

REVIEW ARTICLE

Food Microbiology

Antibiotic resistance of *Listeria monocytogenes* present in raw milk and milk products: mechanisms, prevalence and implications for food safety.

HBC Harshani*, WAS Wijendra and R Ramesh

Medical Research Institute, Colombo-08, Sri Lanka

Submitted: 18 February 2025; Revised: 24 April 2026; Accepted: 29 April 2026

Abstract: Antibiotic resistance has emerged as a major global concern in both clinical and food safety contexts leading to a reduction in the effectiveness of treatments against bacterial infections and contaminations. *Listeria monocytogenes*, which causes severe food borne infections is particularly important due to its increasing tendency to develop resistance to commonly used antibiotics, posing significant challenges to public health. To gain a deeper insight into this issue, a comprehensive literature search was conducted. Based on this extensive review of the available literature, this article describes the mechanisms underlying antibiotic resistance in *L. monocytogenes*, with particular emphasis on its genetic basis and the role of horizontal gene transfer. The review also discusses the prevalence of antibiotic-resistant strains, with a special emphasis on their occurrence in raw milk and dairy products. In addition, key factors contributing to the development and spread of resistance including antibiotic exposure, food processing conditions, and bacterial stress responses were evaluated. Overall, this review highlights the growing public health significance of antibiotic-resistant *L. monocytogenes* and emphasizes the need for continuous surveillance, improved control strategies, and interdisciplinary collaboration to mitigate its emergence and ensure food safety.

Key words: *Listeria monocytogenes*, antibiotic resistance, raw milk, food safety, public health, genetic mechanisms

INTRODUCTION

Listeria monocytogenes, the causative agent of listeriosis, is a pathogenic Gram-positive coccobacillus widely

distributed in environmental sources such as food, water, soil, animal feed, and sewage (Gartley et al., 2022). This bacterium is capable of contaminating a wide range of food products and is responsible for listeriosis, a serious foodborne infection that poses significant health risks to humans. The disease primarily affects vulnerable populations, including pregnant women, neonates, the elderly, and immunocompromised individuals. In humans, listeriosis can result in severe clinical outcomes such as meningitis, meningoencephalitis, septicemia, abortion, and prenatal infections. The infection is associated with high mortality rates, reaching approximately 20–30% among high-risk groups (Disson & Lecuit, 2012; Choi et al., 2018; Hilliard et al., 2018).

L. monocytogenes can be shed in the milk of cows and buffaloes following miscarriage or udder infection, contaminating apparently normal milk with a significant bacterial load (Osman et al., 2016). The potential transmission of listeriosis through raw milk highlights the importance of monitoring and managing dairy herds to prevent outbreaks. Contaminated dairy products, introduced during processing or post-production handling, remain a major vehicle for human infection (Borucki et al., 2005; Wijendra et al., 2014; Ulusoy & Chirkena, 2019).

In recent years, increasing attention has been directed toward antimicrobial resistance in *L. monocytogenes*,

* Corresponding author (hbc.harshani@gmail.com;  <https://orcid.org/0000-0002-7194-1794>)



This article is published under the Creative Commons CC-BY-ND License (<http://creativecommons.org/licenses/by-nd/4.0/>). This license permits use, distribution and reproduction, commercial and non-commercial, provided that the original work is properly cited and is not changed in anyway.

particularly among isolates associated with food and dairy environments. Although the organism has been reported to be susceptible to first-line antibiotics such as ampicillin and penicillin (Morvan et al., 2010; Haase et al., 2014; Wilson et al., 2018), emerging resistance to commonly used antimicrobials, including tetracyclines, macrolides, and sulfonamides, has been reported (Tayeb et al., 2023; Díaz-Martínez et al., 2024; Ramatla et al., 2026). The presence of multidrug-resistant strains raises concerns regarding treatment efficacy and public health risk (Kayode et al., 2020). These factors collectively highlight the importance of integrating antimicrobial resistance surveillance into studies of listeriosis outbreaks, particularly those associated with milk and milk products.

