Supplementary Table S2). Continuous monitoring of these resistance patterns is essential, as the increasing prevalence of resistant strains poses a growing challenge for both clinical treatment and food safety management.

Antibiotic resistance of L. monocytogenes

Antimicrobial susceptibility interpretation in this review was standardized according to the European Committee on Antimicrobial Susceptibility Testing (EUCAST, 2024) clinical breakpoints. Where EUCAST breakpoints were unavailable, epidemiological cutoff values (ECOFFs) or published MIC distribution data were used to classify isolates as susceptible or resistant. Reported findings were further interpreted in accordance with guidance from the Centers for Disease Control and Prevention (CDC, 2024) and the Infectious Diseases Society of America (Tamma et al., 2024) to ensure appropriate clinical context and to avoid overstatement of resistance implications.

L. monocytogenes displays variable resistance to antibiotics across different classes, including β-lactams, macrolides, aminoglycosides, and quinolones. In a survey of 23 antibiotics (Supplementary Table S3), all tested strains were sensitive to aminoglycosides, such as gentamicin, kanamycin, neomycin, and streptomycin, as well as to glycopeptides, including vancomycin. Other antibiotics, including clarithromycin, levofloxacin, and combinations like amoxicillin/clavulanic acid and trimethoprim/sulfamethoxazole, were also effective against all strains. Clindamycin exhibited the highest resistance, affecting a significant number of isolates. Most resistant strains were identified before 2000, with exceptions including two strains detected later. Notably, a strain isolated from pigs in 1967 displayed resistance to penicillin G and enrofloxacin, suggesting the presence of intrinsic resistance mechanisms even decades ago (Andriyanov et al., 2021).

A detailed analysis of resistance mechanisms (Table 8) highlights the genetic basis underlying these phenotypic patterns. Erythromycin resistance is mediated by target site modification via the *ermB* gene (Morvan et al., 2010), while tetracycline resistance arises from efflux pumps or ribosomal protection through *tetM* and *tetS* genes (Luque-Sastre et al., 2018). Ampicillin resistance is rare and not well characterized, whereas ciprofloxacin resistance involves efflux pump activity mediated by the *lde* gene (Elsayed et al., 2022). Gentamicin resistance is caused by enzymatic inactivation through *aac(6′)-Ii* (Wilson et al., 2018), and vancomycin resistance is primarily intrinsic, linked to cell wall thickening (Cheng et al., 2023). Trimethoprim resistance occurs via plasmid- or transposon-encoded dihydrofolate reductases (*dfrA, dfrB, dfrC, dfrD, dfrG, dfrK*) (Korsak and Krawczyk-Balska, 2017).

Enzymatic degradation also plays a key role in antibiotic resistance in *L. monocytogenes*. The bacterium produces phospholipase C enzymes, activated through proteolytic pathways involving proteases and metalloproteases during intracellular infection, converting inactive proenzymes into their active forms (Sun et al., 2023). Additionally, *L. monocytogenes* encodes two chitinase enzymes, LmChiA and LmChiB, which contribute to the breakdown of chitin, a major structural component of biofilm-associated extracellular polymeric substance matrices. The biochemical properties, substrate specificity, and structure–function relationships of these enzymes have been thoroughly characterized (Anupama et al., 2025). Together, these genetic determinants and enzymatic mechanisms explain the observed resistance patterns and underscore the importance of ongoing surveillance to guide effective therapeutic and control strategies. The MdrL efflux pump represents a critical mechanism contributing to antibiotic resistance in *L. monocytogenes*. As illustrated in Figure 3, the tripartite MdrL system consists of an inner membrane protein (IMP), a periplasmic adapter protein (PAP), and an outer membrane protein (OMP). Together, these components form the MdrL superfamily, which actively exports antibiotics and other toxic compounds from the bacterial cell, thereby mediating multidrug resistance. Efflux-mediated resistance in *L. monocytogenes* was first described in 2000 (Mata et al., 2000). The MdrL protein shares high sequence homology with YfmO, a putative chromosomal multidrug efflux transporter of *Bacillus subtilis*. Functional studies have shown that an allele-substituted mutant of the *mdrL* gene loses the ability to efflux ethidium bromide and exhibits increased susceptibility to macrolides, cefotaxime, and heavy metals.

TABLE 8. ANTIBIOTIC RESISTANCE MECHANISMS AND ASSOCIATED GENES IN DIVERSE *LISTERIA MONOCYTOGENES* STRAINS ACROSS MULTIPLE ANTIBIOTIC CLASSES

Antibiotic	*Class*	L. monocytogenes *strains*	*Resistance mechanism*	*Resistance gene(s)*	*Resistance reported*	*References*
Erythromycin	Macrolides	EGD-e, F2365, Scott A	Target site modification	*ermB*	Yes	(Morvan et al., 2010)
Tetracycline	Tetracyclines	10403S, V7	Efflux pump/ribosomal protection	*tetM*, *tetS*	Yes	(Luque-Sastre et al., 2018)
Ampicillin	Beta-lactams	Scott A, EGD-e	β-lactamase production (rare in *Listeria*)	Not well characterized	Rare	(Matereke and Okoh, 2020)
Ciprofloxacin	Fluoroquinolones	F2365, H7858	Efflux pump activity	*lde* (efflux pump)	Yes	(Elsayed et al., 2022)
Chloramphenicol	Amphenicols	F2365, clinical isolates	Efflux pump/acetyltransferase activity	*cat*, *cmlA*		
Gentamicin	Aminoglycosides	V7, 10403S	Enzymatic inactivation	*aac(6′)-Ii*	Yes	(Wilson et al., 2018)
Vancomycin	Glycopeptides	EGD-e	Intrinsic resistance (thickened cell wall)	Not specific	No	(Cheng et al., 2023)
Trimethoprim	Folate pathway inhibitor	*L. seeligeri*, *L. monocytogenes*	Dihydrofolate reductase via plasmid/transposon	*dfrA*, *dfrB*, *dfrC*, *dfrD*, *dfrG*, *dfrK*	Yes	(Korsak and Krawczyk-Balska, 2017)

In addition to MdrL, the Lde efflux pump (*Listeria* drug efflux) has been linked to fluoroquinolone resistance in clinical isolates of *L. monocytogenes* from France (Verraes et al., 2013). The Lde protein shares 44% sequence homology with PmrA, a multidrug transporter of *Streptococcus pneumoniae*, which belongs to the major facilitator superfamily of secondary multidrug transporters. Disruption of the *lde* gene through insertional inactivation increases susceptibility to fluoroquinolones, confirming its essential role in drug efflux and resistance. These efflux systems, therefore, play a central role in the multidrug resistance phenotype of *L. monocytogenes* and highlight the importance of monitoring efflux-mediated mechanisms when assessing antimicrobial susceptibility.

Patterns of antibiotic resistance to L. monocytogenes

Supplementary Table S4 indicates the distribution of *L. monocytogenes* strains showing resistance to 14 different antibiotics that are routinely used in both human and veterinary treatment. The data reveal a relatively high incidence of tetracycline resistance (22.8%) and a low incidence of erythromycin resistance (1.9%), while tigecycline resistance was observed in 38% of strains (Noll et al., 2018). In contrast, Salas et al. (2008) reported excellent activity of tigecycline against *L. monocytogenes* at concentrations ≤0.5 g/mL. Isolates from Romania did not show resistance to tigecycline (Sala et al., 2016), and erythromycin, gentamicin, and trimethoprim/sulfamethoxazole exhibited minimal inhibitory concentration (MIC) diameters between 50 and 90. Similarly, *L. monocytogenes* strains isolated from raw milk, soft cheese, and meat in Italy showed comparable MIC ranges for erythromycin, tetracycline, and vancomycin. Although MIC measurement methods varied among different strain groups, most MIC values were consistent, with only minor differences of one concentration level. This indicates that the inhibition diameters, ranging from 50 to 90 MIC, are generally consistent for *L. monocytogenes* (Noll et al., 2018). Supplementary Table S4 presents the susceptibility and resistance profiles of the different antibiotic-resistant strains, along with the ECOFFs for MICs.