Listeriosis outbreaks

Listeriosis is a severe foodborne infection caused by *L. monocytogenes*, a bacterium capable of surviving in diverse environments, including refrigerated foods (Choi et al., 2018; Gartley et al., 2022). Infection occurs mainly through contaminated food such as ready-to-eat products and unpasteurized milk (Disson & Lecuit, 2012; Osman et al., 2016). Clinical outcomes range from mild febrile illness to septicemia, meningitis, and miscarriage, with case fatality rates reaching 20–30% in high-risk groups (Hilliard et al., 2018; Choi et al., 2018).

L. monocytogenes outbreaks linked to milk and milk products (Table 1) reveal several key trends in product type, outbreak severity, and contamination pathways. Soft and fresh cheeses, including Brie, Queso fresco, Mexican-type cheese, and raw milk cheeses, were the most frequently implicated products. Outbreaks involving these products often resulted in the highest number of cases and deaths, reflecting their susceptibility to contamination and widespread consumption. For example, the 1985 outbreak in California associated with Mexican-type cheese caused 142 cases and 48 deaths (Linnan et al., 1988), while soft cheese outbreaks in Switzerland (1983–1987) and Sweden (2001) accounted for 122 and 120 cases, respectively (Bula et al., 1995; Carrique-Mas et al., 2003).

Pasteurized milk and pasteurized dairy products were also implicated in outbreaks, though typically with lower case numbers. Notably, the 1983 Maryland outbreak of pasteurized milk resulted in 49 cases and 14 deaths (Fleming et al., 1985), highlighting that post-pasteurization contamination remains a significant risk. Products such as butter, chocolate milk, ice cream, and fermented dairy were less frequently associated with outbreaks and generally resulted in fewer cases and

fatalities (e.g., 1987 California butter: 11 cases, Not Reported; 2009 Lebanon Kashk: 6 cases, Not Reported) (FDA, 2003; Harakeh et al., 2009).

Geographically, outbreaks were reported across North America, Europe, and the Middle East, with the USA, France, Canada, and Switzerland experiencing multiple large-scale events. Multi-state outbreaks in the USA (2003–2007, 2020–2024) frequently involved Hispanic-style soft cheeses and Brie/Camembert-type cheeses, reflecting distribution across wider regions (Smith, 2008; CDC, 2021).

Mortality trends indicate that raw milk and soft cheese outbreaks caused the greatest fatalities. Early high-mortality events included the 1985 Mexican-type cheese outbreak in California (48 deaths) and the 1983–1987 soft cheese outbreak in Switzerland (33 deaths) (Linnan et al., 1988; Bula et al., 1995). In contrast, outbreaks involving butter, pasteurized milk, or ice cream generally resulted in fewer deaths.

Contamination of dairy products with *L. monocytogenes* has been attributed to several factors reported in the literature. Raw or unpasteurized products are particularly susceptible due to higher bacterial loads and the absence of heat treatment, which allows the bacteria to survive and proliferate (Allerberger & Guggenbichler, 1989; Osman et al., 2016). Soft cheeses, characterized by high moisture content and nearly neutral pH, provide an environment favorable for bacterial growth (Linnan et al., 1988; Bula et al., 1995). Even pasteurized products are at risk through post-processing contamination, which can occur during handling, storage, or from equipment (Fleming et al., 1985; Schwartz et al., 1989).

Additionally, fresh or minimally aged cheeses often have limited acidity and short shelf lives, which fail to inhibit bacterial proliferation effectively (Harakeh et al., 2009; Osaili et al., 2012). Together, these factors highlight the multiple points at which *L. monocytogenes* contamination can occur in dairy production.

Contamination pathways included direct shedding from infected animals (such as mastitis or miscarriage) (Osman et al., 2016), cross-contamination during processing, and improper storage allowing bacterial proliferation. Multi-country outbreaks in recent years (e.g., in 2023, in Europe) underscore the transboundary risks associated with modern distribution chains. Both industrial and artisanal dairy products are vulnerable, and the absence of mortality reporting in some recent outbreaks may underestimate the public health burden.

Table 1: *Listeria* outbreaks caused by contaminated raw milk and milk products

Year	Country / Region	Type of Milk Product	No. of listeriosis cases and (deaths)	Reference
1979	Maryland, USA	Raw milk cheese	20 (3)	Ho et al., (1986)
1981	England	Dairy products	11 (5)	FDA (2003)
1983	Maryland, USA	Pasteurized milk	49 (14)	Fleming et al., (1985)
1983–1987	Switzerland	Soft cheese	122 (33)	Bula et al., (1995)
1985	California, USA	Mexican-type cheese	142 (48)	Linnan et al., (1988)
1986	Austria	Unpasteurized milk	28 (5)	Allerberger & Guggenbichler (1989)
1986–1987	Pennsylvania, USA	Ice cream, Brie	36 (4)	Schwartz et al., (1989)
1987	California, USA	Butter	11 (NR)	FDA (2003)
1989–1990	Denmark	Blue-mold / hard cheese	26 (6)	Jensen et al., (1994)
1989	Italy	Soft cheese	2 (NR)	Massa et al., (1990)
1991	England & Wales	Soft ripened cheese	63 (NR)	Greenwood et al., (1991)
1994	USA	Chocolate milk	45 (NR)	Dalton et al., (1997)
1995	France	Soft cheese	37 (11)	Goulet et al., (1995)
1997	France	Soft cheese	14 (NR)	Jacquet et al., (1998)
1998–1999	Finland	Butter	25 (6)	Lyytikäinen et al., (2000)
1999	England	Cheese	2 (NR)	Torner (2007)
2000	North Carolina, USA	Queso fresco	12 (5)	CDC (2001); MacDonald et al., (2005)
2001	Sweden	Soft cheese	120 (NR)	Carrique-Mas et al., (2003)
2001	Belgium	Frozen ice cream	2 (NR)	Yde & Genicot (2004)
2001	Japan	Washed-type cheese	38 (NR)	Makino et al., (2005)
2002	British Columbia, Canada	Cheese	47 (NR)	Pagotto et al., (2006)
2002	British Columbia, Canada	Pasteurized cheese	86 (NR)	Pagotto et al., (2006)
2002	Quebec, Canada	Soft & semi-hard cheese	17 (NR)	Gaulin et al., (2003)
2003	Texas, USA	Mexican fresh cheese	13 (2)	Swaminathan & Gerner-Smidt (2007)
2003–2007	USA (multi-state)	Queso fresco	74 (10)	Smith (2008)
2005	Brazil	Minas frescal cheese	6 (NR)	Brito et al., (2008)
2007	Massachusetts, USA	Pasteurized milk	5 (3)	CDC (2008)
2007	Ireland	Farmhouse cheeses	21 (NR)	O'Brien et al., (2009)
2008	Quebec, Canada	Cheese	38 (2)	Gilmour et al., (2010)
2008	Chile	Brie cheese	119 (5)	Jordan, 2016
2009	Lebanon	Kashk (fermented dairy)	6 (NR)	Harakeh et al., (2009)
2011	Jordan	Cheese	39 (NR)	Osaili et al., (2012)
2020	USA (multi-state)	Hispanic-style soft cheeses	13 (1)	CDC (2021)
2021	France	Raw milk soft cheeses	14 (NR)	Robinson et al., 2020)
2022	USA (Florida)	Ice cream	23 (1)	CDC (2022)
2022	USA (multi-state)	Brie & Camembert-style cheese	6 (1)	CDC (2022)
2023	Europe (multi-country)	Raw milk soft cheeses	16 (NR)	EFSA & ECDC (2023)
2024	USA (multi-state)	Cottage cheese & dairy desserts	8 (NR)	CDC (2024)