The resistance patterns observed in Supplementary Table S4 have significant clinical and public health consequences. High resistance rates to tetracycline (22.8%) and tigecycline (38%) indicate that these antibiotics may have reduced therapeutic efficacy for certain *L. monocytogenes* infections, particularly in vulnerable populations such as pregnant women, neonates, and immunocompromised individuals. Conversely, low resistance rates to erythromycin (1.9%), vancomycin, and ampicillin highlight their continued effectiveness for empirical therapy. The widespread occurrence of resistance in field strains, particularly to broad-spectrum agents like daptomycin and ciprofloxacin, underscores the potential risk of treatment failure and emphasizes the necessity for continuous antimicrobial susceptibility monitoring. From a public health perspective, the detection of resistant strains in food products such as raw milk, cheese, and meat poses a risk for transmission to humans. To mitigate this risk, rigorous food safety measures and prudent antibiotic use in both human and veterinary medicine are essential to prevent the spread of resistant *L. monocytogenes* strains. Overall, the resistance patterns observed in *L. monocytogenes* remain consistent

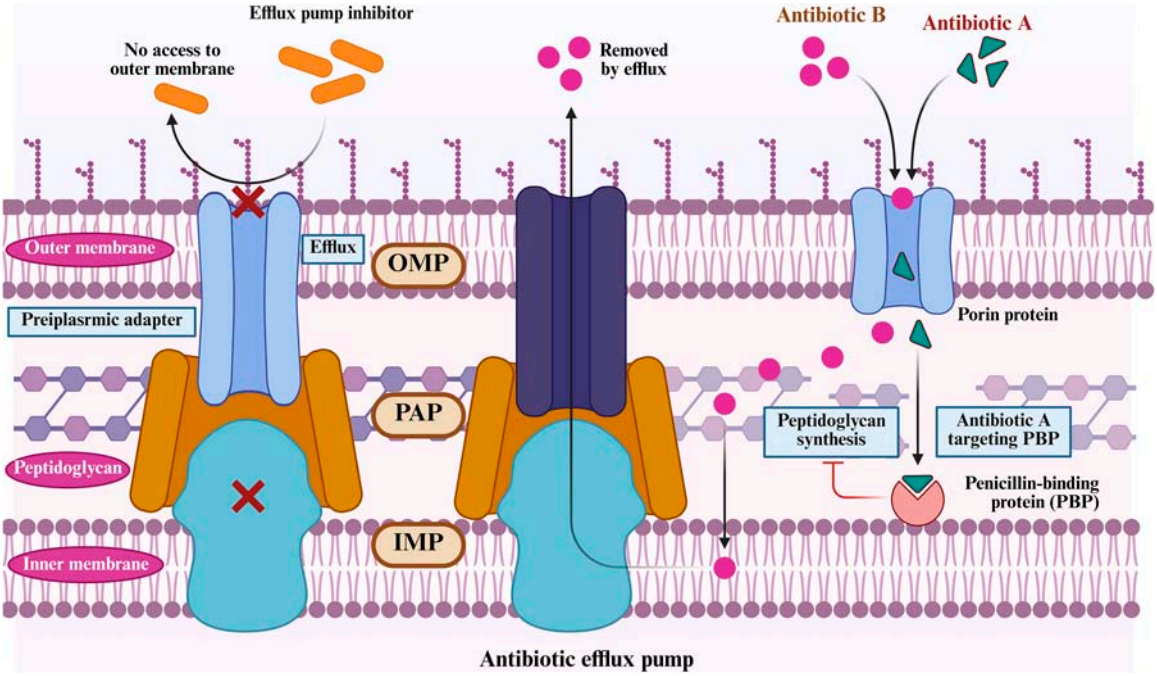

FIG. 3. Structural organization of the MdrL multidrug efflux pump in *Listeria monocytogenes*, showing the inner membrane protein (IMP), periplasmic adapter protein (PAP), and outer membrane protein (OMP) forming the functional efflux pump.

with EUCAST interpretive criteria and CDC guidance, indicating that while emerging resistance to tetracycline and macrolides is concerning, β-lactams and glycopeptides continue to exhibit reliable clinical efficacy.

Green Antimicrobials: Natural Approaches to Combat Pathogens

One of the major challenges in the meat industry is controlling foodborne pathogens. Although thermal treatments are highly effective for inactivating key pathogens such as *L. monocytogenes*, they often negatively affect the sensory and nutritional quality of the final product. Consequently, the rising demand for organically processed and natural meats is driven by perceived health and safety benefits associated with minimizing exposure to chemical preservatives and pesticides (Tan et al., 2018). Antimicrobial treatments for ready-to-eat meat and poultry products are strictly regulated, with comprehensive lists of approved compounds and procedures specified by governing authorities (Mie et al., 2017). This review critically evaluates natural antimicrobial agents currently applied in ready-to-eat products, with a focus on their efficacy against *L. monocytogenes*, in line with increasing consumer interest in clean-label strategies. There is also growing interest in adopting green technologies in the food industry, as they provide sustainable, environmentally friendly alternatives that can enhance both product safety and quality (Heredia and García, 2018; Taha et al., 2024).

Emerging nonthermal technologies, including high-pressure processing, pulsed electric fields, cold plasma, and ultrasound, are gaining traction for controlling *L. monocytogenes* in food products. These approaches effectively inactivate pathogens while preserving the nutritional and sensory attributes of foods. For example, high-pressure processing has been shown to achieve up to a 5-log reduction of *L. monocytogenes* in meat products, extending shelf life without compromising quality (Ghazali et al., 2025). Pulsed electric fields use short bursts of high voltage to disrupt microbial cell membranes, significantly reducing *Listeria* populations in liquid foods (Safwa et al., 2024). Cold plasma generates reactive species that damage microbial DNA and cell membranes, effectively inactivating *Listeria* on food surfaces (Sainz-García and Alba-Elías, 2023). Ultrasound, especially when combined with pressure (manosonication), has demonstrated enhanced lethality against *Listeria* in dairy products, achieving rapid microbial inactivation (Sawale et al., 2024). These nonthermal technologies not only improve food safety but also align with consumer demand for minimally processed, clean-label foods, highlighting their potential as sustainable interventions in the meat industry.

*Comprehensive insights into natural anti-*Listeria *strategies for food safety*

Bacteriocins are microbially produced ribosomal antimicrobial peptides or short proteins with strong antimicrobial potential against pathogens such as *L. monocytogenes*. Well-characterized examples include garviecin LG34, bifidocin A, leucocin C-607, pediocin GS4, plantaricin LPL1, sakacins, and nisin. Producer microorganisms naturally possess self-immunity to their bacteriocins through specific enzymes, and these compounds are generally considered safe for human consumption because gastrointestinal proteases readily degrade them. Most bacteriocins are classified according to structural features, such as unmodified linear peptides, and exert their antimicrobial activity by disrupting target cell

membrane integrity, often via receptor–ligand interactions. Upon binding, the hydrophobic domains of bacteriocins insert into the lipid bilayer and oligomerize to form ion-selective pores, leading to dissipation of the proton motive force (PMF), depletion of intracellular ATP, efflux of cellular solutes, and eventual cell death. Receptor specificity is a key determinant of the target range: some bacteriocins interact with universally expressed molecules such as lipid II or mannose permease, whereas others, such as the circular bacteriocin Garvicin ML from *Lactococcus garvieae* DCC43, specifically target the maltose ABC transporter and permease. Class I bacteriocins (lantibiotics) are posttranslationally modified peptides containing lanthionine and methyllanthionine residues that form intramolecular thioether rings and defined wedge-like pores. In contrast, Class II bacteriocins increase membrane permeability through diverse biophysical mechanisms, ultimately causing similar disruption of cellular homeostasis (Bodie et al., 2023).

In addition to bacteriocins, plant-derived secondary metabolites, including polyphenols, lignans, alkaloids, glycosides, saponins, and tannins, as well as antimicrobial peptides, exhibit anti-*Listeria* activity (Ricci et al., 2023; Shehata et al., 2023). Polyphenols are among the most abundant and functionally significant classes of secondary metabolites, playing key roles in plant defense against abiotic stressors such as oxidizing agents and ultraviolet radiation, as well as biotic challenges including phytopathogens (Hamad et al., 2023). Numerous studies have demonstrated their efficacy against *Listeria* species, with specific compounds including hydroxycinnamic acids, anthocyanins, flavan-3-ols, flavonols, oleuropein, verbascoside, luteolin-7-*O*-glucoside, luteolin-4-*O*-glucoside, phenolic acids, tannins, flavonoids, and quercetin. The antimicrobial activity of phenolic compounds is primarily determined by the presence and configuration of hydroxyl (-OH) groups, which facilitate interactions with microbial membranes via hydrogen bonding. This leads to multiple cytotoxic effects: (a) membrane disruption through altered permeability and structural disintegration; (b) bioenergetic collapse caused by dysregulation of H^+ and K^+ ion gradients, intracellular pH reduction, and PMF disruption; and (c) intracellular damage via inhibition of enzymes or cellular energy pathways. Essential oils such as carvacrol, thymol, clove, cinnamon, oregano, and ginger, as well as organic and inorganic acids including citric, lactic, acetic, and tartaric acids, sodium chloride, and nitrite, also exhibit anti-*Listeria* activity. Recent research highlights organic acid extracts derived from plants, fruits, and bacteria as sustainable and environmentally friendly alternatives with promising potential as natural anti-*Listeria* agents for food safety and therapeutic applications (Hamad et al., 2023).

Future Challenges, Recommendations, and Conclusions

L. monocytogenes remains a significant global foodborne pathogen, contaminating not only meat and meat products but a wide range of animal-derived and processed foods. Its persistence in food-processing environments, ability to survive under diverse conditions, and increasing multidrug resistance pose serious challenges to both public health and food safety. Addressing these challenges requires a multifaceted approach. Strict enforcement of Good Hygiene Practices and Hazard Analysis and Critical Control Points in food production and processing is essential to minimize contamination risks. Routine surveillance using genomic, phenotypic, and molecular approaches can improve outbreak detection and source tracking, while rapid and sensitive diagnostic tools, including PCR-based assays, API *Listeria* systems, MALDI-TOF-MS, and emerging biosensors, are critical for timely identification of the pathogen. Public education on proper food handling, storage, and cooking practices further reduces the risk of listeriosis, and rational antibiotic use in clinical and agricultural settings is necessary to curb the development of resistance. Future research should focus on innovative detection technologies, including real-time sensors and point-of-care diagnostics, as well as strategies to manage antibiotic resistance effectively. By integrating stringent hygiene practices, advanced surveillance, rapid diagnostics, public awareness, and antimicrobial stewardship, it is possible to enhance food safety, protect consumer health, and reduce the global burden of *L. monocytogenes* infections.

Ethical Statement

In accordance with the regulations, this study is classified as a routine literature review and therefore does not require approval from an Ethics Committee or Institutional Review Board. The study does not involve animal or human clinical trials and is not unethical.

Authors' Contributions

S.A.A.-H.: Writing—original draft, supervision, data curation, project administration; S.S.G.: Writing—original draft, resources, data curation; S.A.K.: Writing—original draft, formal analysis. M.T.: Writing—review and editing, investigation; A.T.P.: Writing—review and editing, resources, conceptualization; A.A.-F.: Resources, writing—review and editing; S.P.: Writing—review and editing; M.A.F.: Writing—review and editing, resources, conceptualization; S.A.K.: Writing—review and editing, data curation, supervision, resources, conceptualization. All authors made significant contributions to the article and reviewed the article in its final form.

Disclosure Statement

The authors declare that they have no known competing financial interests or personal relationships that could have influenced the work reported in this article.

Funding Information

This work was also supported by research team members from various universities in Iraq, Egypt, Saudi Arabia, India, North Macedonia, Korea, Iran, and China, who contributed relevant scientific data collected from different sources in the literature. S.A.K. would like to thank the China Postdoctoral Science Foundation for providing a postdoctoral research fellowship and supporting his research.

Supplementary Material

Supplementary Data

References

Aalto-Araneda M, Lundén J, Markkula A, et al. Processing plant and machinery sanitation and hygiene practices associate with *Listeria monocytogenes* occurrence in ready-to-eat fish products. Food Microbiol 2019;82:455–464; doi: 10.1016/j.fm.2019.03.017

Abdelhamed H, Nho SW, Kim SW, et al. Serotype-identifying ions in *Listeria monocytogenes* using matrix-associated laser desorption ionization-time of flight mass spectrometry. Heliyon 2022;8(12):e11769; doi: 10.1016/j.heliyon.2022.e11769

Abdul Karim S, George SS, Al-Hilifi SA. Antibacterial activity of plant extracts against *Listeria monocytogenes* isolated from some fresh meat from local markets in the city of Basrah. Arab Univ J Agric Sci 2024;7(22):25–48; doi: 10.21608/asajs.2024.349808

Adebesin IO, Amoka SO, Olomoko CR, et al. *Listeria monocytogenes* in food production and food safety. J Food Sci Nutr The 2024;10(1):57–68; doi: 10.17352/jfsnt.000050

Aladhadh M. A review of modern methods for the detection of foodborne pathogens. Microorganisms 2023;11(5):1111; doi: 10.3390/microorganisms11051111

Al-Ghanim AM, Abbas BA. Detection of *Listeria monocytogenes* in frozen food using a specific *inlB* virulence gene. J Phys: Conf Ser 2021;1879(2):22011; doi: 10.1088/1742-6596/1879/2/022011

Allerberger F. *Listeria*: Growth, phenotypic differentiation and molecular microbiology. FEMS Immunol Med Microbiol 2003;35(3):183–189; doi: 10.1016/S0928-8244(02)00447-9

An T, Song M, Li X, et al. Development of visual loop-mediated isothermal amplification assays for foodborne hepatitis a virus. Foods 2025;14(6):934; doi: 10.3390/foods14060934

Andareas P, Aruan M, Lusiana DIG, et al. Pelatihan identifikasi enterobacteriaceae secara biokimia menggunakan analytical profile index (API) 20-E kedapa guru dan siswa teknologi laboratorium medik SMK Negeri 9 Kota Tangerang. PKM 2023;6(9):3758–3773; doi: 10.33024/jkpm.v6i9.11067

Andriyanov PA, Zhurilov PA, Liskova EA, et al. Antimicrobial resistance of *Listeria monocytogenes* strains isolated from humans, animals, and food products in Russia in 1950–1980, 2000–2005, and 2018–2021. Antibiotics (Basel) 2021;10(10):1206; doi: 10.3390/antibiotics10101206

Angeletti S. Matrix assisted laser desorption time of flight mass spectrometry (MALDI-TOF MS) in clinical microbiology. J Microbiol Methods 2017;138:20–29; doi: 10.1016/j.mimet.2016.09.003

Anupama A, Pattapulavar V, Christopher G. The past, present, future of *Listeria monocytogenes*: Understanding the molecular pathways, antibiotic resistance and public health implications. Med Microecol 2025;25:100127; doi: 10.1016/j.medmic.2025.100127

Atasever M. *Listeria monocytogenes*: An overview. Asian J Med Biol Res 2025;11(1):5–12; doi: 10.3329/ajmbr.v11i1.68241

Awaiwanont N, Smulders FJM, Paulsen P. Growth potential of *Listeria monocytogenes* in traditional Austrian cooked-cured meat products. Food Control 2015;50:150–156; doi: 10.1016/j.foodcont.2014.08.043

Barbuddhe S, Hain T, Doijad SP, et al. The genus *Listeria*. In: Practical Handbook of Microbiology. Lorrence HGE, Goldman, eds. 4th ed. CRC Press: Boca Raton, FL; 2021, 411–442.