NR-Not Recorded

Treatment of listeriosis

Antibiotics are the primary therapeutic option for listeriosis, as no vaccines are currently available for its prevention. Early diagnosis of *L. monocytogenes* infection is critical due to the potentially severe outcomes of the disease, including septicemia, meningitis, and complications in pregnant women. One factor that complicates timely diagnosis and outbreak investigations is the pathogen's unusually long incubation period, which can last up to 70 days. Symptoms may appear weeks after exposure, and thus patients often fail to accurately recall, the relevant details making it difficult for public health authorities to trace the source of infection and implement control measures (Dortet et al., 2009; Rhoades et al., 2009). First-line treatments include penicillin, ampicillin, and gentamicin, while trimethoprim-sulfamethoxazole serves as an alternative for penicillin-allergic individuals. Erythromycin is often recommended for infected pregnant women, and vancomycin is used for cases of bacteremia. Other antibiotics, including rifampicin, doxycycline, chloramphenicol, and fluoroquinolones, may also be effective depending on the clinical context (Ramaswamy et al., 2007; Conter et al., 2009; Allerberger & Wagner, 2010; Alonso-Hernando et al., 2012).

However, the emergence of antibiotic-resistant strains of *L. monocytogenes* in raw milk and dairy products has complicated the control of this pathogen and may compromise the effectiveness of antimicrobial therapy for listeriosis, thereby posing significant public health concerns (Basu et al., 2017; Akrami-Mohajeri et al., 2018; Badawy et al., 2022).

Antibiotic resistance in *Listeria monocytogenes*

Antibiotic resistance in bacteria appears to be driven, in part, by the extensive and sometimes inappropriate use of antibiotics in both animal husbandry and human medicine, where they have been used not only for therapeutic purposes but also, in some regions, as growth promoters in livestock or applied without strict regulatory oversight (Marshall and Levy, 2011; Van Boeckel et al., 2015; O'Neill Review on Antimicrobial Resistance, 2016; Food and Agriculture Organization, 2016; World Health Organization, 2017). Exposure to sub-therapeutic antibiotic levels in animal production can select for resistant *L. monocytogenes* strains, and horizontal gene transfer via mobile genetic elements (plasmids, transposons), which further facilitates acquisition of resistance genes. In addition, stressful conditions in food-processing environments and the formation of

biofilms can enhance survival of resistant bacteria. As a result, multidrug-resistant *L. monocytogenes* isolates have been increasingly recovered from raw milk, pasteurized products, and other dairy foods, reducing the therapeutic options for listeriosis and underscoring the need for prudent antibiotic stewardship and ongoing surveillance across the farm-to-fork continuum.

Prevalence of antibiotic-resistant *Listeria monocytogenes* in raw milk and dairy products

Numerous studies over the past four decades have documented the prevalence of antibiotic-resistant *L. monocytogenes* in raw milk and dairy products (Akrami-Mohajeri et al., 2018; Aksem et al., 2018; Badawy et al., 2022; Kayode & Okoh, 2022; Harshani et al., 2022). More recent studies have reported multidrug-resistant (MDR) strains in raw milk and dairy products across multiple regions, with resistance commonly observed against penicillin, ampicillin, tetracycline, oxacillin, and aminoglycosides (Harshani et al., 2022, 2024; Suryawanshi et al., 2023; He et al., 2025). Many isolates also harbor virulence genes, underscoring the potential for both antimicrobial resistance and pathogenicity to co-exist in dairy-associated *L. monocytogenes* (Parussolo et al., 2021; Mohamed et al., 2022).

Mechanisms of antibiotic resistance in *Listeria monocytogenes*

Antibiotic resistance in *L. monocytogenes* is mediated by a combination of intrinsic and acquired mechanisms, involving horizontal gene transfer, mobile genetic elements, active efflux systems, and genetic modifications affecting antibiotic targets.

(i) Plasmid- and conjugation-mediated resistance

The acquisition of resistance genes via plasmids and conjugative transposons represents a major mechanism contributing to antimicrobial resistance in *L. monocytogenes*. Early studies demonstrated that resistance plasmids can be transferred between bacteria through conjugation (Evans & Macrina, 1983; Flamm et al., 1984). In addition, conjugative transposons carrying tetracycline resistance genes have been shown to transfer between *Listeria* species (Vicente et al., 1988). Certain studies indicate that such mobile elements continue to play a significant role in the dissemination of resistance traits, including fluoroquinolone resistance and multidrug resistance (Allen et al., 2016; Barker et al., 2025).