Befa Kinki A, Atlaw T, Haile T, et al. Preservation of minced raw meat using rosemary (*Rosmarinus officinalis*) and basil (*Ocimum basilicum*) essential oils. Cogent Food Agric 2024;10(1):2306016; doi: 10.1080/23311932.2024.2306016

Bersisa A, Tulu D, Negera C. Investigation of bacteriological quality of meat from Abattoir and Butcher shops in Bishoftu, Central Ethiopia. Int J Microbiol 2019;2019(1):6416803; doi: 10.1155/2019/6416803

Bertsch D, Rau J, Eugster MR, et al. *Listeria fleischmannii* sp. nov., isolated from cheese. Int J Syst Evol Microbiol 2013;63(Pt 2):526–532; doi: 10.1099/ijs.0.036947-0

Bodie AR, O'Bryan CA, Olson EG, et al. Natural antimicrobials for *Listeria monocytogenes* in ready-to-eat meats: Current challenges and future prospects. Microorganisms 2023;11(5):1301; doi: 10.3390/microorganisms11051301

Bonos E, Skoufos I, Petrotos K, et al. Innovative use of olive, winery and cheese waste by-products as functional ingredients in broiler nutrition. Vet Sci 2022;9(6):290; doi: 10.3390/vetsci9060290

Bouayad L, Hamdi T-M. Prevalence of *Listeria* spp. in ready to eat foods (RTE) from Algiers (Algeria). Food Control 2012;23(2):397–399; doi: 10.1016/j.foodcont.2011.08.006

Budiarto R, Ujilestari T, Rumhayati B, et al. Meta-analysis of citrus-derived additives on chicken meat quality and safety: A comprehensive evaluation of acceptability, physicochemical properties, and microbial contamination. Poult Sci 2024;103(5):103556; doi: 10.1016/j.psj.2024.103556

Buncic S, Nychas G-J, Lee MRF, et al. Microbial pathogen control in the beef chain: Recent research advances. Meat Sci 2014;97(3):288–297; doi: 10.1016/j.meatsci.2013.04.040

Burnett E, Kucerova Z, Freeman M, et al. Whole-genome sequencing reveals multiple subpopulations of dominant and persistent lineage I isolates of *Listeria monocytogenes* in two meat processing facilities during 2011-2015. Microorganisms 2022;10(5):1070; doi: 10.3390/microorganisms10051070

Burnett J, Wu ST, den Bakker HC, et al. *Listeria monocytogenes* is prevalent in retail produce environments but *Salmonella enterica* is rare. Food Control 2020;113:107173; doi: 10.1016/j.foodcont.2020.107173

Bustamante F, Maury-Sintjago E, Leal FC, et al. Presence of *Listeria monocytogenes* in ready-to-eat Artisanal chilean foods. Microorganisms 2020;8(11):1669; doi: 10.3390/microorganisms8111669

Calderón-Miranda ML, Barbosa-Cánovas GV, Swanson BG. Inactivation of *Listeria innocua* in skim milk by pulsed electric fields and nisin. Int J Food Microbiol 1999;51(1):19–30; doi: 10.1016/s0168-1605(99)00069-0

Canciu A, Tertis M, Hosu O, et al. Modern analytical techniques for detection of bacteria in surface and wastewaters. Sustainability 2021;13(13):7229; doi: 10.3390/su13137229

Carpentier B, Cerf O. Review - Persistence of *Listeria monocytogenes* in food industry equipment and premises. Int J Food Microbiol 2011;145(1):1–8; doi: 10.1016/j.ijfoodmicro.2011.01.005

Cavalcanti AAC, Limeira CH, Siqueira I, et al. The prevalence of *Listeria monocytogenes* in meat products in Brazil: A systematic literature review and meta-analysis. Res Vet Sci 2022;145:169–176; doi: 10.1016/j.rvsc.2022.02.015

CDC. Reference Antimicrobial-Susceptibility-Testing (AST) Data. Volume 2025. Centers for Disease Control and Prevention: Atlanta, GA; 2024.

Cheng Y, Mousavi ZE, Pennone V, et al. Association between the presence of resistance genes and sanitiser resistance of *Listeria monocytogenes* isolates recovered from different

food-processing facilities. Microorganisms 2023;11(12): 2989; doi: 10.3390/microorganisms11122989

Cosgrove M, Flynn A, Kiely M. Consumption of red meat, white meat and processed meat in Irish adults in relation to dietary quality. Br J Nutr 2005;93(6):933–942; doi: 10.1079/bjn20051427

da Silva GN, Holt JG. Numerical taxonomy of certain Coryneform bacteria. J Bacteriol 1965;90(4):921–927; doi: 10.1128/jb.90.4.921-927.1965

den Bakker HC, Warchocki S, Wright EM, et al. *Listeria floridensis* sp. nov., *Listeria aquatica* sp. nov., *Listeria cornellensis* sp. nov., *Listeria riparia* sp. nov. and *Listeria grandensis* sp. nov., from agricultural and natural environments. Int J Syst Evol Microbiol 2014;64(Pt 6):1882–1889; doi: 10.1099/ijs.0.052720-0

Deniz A, Ruiz-Llacsahuanga B, Critzer F, et al. Formation and control of *Listeria monocytogenes* growth and accumulation on food processing surfaces in the fresh produce industry. J Food Prot 2025;88(11):100619; doi: 10.1016/j.jfp.2025.100619

Dhama K, Karthik K, Tiwari R, et al. Listeriosis in animals, its public health significance (food-borne zoonosis) and advances in diagnosis and control: A comprehensive review. Vet Q 2015;35(4):211–235; doi: 10.1080/01652176.2015.1063023

Doijad SP, Poharkar KV, Kale SB, et al. *Listeria* goaensis sp. nov. Int J Syst Evol Microbiol 2018;68(10):3285–3291; doi: 10.1099/ijsem.0.002980

Du J, Wu S, Niu L, et al. A gold nanoparticles-assisted multiplex PCR assay for simultaneous detection of *Salmonella typhimurium*, *Listeria monocytogenes* and *Escherichia coli* O157: H7. Anal Methods 2020;12(2):212–217; doi: 10.1039/C9AY02282A

EC. Regulation (European Commission) No 2073/2005 on Microbiological Criteria for Foodstuffs. Volume 2024. European Commission: Brussels, Belgium; 2005.

Elbehiry A, Aldubaib M, Abalkhail A, et al. How MALDI-TOF mass spectrometry technology contributes to microbial infection control in healthcare settings. Vaccines (Basel) 2022; 10(11):1881; doi: 10.3390/vaccines10111881

Elmali M, Can HY, Yaman H. Prevalence of *Listeria monocytogenes* in poultry meat. Food Sci Technol 2015;35(4):672–675; doi: 10.1590/1678-457X.6808

Elsayed ME, Abd El-Hamid MI, El-Gedawy A, et al. New insights into *Listeria monocytogenes* antimicrobial resistance, virulence attributes and their prospective correlation. Antibiotics (Basel) 2022;11(10):1447; doi: 10.3390/antibiotics11101447

El-Shenawy M, El-Shenawy M, Mañes J, et al. *Listeria* spp. in street-vended ready-to-eat foods. Interdiscip Perspect Infect Dis 2011;2011(1):968031; doi: 10.1155/2011/968031

Ennaji H, Timinouni M, Ennaji MM, et al. Characterization and antibiotic susceptibility of *Listeria monocytogenes* isolated from poultry and red meat in Morocco. Infect Drug Resist 2008;1:45–50; doi: 10.2147/idr.s3632

EUCAST. Breakpoint Tables for Interpretation of MICs and Zone Diameters: Version 14.0. Volume 2025. European Committee on Antimicrobial Susceptibility Testing; 2024.

Fagerlund A, Langsrud S, Møretrø T. In-depth longitudinal study of *Listeria monocytogenes* ST9 isolates from the meat processing industry: Resolving diversity and transmission patterns using whole-genome sequencing. Appl Environ Microbiol 2020;86(14):e00579–e520; doi: 10.1128/AEM.00579-20

Fallah AA, Saei-Dehkordi SS, Mahzounieh M. Occurrence and antibiotic resistance profiles of *Listeria monocytogenes* isolated from seafood products and market and processing environments in Iran. Food Control 2013;34(2):630–636; doi: 10.1016/j.foodcont.2013.06.015

FDA. *Listeria Monocytogenes*: Guidance for Industry. Volume 2025. U.S. Food and Drug Administration: Silver Spring, MD; 2022.

Filipello V, Mughini-Gras L, Gallina S, et al. Attribution of *Listeria monocytogenes* human infections to food and animal sources in Northern Italy. Food Microbiol 2020;89:103433; doi: 10.1016/j.fm.2020.103433

Fouladynezhad N, Afsah-Hejri L, Rukayadi Y, et al. Assessing biofilm formation by *Listeria monocytogenes*. Int Food Res J 2013;20(2):987–990.

Frece J, Kos B, Svetec IK, et al. Importance of S-layer proteins in probiotic activity of *Lactobacillus acidophilus* M92. J Appl Microbiol 2005;98(2):285–292; doi: 10.1111/j.1365-2672.2004.02473.x

Frece J, Markov K, Cvek D, et al. Comparison of conventional and molecular methods for the routine confirmation of *Listeria monocytogenes* in milk products produced domestically in Croatia. J Dairy Res 2010;77(1):112–116; doi: 10.1017/s0022029909990379

Gál R, Zapletal D, Jakešová P, et al. Proximate chemical composition, amino acids profile and minerals content of meat depending on carcass part, sire genotype and sex of meat rabbits. Animals (Basel) 2022;12(12):1537; doi: 10.3390/ani12121537

Gebretsadik S, Kassa T, Alemayehu H, et al. Isolation and characterization of *Listeria monocytogenes* and other *Listeria* species in foods of animal origin in Addis Ababa, Ethiopia. J Infect Public Health 2011;4(1):22–29; doi: 10.1016/j.jiph.2010.10.002

Getaneh A, Berhanu L, Gume B, et al. Occurrences and antibiotic susceptibility patterns of *Listeria monocytogenes* in raw meat samples from abattoir and butcher shops in Jimma Town, Southwest Ethiopia. Heliyon 2025;11(4):e42589; doi: 10.1016/j.heliyon.2025.e42589

Ghazali MH, Saleem F, Bashir L. Cold plasma and high-pressure processing in sustainable meat preservation: A review. Food Nutr Health 2025;2(1):22; doi: 10.1007/s44403-025-00032-1

Gil MI, Truchado P, Tudela JA, et al. Environmental monitoring of three fresh-cut processing facilities reveals harborage sites for *Listeria monocytogenes*. Food Control 2024;155:110093; doi: 10.1016/j.foodcont.2023.110093

Gombas DE, Chen Y, Clavero RS, et al. Survey of *Listeria monocytogenes* in ready-to-eat foods. J Food Prot 2003; 66(4):559–569; doi: 10.4315/0362-028X-66.4.559

Goudar V, Kanthesh B, Prasad N. Isolation and identification of *Listeria monocytogenes* in Bangalore city from various food samples. Biomed Pharmacol J 2021;14(4):2271–2276; doi: 10.13005/bpj/2327

Gouws PA, Liedemann I. Evaluation of diagnostic PCR for the detection of *Listeria monocytogenes* in food products. Food Technol Biotechnol 2005;43(2):201–205.

Graves LM, Helsel LO, Steigerwalt AG, et al. *Listeria marthii* sp. nov., isolated from the natural environment, finger lakes national forest. Int J Syst Evol Microbiol 2010;60(Pt 6): 1280–1288; doi: 10.1099/ijs.0.014118-0

Hadi AJ, Medicine ANJ. Isolation and identification of zoonotic importance bacteria from meat, meat products and human in Diyala, Iraq. Plant Arch 2020;20(2):8745–8755.

Hamad G, Hafez EE, Sobhy SE, et al. Detection of *Clostridium botulinum* in some Egyptian fish products, Its control *in vitro* using citrus leaves extracts, and applicability of *Citrus limon* leaf extract in tuna. Foods 2023;12(7):1466; doi: 10.3390/foods12071466

Hamidiyan N, Salehi-Abargouei A, Rezaei Z, et al. The prevalence of *Listeria* spp. food contamination in Iran: A systematic review and meta-analysis. Food Res Int 2018;107:437–450; doi: 10.1016/j.foodres.2018.02.038

Harakeh S, Saleh I, Zouhairi O, et al. Antimicrobial resistance of *Listeria monocytogenes* isolated from dairy-based food products. Sci Total Environ 2009;407(13):4022–4027; doi: 10.1016/j.scitotenv.2009.04.010

Hassan HA, Ali ZI. Assessment of *Listeria monocytogenes* presence in raw milk samples and certain cheese varieties. Assiut Vet Med J 2024;70(183); doi: 10.21608/avmj.2024.305177.1308

Henri C, Félix B, Guillier L, et al. Population genetic structure of *Listeria monocytogenes* strains as determined by pulsed-field gel electrophoresis and multilocus sequence typing. Appl Environ Microbiol 2016;82(18):5720–5728; doi: 10.1128/AEM.00583-16

Heredia N, García S. Animals as sources of food-borne pathogens: A review. Anim Nutr 2018;4(3):250–255; doi: 10.1016/j.aninu.2018.04.006

Indrawattana N, Nibaddhasobon T, Sookrung N, et al. Prevalence of *Listeria monocytogenes* in raw meats marketed in Bangkok and characterization of the isolates by phenotypic and molecular methods. J Health Popul Nutr 2011;29(1):26–38; doi: 10.3329/jhpn.v29i1.7565

Jadhav S, Bhave M, Palombo EA. Methods used for the detection and subtyping of *Listeria monocytogenes*. J Microbiol Methods 2012;88(3):327–341; doi: 10.1016/j.mimet.2012.01.002

Jamali H, Chai LC, Thong KL. Detection and isolation of *Listeria* spp. and *Listeria monocytogenes* in ready-to-eat foods with various selective culture media. Food Control 2013;32(1):19–24; doi: 10.1016/j.foodcont.2012.11.033

Jamshidi A, Zeinali T. Significance and characteristics of *Listeria monocytogenes* in poultry products. Int J Food Sci 2019;2019(1):7835253; doi: 10.1155/2019/7835253

Janković V, Mitrović R, Lakicevic B, et al. *Listeria monocytogenes* presence during fermentation, drying and storage of Petrovská klobása sausage. IOP Conf Ser: Earth Environ Sci 2017;85:12051; doi: 10.1088/1755-1315/85/1/012051

Jones D, Sneath P, Woodbine M. The relations between Listeria and other bacteria. In Proceedings of the 3rd International Symposium of Listeriosis Bilthoven, *The Netherlands*, 1966, pp. 161–164.

Kaszoni-Rückerl I, Mustedanagic A, Muri-Klinger S, et al. Predominance of distinct *Listeria innocua* and *Listeria monocytogenes* in recurrent contamination events at dairy processing facilities. Microorganisms 2020;8(2):234; doi: 10.3390/microorganisms8020234

Khan JA, Rathore RS, Khan S, et al. Role of *Listeria monocytogenes* in human health: Disadvantages and advantages. In: The Handbook of Microbial Bioresources. Gaur VKGGDSMGTR, eds. CABI: Wallingford, UK; 2016, 193–203.

Korsak D, Krawczyk-Balska A. Identification of the molecular mechanism of trimethoprim resistance in *Listeria monocytogenes*. Foodborne Pathog Dis 2017;14(12):696–700; doi: 10.1089/fpd.2017.2323

Korthals M, Ege M, Lick S, et al. Occurrence of *Listeria* spp. in mattress dust of farm children in Bavaria. Environ Res 2008;107(3):299–304; doi: 10.1016/j.envres.2008.02.007

Kramarenko T, Roasto M, Meremäe K, et al. *Listeria monocytogenes* prevalence and serotype diversity in various foods. Food Control 2013;30(1):24–29; doi: 10.1016/j.foodcont.2012.06.047

Kuan CH, Goh SG, Loo YY, et al. Prevalence and quantification of *Listeria monocytogenes* in chicken offal at the retail level in Malaysia. Poult Sci 2013;92(6):1664–1669; doi: 10.3382/ps.2012-02974

Kureljušić J, Roković N, Jezdimirović N, et al. Isolation and detection of *Listeria monocytogenes* in poultry meat by standard culture methods and PCR. IOP Conf Ser: Earth Environ Sci 2017;85:12069; doi: 10.1088/1755-1315/85/1/012069

Lado B, Yousef AE. 6 Characteristics of Listeria monocytogenes important to food processors. In: Listeria, Listeriosis and Food Safety. Ryser ETM, E. H., eds. 3rd edition. CRC Press: Boca Raton, FL; 2007, 157–213.