(ii) Mobile genetic elements in the gastrointestinal tract

Horizontal gene transfer within the gastrointestinal tract is another important pathway for the acquisition of resistance. In this environment, *L. monocytogenes* interacts with a diverse microbial community, facilitating the exchange of genetic material. Mobile genetic elements such as transposons and integrative conjugative elements have been reported to carry resistance genes, including those conferring resistance to tetracycline and ampicillin (Charpentier & Courvalin, 1999; Aminov et al., 2001; Walsh et al., 2001; Périchon & Courvalin, 2009). This contributes to the persistence and spread of resistance determinants across bacterial populations.

(iii) Efflux pumps and regulatory mutations

Efflux-mediated resistance is another key mechanism in *L. monocytogenes*. Efflux pumps, particularly MdrL (also referred to as Mdr1), actively expel antibiotics from the bacterial cell, thereby reducing intracellular drug concentrations. Resistance to fluoroquinolones such as ciprofloxacin has been associated with mutations in regulatory genes, including *fepR*, which control the expression of efflux systems (Romanova et al., 2006; Guérin et al., 2014; Wilson et al., 2018). These mutations can lead to overexpression of efflux pumps and enhanced resistance.

(iv) Modification of antibiotic targets and genetic determinants

Modification of antibiotic target sites is a major mechanism underlying resistance in *L. monocytogenes*. Genetic alterations can affect structures such as ribosomal subunits and penicillin-binding proteins, reducing the binding affinity of antibiotics, particularly macrolides and β -lactams.

At the molecular level, a wide range of antimicrobial resistance genes have been identified in *L. monocytogenes* isolates from diverse sources. Tetracycline resistance is among the most frequently reported and is associated with genes such as *tetA*, *tetC*, *tetD*, *tetG*, *tetK*, and *tetM* (Srinivasan et al., 2005; Kayode et al., 2022; Parra-Flores et al., 2022). Resistance to β -lactam antibiotics has been linked to genes such as *ampC* and *blaZ*, which may contribute to reduced susceptibility through target modification or enzymatic activity (Mohamed et al., 2022; He et al., 2025).

Aminoglycoside resistance is mediated by genes including *aph(3')-IIa* and *aad6*, which encode enzymes capable of modifying and inactivating these antibiotics (Kayode et al., 2022; Mohamed et al., 2022). Similarly, macrolide resistance involves genes such as *lnuG*, *mphB*, *msr(A/D)*, and *mef(A)*, which act through mechanisms including target modification, enzymatic inactivation, and active efflux (Barker et al., 2025; He et al., 2025).

In addition, other resistance determinants such as *fosX*, *lin*, *norB*, and *mprF* have been reported, reflecting a diversity of mechanisms including antibiotic inactivation, efflux activity, and cell membrane modification (Srinivasan et al., 2005; Parra-Flores et al., 2022).

(v) Multidrug resistance and environmental adaptation

Several studies have reported the occurrence of multidrug-resistant (MDR) isolates in dairy products, often associated with high antibiotic resistance indices and the ability to persist under environmental stress, including exposure to disinfectants (Frieri et al., 2017; Suryawanshi et al., 2023; Harshani et al., 2024). These findings highlight that both genetic determinants and environmental pressures play a critical role in the evolution and maintenance of antimicrobial resistance. Environmental conditions encountered during food processing and storage significantly influence the development of antibiotic resistance in *L. monocytogenes* and other foodborne pathogens. A range of biological, physical, and chemical stresses can trigger adaptive responses that enhance bacterial survival and tolerance to antimicrobial agents (Wesche et al., 2009). A key regulator in this process is the sigma factor B (SigB), which controls stress response pathways in Gram-positive bacteria. In *L. monocytogenes*, activation of SigB has been linked to increased expression of genes associated with cell wall integrity and resistance to antibiotics such as vancomycin (Palmer et al., 2009; Shin et al., 2010).