Lambertz ST, Nilsson C, Brådenmark A, et al. Prevalence and level of *Listeria monocytogenes* in ready-to-eat foods in Sweden 2010. Int J Food Microbiol 2012;160(1):24–31; doi: 10.1016/j.ijfoodmicro.2012.09.010

Lang Halter E, Neuhaus K, Scherer S. *Listeria weihenstephanensis* sp. nov., isolated from the water plant Lemna trisulca taken from a freshwater pond. Int J Syst Evol Microbiol 2013;63(Pt 2):641–647; doi: 10.1099/ijs.0.036830-0

Law JW-F, Ab Mutalib N-S, Chan K-G, et al. Rapid methods for the detection of foodborne bacterial pathogens: Principles, applications, advantages and limitations. Front Microbiol 2014;5:770; doi: 10.3389/fmicb.2014.00770

Leclercq A, Clermont D, Bizet C, et al. *Listeria rocourtiae* sp. nov. Int J Syst Evol Microbiol 2010;60(Pt 9):2210–2214; doi: 10.1099/ijs.0.017376-0

Leclercq A, Moura A, Vales G, et al. *Listeria thailandensis* sp. nov. Int J Syst Evol Microbiol 2019;69(1):74–81; doi: 10.1099/ijsem.0.003097

Legba B, Dougnon V, Chabi Y, et al. Evaluation of in-vivo anti-Salmonella activity of *Uvaria chamae*, *Lantana camara* and *Phyllantus amarus* used in Benin, West Africa. BMC Vet Res 2020;16(1):49; doi: 10.1186/s12917-020-2266-1

Leong D, Alvarez-Ordóñez A, Jooste P, et al. *Listeria monocytogenes* in food: Control by monitoring the food processing environment. Afr J Microbiol Res 2016;10(1):1–14; doi: 10.5897/AJMR2015.7832

Linke K, Rückerl I, Brugger K, et al. Reservoirs of *Listeria* species in three environmental ecosystems. Appl Environ Microbiol 2014;80(18):5583–5592; doi: 10.1128/AEM.01018-14

Liu Y, Zhu H, Dou X, et al. The influence of nutrients on biofilm formation of an ST87 strain of *Listeria monocytogenes*. LWT 2024;191:115658; doi: 10.1016/j.lwt.2023.115658

Lomonaco S, Nucera D, Filipello V. The evolution and epidemiology of *Listeria monocytogenes* in Europe and the United States. Infect Genet Evol 2015;35:172–183; doi: 10.1016/j.meegid.2015.08.008

Lourenco A, Linke K, Wagner M, et al. The saprophytic lifestyle of *Listeria monocytogenes* and entry into the food-

processing environment. Front Microbiol 2022;13:789801; doi: 10.3389/fmicb.2022.789801

Luque-Sastre L, Arroyo C, Fox EM, et al. Antimicrobial resistance in *Listeria* species. Microbiol Spectr 2018;6(4); doi: 10.1128/microbiolspec.ARBA-0031-2017

Maćkiw E, Stasiak M, Kowalska J, et al. Occurrence and characteristics of Listeria monocytogenes in ready-to-eat meat products in Poland. J Food Prot 2020;83(6):1002–1009; doi: 10.4315/jfp-19-525

Madharsha N, Veeramani V, Kannaiyan J, et al. Isolation and identification of *Listeria monocytogenes* from fish intestines and phylogenetic analysis. IntJCurrMicrobiolAppSci 2018; 7(11):1177–1187; doi: 10.20546/ijcmas.2018.711.137

Markov K, Frece J, Čvek D, et al. *Listeria monocytogenes* and other contaminants in fresh cheese and cream from Zagreb city area domestic production. Mljekarstvo 2009;59(3): 225–231.

Martín B, Perich A, Gómez D, et al. Diversity and distribution of *Listeria monocytogenes* in meat processing plants. Food Microbiol 2014;44:119–127; doi: 10.1016/j.fm.2014.05.014

Massawe HF, Makingi GI, Shija DS, et al. Prevalence of the *Staphylococcal enterotoxins* genes in raw and milk products along the value chain in Mbeya and Mbozi Districts, Tanzania. J Nat Sci Res 2017;7(18).

Mata MT, Baquero F, Pérez-Díaz JC. A multidrug efflux transporter in *Listeria monocytogenes*. FEMS Microbiol Lett 2000; 187(2):185–188; doi: 10.1111/j.1574-6968.2000.tb09158.x

Matereke LT, Okoh AI. *Listeria monocytogenes* virulence, antimicrobial resistance and environmental persistence: A review. Pathogens 2020;9(7):528; doi: 10.3390/pathogens9070528

Matle I, Mbatha KR, Lentsoane O, et al. Occurrence, serotypes, and characteristics of *Listeria monocytogenes* in meat and meat products in South Africa between 2014 and 2016. J Food Saf 2019;39(4):e12629; doi: 10.1111/jfs.12629

Matle I, Mbatha KR, Madoroba E. A review of *Listeria monocytogenes* from meat and meat products: Epidemiology, virulence factors, antimicrobial resistance and diagnosis. Onderstepoort J Vet Res 2020;87(1):e1–e20; doi: 10.4102/ojvr.v87i1.1869

Meshref A, Zeinhom M, Abdel-Atty NS. Occurrence and distribution of *Listeria* species in some Egyptian foods. AJVS 2015;46(1):42–47; doi: 10.5455/ajvs.187647

Meza-Bone GA, Meza Bone JS, Cedeño Á, et al. Prevalence of *Listeria monocytogenes* in RTE Meat Products of Quevedo (Ecuador). Foods 2023;12(15):2956; doi: 10.3390/foods12152956

Michelet C, Avril J, Cartier F, et al. Inhibition of intracellular growth of *Listeria monocytogenes* by antibiotics. Antimicrob Agents Chemother 1994;38(3):438–446; doi: 10.1128/AAC.38.3.438

Mie A, Andersen HR, Gunnarsson S, et al. Human health implications of organic food and organic agriculture: A comprehensive review. Environ Health 2017;16(1):111; doi: 10.1186/s12940-017-0315-4

Mohammad H, Al-Farwachi M, Al-Shakarji B. First detection of *Listeria ivanovii* in aborted sheep fetuses in the Iraqi Nineveh Governorate. Egyp J Vet Sci 2024;55(3):625–632; doi: 10.21608/EJVS.2023.236083.1612

Morvan A, Moubareck C, Leclercq A, et al. Antimicrobial resistance of *Listeria monocytogenes* strains isolated from humans in France. Antimicrob Agents Chemother 2010; 54(6):2728–2731; doi: 10.1128/AAC.01557-09

Moura A, Leclercq A, Vales G, et al. Phenotypic and genotypic antimicrobial resistance of *Listeria monocytogenes*: An observational study in France. Lancet Reg Health Eur 2024; 37:100800; doi: 10.1016/j.lanepe.2023.100800

Mpundu P, Muma JB, Mukubesa AN, et al. Antibiotic resistance patterns of *Listeria* species isolated from broiler abattoirs in Lusaka, Zambia. Antibiotics (Basel) 2022;11(5):591; doi: 10.3390/antibiotics11050591

Mpundu P. Public Health Importance and Antibiotic Resistance Patterns of *Listeria* Species in Food and Food Processing Environments in Selected Districts of Zambia. The University of Zambia; 2023.

Mustafa A, Al-Nazal AI. Isolation and diagnosis of Listeria monocytogenes from some types of frozen meat. 2019.

Nayak DN, Savalia CV, Kalyani IH, et al. Isolation, identification, and characterization of *Listeria* spp. from various animal origin foods. Vet World 2015;8(6):695–701; doi: 10.14202/vetworld.2015.695-701

Noll M, Kleta S, Al Dahouk S. Antibiotic susceptibility of 259 *Listeria monocytogenes* strains isolated from food, food-processing plants and human samples in Germany. J Infect Public Health 2018;11(4):572–577; doi: 10.1016/j.jiph.2017.12.007

Nørrung B, Buncic S. Microbial safety of meat in the European Union. Meat Sci 2008;78(1–2):14–24; doi: 10.1016/j.meatsci.2007.07.032

Núñez-Montero K, Leclercq A, Moura A, et al. *Listeria costaricensi*s sp. nov. Int J Syst Evol Microbiol 2018;68(3):844–850; doi: 10.1099/ijsem.0.002596

Nwaiwu O. What are the recognized species of the genus *Listeria*? Access Microbiol 2020;2(9):acmi000153; doi: 10.1099/acmi.0.000153

O'Connor L, O'Leary M, Leonard N, et al. The characterization of *Listeria* spp. isolated from food products and the food-processing environment. Lett Appl Microbiol 2010;51(5): 490–498; doi: 10.1111/j.1472-765X.2010.02928.x

Obi L, Morobe I, Nyila MA, et al. Molecular characterization and serotyping of Listeria monocytogenes with a focus on food safety and disease prevention. In: Biochemical Testing. Jimenez-Lopez JC, eds. IntechOpen: Rijeka; 2012.