Exposure to environmental stressors including fluctuations in pH, temperature, and osmotic pressure has been shown to increase bacterial resistance to antibiotics. For instance, *L. monocytogenes* subjected to low pH, high salt concentrations, or refrigeration temperatures demonstrates enhanced tolerance to multiple antimicrobial agents (Al-Nabulsi et al., 2015; Olaimat et al., 2018). Similarly, prior exposure to certain antibiotics, such as ampicillin, tetracycline (achromycin), gentamicin, rifampicin, and trimethoprim-sulfamethoxazole, may

confer cross-protection against non-lethal stresses, including oxidative stress and sublethal heat (Faezi Ghasemi and Kazemi, 2015).

In addition, environmental stresses commonly applied in food preservation such as low water activity, acidic conditions, and high osmotic pressure can facilitate the horizontal transfer of conjugative plasmids carrying resistance genes (Beuls et al., 2012). Starvation stress further enhances bacterial resistance to preservation methods like heat and irradiation (Mendonca et al., 2004). Moreover, both horizontal and vertical gene transfer between *Listeria* spp. and other Gram-positive bacteria, including *Staphylococcus* and *Enterococcus*, contribute to the dissemination of antimicrobial resistance determinants (Charpentier and Courvalin, 1999; Lyon et al., 2008).

The use of approved food antimicrobials, such as sodium diacetate, potassium lactate, and nisin, may also influence resistance by inducing efflux pump activity (Stasiewicz et al., 2011). Additionally, natural plant-derived antimicrobials such as clove oil, cinnamaldehyde, and vanillin are increasingly used in food preservation; however, their potential to induce cross-protection against clinically relevant antibiotics in *L. monocytogenes* remains limited (Oussalah et al., 2005; Zanini et al., 2014).

Biofilm formation further complicates control strategies, as *L. monocytogenes* embedded within biofilms exhibit intrinsic resistance to disinfectants and sanitation procedures. Mechanisms such as exopolysaccharide production, persister cell formation, quorum sensing, and efflux pump activity enhance bacterial persistence in food processing environments, posing ongoing challenges for food safety and public health (Jahid and Ha, 2012; De La Fuente Nunez et al., 2013; Buchanan et al., 2017; Li et al., 2023).

Implications of the emergence of antibiotic-resistant strains of *Listeria monocytogenes* in raw milk and milk products

The emergence of antibiotic-resistant strains of *L. monocytogenes* in raw milk and milk products presents a complex public health challenge with significant implications for food safety (Harakeh et al., 2009; Wilson et al., 2018). Consumption of products containing these strains exposes diverse populations to antibiotic-resistant pathogens, potentially resulting in severe and difficult-to-treat infections, particularly among immunocompromised individuals, (Ramaswamy et al., 2007; Choi et al., 2018).

The well-documented link between raw milk and milk products and listeriosis outbreaks further amplifies the risk, highlighting the need for robust public health interventions (Dalton et al., 1997; Osman et al., 2016). Moreover, the potential for horizontal gene transfer of antibiotic resistance genes among microbial communities raises broader concerns regarding the dissemination of resistance determinants (Charpentier & Courvalin, 1999; Aminov et al., 2001).

This scenario underscores the necessity for responsible antibiotic use in both clinical and agricultural settings, alongside effective monitoring, surveillance, and intervention strategies to limit the spread of antibiotic-resistant *L. monocytogenes* within the food supply chain (Frieri et al., 2017; Guérin et al., 2014). The safety of milk and dairy products is therefore a critical concern, as the presence of resistant *Listeria* strains threatens both consumer health and the integrity of the dairy industry (Noll et al., 2017; Harshani et al., 2022). Continuous surveillance, strong collaboration between food regulatory authorities and the dairy industry, and the adoption of innovative strategies are crucial to effectively mitigate this threat. Alternative antimicrobials such as bacteriophages, plant extracts, and essential oils have shown potential in controlling resistant strains, while advanced detection methods, including biosensor technologies, enable rapid and accurate identification of contamination (Oussalah et al., 2005; Stasiewicz et al., 2011; Zanini et al., 2014). Predictive analytics further support proactive interventions, helping to prevent outbreaks and safeguard public health (Jahid & Ha, 2012).

The integration of alternative antimicrobials, advanced detection techniques, and predictive tools represents a paradigm shift in combating antibiotic-resistant *L. monocytogenes*, addressing immediate risks while promoting long-term food safety. Collectively, these strategies highlight the importance of One Health approaches, ongoing surveillance, stricter food safety regulations, and consumer education to ensure the safety of milk and milk products and the protection of public health (Buchanan et al., 2017; Li et al., 2023).

Study gaps in antibiotic resistance of *Listeria monocytogenes* in raw milk and milk products

Despite reported antibiotic resistance, critical gaps exist in understanding genetic mechanisms driving resistance development in *L. monocytogenes* in raw milk and milk products. Comprehensive studies exploring these pathways are inadequate for understanding how

L. monocytogenes acquires resistance genes, how these genes are transferred between strains or species, and how resistant strains persist and spread in dairy environments and the food chain.

Limited research on environmental conditions within dairy production facilities has also limited the understanding of the factors that influence the survival and persistence of antibiotic-resistant *L. monocytogenes*. Variables such as temperature fluctuations, sanitation practices, biofilm formation on equipment, and exposure to disinfectants or sub-lethal stressors can affect the ability of resistant strains to survive and spread, but these factors remain poorly characterized. Understanding these factors is essential for insights into resistance development within raw milk environments. Further investigations are necessary in the realm of DNA repair following exposure to such environmental conditions. Enhanced comprehension of this pathogen would advance our understanding of how its adaptation to anaerobiosis contributes to its pathogenesis (Roberts et al., 2020).

There is still a significant lack of knowledge regarding the functions of specific proteins and their contributions to the pathogenesis and virulence of *L. monocytogenes*. Additionally, understanding how this information relates to strains obtained from various environments remains incomplete (Wiktorczyk-Kapischke et al., 2023).

Additional research is essential to quantify the release of antibiotics into agricultural ecosystems and to assess the extent of human exposure not only to antibiotics but also to antibiotic-resistant bacteria (ARB) and antibiotic resistance genes (ARGs). While much of the focus has been on *L. monocytogenes*, similar concerns apply to other foodborne and environmental bacterial species, including *Escherichia coli*, *Salmonella spp.*, *Staphylococcus aureus*, and *Enterococcus spp.*, which can acquire and disseminate resistance genes. Comprehensive studies are needed to evaluate the potential risks that antibiotics, ARB, and ARGs in the environment pose to human health and ecological systems, as well as to inform strategies for mitigating the spread of resistance across bacterial populations (Iwu et al., 2020).

In summary, targeted research efforts are needed to address these gaps in understanding antibiotic resistance in *L. monocytogenes* associated with raw milk, offering insights into mechanisms, drivers, and effective mitigation strategies.

CONCLUSIONS

In conclusion, antibiotic-resistant *L. monocytogenes* in raw milk poses significant challenges for public health, food safety, and the dairy industry. Resistance mechanisms, including mobile genetic elements and efflux pumps, lead to multidrug resistance. Environmental stressors like pH, temperature, and salt contribute to antibiotic resistance, highlighting the pathogen's adaptability. Implications include challenges in clinical management, increased healthcare burdens, and strains on public health resources. Horizontal gene transfer underscores the need for comprehensive strategies, including responsible antibiotic use, continuous surveillance, and interventions. Despite progress, gaps persist in understanding genetic mechanisms, environmental factors, and clinical implications of antibiotic resistance in raw milk strains. Continuous surveillance, innovative strategies, and interdisciplinary collaboration are crucial. Alternative antimicrobials, advanced testing, and predictive analytics offer promising avenues. The convergence of these strategies emphasizes prevention, consumer safety, and dairy industry sustainability. Targeted research is essential to fill knowledge gaps and develop effective mitigation strategies for antibiotic-resistant strains in raw milk.