Oravcová K, Trncíková T, Kuchta T, et al. Limitation in the detection of *Listeria monocytogenes* in food in the presence of competing *Listeria innocua*. J Appl Microbiol 2008; 104(2):429–437; doi: 10.1111/j.1365-2672.2007.03554.x

Orsi RH, Wiedmann M. Characteristics and distribution of *Listeria* spp., including *Listeria* species newly described since 2009. Appl Microbiol Biotechnol 2016;100(12):5273–5287; doi: 10.1007/s00253-016-7552-2

Osek J, Lachtara B, Wieczorek K. *Listeria monocytogenes* in foods-from culture identification to whole-genome characteristics. Food Sci Nutr 2022;10(9):2825–2854; doi: 10.1002/fsn3.2910

Painter J, Slutsker L. Listeriosis in Humans. Food Science and Technology-New York-Marcel Dekker; 2007;161:85.

Panebianco F, Rubiola S, Buttieri C, et al. Understanding the effect of ozone on *Listeria monocytogenes* and resident microbiota of Gorgonzola cheese surface: A Culturomic approach. Foods 2022;11(17):2640; doi: 10.3390/foods11172640

Park J, Han S, Shin S. Comparison of growth performance of the BacT/ALERT VIRTUO and BACTEC FX blood culture systems under simulated bloodstream infection conditions.

Clin Lab 2017;63(1):39–46; doi: 10.7754/Clin.Lab.2016.160502

Parra-Flores J, Holý O, Bustamante F, et al. Virulence and antibiotic resistance genes in *Listeria monocytogenes* strains isolated from ready-to-eat foods in Chile. Front Microbiol 2021;12:796040; doi: 10.3389/fmicb.2021.796040

Paul M. Monitoring and analytics of *Listeria monocytogenes*: Key facts for authorities, food manufacturers, and retailers. J Consum Prot Food Saf 2020;15(1):1–3; doi: 10.1007/s00003-020-01273-2

Peri AM, Stewart A, Hume A, et al. New microbiological techniques for the diagnosis of bacterial infections and sepsis in ICU including point of care. Curr Infect Dis Rep 2021;23(8):12; doi: 10.1007/s11908-021-00755-0

Pleadin J, Lešić T, Vujačić V, et al. Comparison of chemical composition and fatty acid profile of traditional meat products from Croatia and Montenegro. J Food Qual 2021;2021:1–10; doi: 10.1155/2021/5586436

Rajalingam N, Van Haute S. Adaptive tolerance of *Listeria monocytogenes* to chemical oxidants: Comparative analysis of transcriptomic studies. Compr Rev Food Sci Food Saf 2025;24(5):e70260; doi: 10.1111/1541-4337.70260

Rapeanu G, Parfene GHV, Polcovnicu C, et al. Confirmation and identification of *Listeria* species from fresh lettuce. Periodico di Mineralogia 2017;86(6):32–36.

Ravindhiran R, Sivarajan K, Sekar JN, et al. *Listeria monocytogenes* an emerging pathogen: A comprehensive overview on listeriosis, virulence determinants, detection, and anti-listerial interventions. Microb Ecol 2023;86(4):2231–2251; doi: 10.1007/s00248-023-02269-9

Ribeiro AC, Almeida F, Medeiros MM, et al. *Listeria monocytogenes*: An inconvenient hurdle for the dairy industry. Dairy 2023;4(2):316–344; doi: 10.3390/dairy4020022

Ricci A, Lazzi C, Bernini V. Natural antimicrobials: A reservoir to contrast *Listeria monocytogenes*. Microorganisms 2023;11(10):2568; doi: 10.3390/microorganisms11102568

Rincón-Gamboa SM, Poutou-Piñales RA, Carrascal-Camacho AK. Distribution of *Listeria* spp., and *Listeria monocytogenes* in micro- and small-scale meat product processing plants. Heliyon 2024;10(7):e28662; doi: 10.1016/j.heliyon.2024.e28662

Rodrigues CS, Sá C, Melo C. An overview of *Listeria monocytogenes* contamination in ready to eat meat, dairy and fishery foods. Cienc Rural 2017;47(2):e20160721; doi: 10.1590/0103-8478cr20160721

Rohilla A, Kumar V, Ahire J. Unveiling the persistent threat: Recent insights into *Listeria monocytogenes* adaptation, biofilm formation, and pathogenicity in foodborne infections. J Food Sci Technol 2024;61(8):1428–1438; doi: 10.1007/s13197-023-05918-6

Romão B, Botelho RBA, Torres ML, et al. Nutritional profile of commercialized plant-based meat: An integrative review with a systematic approach. Foods 2023;12(3):448; doi: 10.3390/foods12030448

Rossi F, Giaccone V, Colavita G, et al. Virulence characteristics and distribution of the pathogen *Listeria ivanovii* in the environment and in food. Microorganisms 2022;10(8):1679; doi: 10.3390/microorganisms10081679

Safwa SM, Ahmed T, Talukder S, et al. Applications of non-thermal technologies in food processing Industries-a review. J Agric Food Res 2024;18:100917; doi: 10.1016/j.jafr.2023.100917

Sainz-García E, Alba-Elías F. Advances in the application of cold plasma technology in foods. Foods 2023;12(7):1388; doi: 10.3390/foods12071388

Sala C, Morar A, Tîrziu E, et al. Environmental occurrence and antibiotic susceptibility profile of *Listeria monocytogenes* at a slaughterhouse raw processing plant in Romania. J Food Prot 2016;79(10):1794–1797; doi: 10.4315/0362-028x.jfp-16-052

Salas C, Calvo J, Martínez-Martínez L. Activity of tigecycline against coryneform bacteria of clinical interest and *Listeria monocytogenes*. Antimicrob Agents Chemother 2008;52(4):1503–1505; doi: 10.1128/AAC.01129-07

Santorum P, Garcia RV, López V, et al. Review. Dairy farm management and production practices associated with the presence of *Listeria monocytogenes* in raw milk and beef. Span j agric res 2012;10(2):360–371; doi: 10.5424/sjar/2012102-314-11

Sasakawa C., eds. Molecular Mechanisms of Bacterial Infection via the Gut. Springer Science & Business Media: Berlin, Heidelberg; 2009.

Sauders BD, Overdevest J, Fortes E, et al. Diversity of *Listeria* species in urban and natural environments. Appl Environ Microbiol 2012;78(12):4420–4433; doi: 10.1128/AEM.00282-12

Sauders BD, Sanchez MD, Rice DH, et al. Prevalence and molecular diversity of *Listeria monocytogenes* in retail establishments. J Food Prot 2009;72(11):2337–2349; doi: 10.4315/0362-028X-72.11.2337

Sawale P, Patil P, Singh A, et al. Non-thermal techniques for microbiological safety, nutritional preservation, and enhanced efficiency in dairy processing. FFS 2024;4(5):180–203; doi: 10.31989/ffs.v4i5.1326

Shamloo E, Hosseini H, Abdi Moghadam Z, et al. Importance of *Listeria monocytogenes* in food safety: A review of its prevalence, detection, and antibiotic resistance. Iran J Vet Res 2019;20(4):241–254.

Sharma RK, Jalalpure SS, Pathak S, et al. Molecular detection of *Listeria monocytogenes* from different dairy and street food sources in North Karnataka, India. J Infect Public Health 2024;17(4):696–703; doi: 10.1016/j.jiph.2024.02.014

Shehata MG, Abd El-Aziz NM, Mehany T, et al. Taro leaves extract and probiotic lactic acid bacteria: A synergistic approach to improve antioxidant capacity and bioaccessibility in fermented milk beverages. LWT 2023;187:115280; doi: 10.1016/j.lwt.2023.115280

Smith CL, Gonzalez SV, Metcalf JL, et al. Differences in spoilage microflora growth kinetics could be contributing to beef muscle-specific color stability. Meat Muscle Biol 2024;8(1):16915, 16911–16914; doi: 10.22175/mmb.16915

Sneath P, Cowan S. An electro-taxonomic survey of bacteria. J Gen Microbiol 1958;19(3):551–565; doi: 10.1099/00221287-19-3-551

Sofos JN, Geornaras I. Overview of current meat hygiene and safety risks and summary of recent studies on biofilms, and control of *Escherichia coli* O157:H7 in nonintact, and *Listeria monocytogenes* in ready-to-eat, meat products. Meat Sci 2010;86(1):2–14; doi: 10.1016/j.meatsci.2010.04.015

Song C, Wang B, Wang Y, et al. Detection of *Listeria monocytogenes* in food using the Proofman-LMTIA assay. Molecules 2023;28(14):5457; doi: 10.3390/molecules28145457

Stuart SE, Welshimer HJ. Taxonomic reexamination of *Listeria Pirie* and transfer of *Listeria grayi* and *Listeria murrayi* to a

New Genus, Murraya. Int J Syst Evol Microbiol 1974;24(2): 177–185; doi: 10.1099/00207713-24-2-177

Sun L, Van Loey A, Buvé C, et al. Experimental evolution reveals a novel ene reductase that detoxifies α, β-unsaturated aldehydes in *Listeria monocytogenes*. Microbiol Spectr 2023; 11(3):e04877–e4822; doi: 10.1128/spectrum.04877-22

Szymczak B, Szymczak M, Sawicki W, et al. Anthropogenic impact on the presence of *L. monocytogenes* in soil, fruits, and vegetables. Folia Microbiol (Praha) 2014;59(1):23–29; doi: 10.1007/s12223-013-0260-8

Taha A, Mehany T, Pandiselvam R, et al. Sonoprocessing: Mechanisms and recent applications of power ultrasound in food. Crit Rev Food Sci Nutr 2024;64(17):6016–6054; doi: 10.1080/10408398.2022.2161464

Tamma PD, Heil EL, Justo JA, et al. Infectious diseases society of America 2024 guidance on the treatment of antimicrobial-resistant gram-negative infections. Clin Infect Dis 2024: ciae403; doi: 10.1093/cid/ciae403

Tan SM, De Kock HL, Dykes GA, et al. Enhancement of poultry meat: Trends, nutritional profile, legislation and challenges. SA J An Sci 2018;48(2):199–212; doi: 10.4314/sajas.v48i2.1

Thi Le H, Vu HT, Tran NTH, et al. Ultrasensitive and rapid fluorescence immunoassay for *Listeria monocytogenes* detection using size-compatible magnetic beads and core-shell quantum dots. J Sci: Adv Mater Dev 2025;10(3):100936; doi: 10 .1016/j.jsamd.2025.100936

Tirloni E, Centorotola G, Pomilio F, et al. *Listeria monocytogenes* in ready-to-eat (RTE) delicatessen foods: Prevalence, genomic characterization of isolates and growth potential. Int J Food Microbiol 2024;410:110515; doi: 10.1016/j .ijfoodmicro.2023.110515

Toplu MS, Tuncer BÖ. Evaluation of the functional properties and safety of enterocin-producing *Enterococcus faecium* BT29. 11 isolated from Turkish Beyaz cheese and its inhibitory activity against *Listeria monocytogenes* in UHT whole milk. Ital J Food Sci 2023;35(2):54–70; doi: 10.15586/ijfs .v35i2.2316

Troxler R, von Graevenitz A, Funke G, et al. Natural antibiotic susceptibility of *Listeria* species: *L. grayi, L. innocua, L. ivanovii, L. monocytogenes, L. seeligeri* and *L. welshimeri* strains. Clin Microbiol Infect 2000;6(10):525–535; doi: 10 .1046/j.1469-0691.2000.00168.x

Verraes C, Van Boxstael S, Van Meervenne E, et al. Antimicrobial resistance in the food chain: A review. Int J Environ Res Public Health 2013;10(7):2643–2669; doi: 10 .3390/ijerph10072643

Vitas AI, Garcia-Jalon VA. Occurrence of *Listeria monocytogenes* in fresh and processed foods in Navarra (Spain). Int J Food Microbiol 2004;90(3):349–356; doi: 10.1016/s0168-1605(03)00314-3

Vrioni G, Tsiamis C, Oikonomidis G, et al. MALDI-TOF mass spectrometry technology for detecting biomarkers of antimicrobial resistance: Current achievements and future perspectives. Ann Transl Med 2018;6(12):240; doi: 10.21037/atm .2018.06.28

Wang L, Zhao P, Si X, et al. Rapid and specific detection of *Listeria monocytogenes* with an isothermal amplification and lateral flow strip combined method that eliminates false-positive signals from primer-dimers. Front Microbiol 2019;10:2959; doi: 10.3389/fmicb.2019.02959

Wang X-X, Chen X, Zhou Z-K. Digestive and metabolic characteristics of dietary meat proteins: Meat source and thermal processing matter. Food Rev Int 2024;40(9):3020–3035; doi: 10.1080/87559129.2024.2325693

Weller D, Andrus A, Wiedmann M, et al. *Listeria booriae* sp. nov. and *Listeria newyorkensis* sp. nov., from food processing environments in the USA. Int J Syst Evol Microbiol 2015;65(Pt 1):286–292; doi: 10.1099/ijs.0.070839-0

WHO. Estimates of the global burden of foodborne diseases: Foodborne disease burden epidemiology reference group 2007–2015. WHO: Geneva; 2015.

Wilson A, Gray J, Chandry PS, et al. Phenotypic and genotypic analysis of antimicrobial resistance among *Listeria monocytogenes* isolated from Australian food production chains. Genes (Basel) 2018;9(2):80; doi: 10.3390/genes9020080

Wu Z, Xu M, He W, et al. Unraveling the physicochemical properties and bacterial communities in rabbit meat during chilled storage. Foods 2024;13(4):623; doi: 10.3390/foods13040623

Yong S-S, Lee J-I, Kang D-H. Identifying a novel *Listeria innocua* subgroup and enhancing *Listeria* detection in grain: A duplex real-time PCR approach informed by comparative genomic analysis. LWT 2024;199:116108; doi: 10.1016/j.lwt .2024.116108

Yordanova R, Andonova A. Rapid methods for detection of foodborne pathogens and their toxins - a review of current trends and future perspectives. J IMAB 2024;30(2):5587–5592; doi: 10.5272/jimab.2024302.5587

Zakaria AI, Sabala RF. Potential public health hazards related to consumption of poultry contaminated with antibiotic resistant *Listeria monocytogenes* in Egypt. BMC Microbiol 2024; 24(1):41; doi: 10.1186/s12866-024-03183-x

Zeinali T, Jamshidi A, Bassami M, et al. Isolation and identification of *Listeria* spp. in chicken carcasses marketed in northeast of Iran. Int Food Res J 2017;24(2):881–887.

Zhang H, Que F, Xu B, et al. Identification of *Listeria monocytogenes* contamination in a ready-to-eat meat processing plant in China. Front Microbiol 2021a;12:628204; doi: 10.3389/ fmicb.2021.628204

Zhang H, Wang J, Chang Z, et al. *Listeria monocytogenes* contamination characteristics in two ready-to-eat meat plants from 2019 to 2020 in Shanghai. Front Microbiol 2021b;12: 729114; doi: 10.3389/fmicb.2021.729114

Zhang J, Ma C, Du Y, et al. Microfluidic biosensors for rapid detection of foodborne pathogenic bacteria: Recent advances and future perspectives. Front Chem 2025;13:1536928; doi: 10.3389/fchem.2025.1536928

Zhang P, Ji L, Wu X, et al. Prevalence, genotypic characteristics, and antibiotic resistance of *Listeria monocytogenes* from retail foods in Huzhou, China. J Food Prot 2024a;87(7): 100307; doi: 10.1016/j.jfp.2024.100307

Zhang Y, Zhu C, Du B, et al. Preservative effect of chitosan-gelatine composite incorporated with pomegranate peel polyphenol on fresh meat. IFRJ 2024b;31(1):239–252; doi: 10 .47836/ifrj.31.1.21

Zhu Q, Gooneratne R, Hussain MA. *Listeria monocytogenes* in fresh produce: Outbreaks, prevalence and contamination levels. Foods 2017;6(3):21; doi: 10.3390/foods6030021

Zuerner RLLeptospira. In: Bergey's Manual of Systematics of Archaea and Bacteria. Trujillo ME, Dedysh S, DeVos P, et al. eds. Wiley; 2015, 1–19.

Address correspondence to:
Sawsan A. Al-Hilifi, PhD
Department of Food Science
College of Agriculture
University of Basrah
Basrah 61014
Iraq

E-mail: sawsan.hameed@uobasrah.edu.iq

Sameh A. Korma, PhD
School of Food Science and Engineering
South China University of Technology
Guangzhou 510641
China

E-mails: sameh9251@scut.edu.cn*;*
sameh.hosny@zu.edu.eg