Based on guidance from the Food and Agriculture Organization (FAO) of the United Nations and the World Health Organization (WHO), addressing antibiotic-resistant *L. monocytogenes* in raw milk and milk products requires coordinated, risk-based interventions across the food chain. Joint FAO/WHO expert reports emphasize strengthening integrated surveillance systems to monitor *L. monocytogenes* contamination and antimicrobial resistance trends in dairy production, processing environments, and final products (FAO/WHO, 2020; FAO, 2022). The adoption of a One Health approach is strongly recommended, recognizing the interconnected roles of human health, animal husbandry, food safety, and the environment in the emergence and dissemination of antimicrobial resistance (WHO, 2017; FAO/WHO, 2021). Responsible and regulated use of antibiotics in livestock production, coupled with strict enforcement of good hygienic practices, good manufacturing practices, and Hazard Analysis and Critical Control Point (HACCP) based controls, is critical to reducing selective pressure that drives resistance (FAO/WHO, 2019). Furthermore, FAO/WHO reports advocate pasteurization as a key control measure and stress the importance of consumer risk

communication, particularly for vulnerable populations, regarding the hazards of raw milk consumption. Continued research into alternative antimicrobials, rapid detection tools, and updated quantitative microbial risk assessments is also encouraged to support evidence-based policy development and ensure long-term protection of public health and dairy food safety (FAO/WHO, 2022).

REFERENCES

- Akrami-Mohajeri, F., Derakhshan, Z., Ferrante, M., Hamidiyan, N., Soleymani, M., Conti, G. O., & Tafti, R. D. (2018). The prevalence and antimicrobial resistance of *Listeria* spp. in raw milk and traditional dairy products delivered in Yazd, central Iran (2016). *Food and Chemical Toxicology*, 114, 141–144. <https://doi.org/10.1016/j.fct.2018.02.006>
- Aksoy, A., Sezer, Ç., Vatansever, L., & Gülbaz, G. (2018). Presence and antibiotic resistance of *Listeria monocytogenes* in raw milk and dairy products. *Kafkas Üniversitesi Veteriner Fakültesi Dergisi*, 24(3), 415–421. <https://doi.org/10.9775/kvfd.2017.19081>
- Akya, A., Najafi, A., Moradi, J., Mohebi, Z., & Adabagher, S. (2013). Prevalence of food contamination with *Listeria* spp. in Kermanshah, Islamic Republic of Iran. *Eastern Mediterranean Health Journal*, 19(5), 474–477. <https://doi.org/10.26719/2013.19.5.474>
- Al-Brefkani, A. M. T., & Mammani, I. M. A. (2019). Characterisation of *Listeria monocytogenes* from food and human clinical samples at Duhok, Kurdistan Region of Iraq. *Journal of Pure and Applied Microbiology*, 13(4), 2215–2226. <https://doi.org/10.22207/JPAM.13.4.35>
- Allen, K. J., Walecka-Zacharska, E., Chen, J. C., Kosek-Paszkowska, K., Devlieghere, F., Van Meerven, E., Osek, J., Wiczorek, K., & Bania, J. (2016). *Listeria monocytogenes* – An examination of food chain factors potentially contributing to antimicrobial resistance. *Food Microbiology*, 54, 178–189. <https://doi.org/10.1016/j.fm.2014.08.006>
- Allerberger, F., & Guggenbichler, J. P. (1989). Listeriosis in Austria—Report of an outbreak in 1986. *Acta Microbiologica Hungarica*, 36(2–3), 149–152.
- Allerberger, F., & Wagner, M. (2010). Listeriosis: A resurgent foodborne infection. *Clinical Microbiology and Infection*, 16(1), 16–23. <https://doi.org/10.1111/j.1469-0691.2009.03109.x>
- Al-Nabulsi, A., Osaili, T., Awad, A., Olaimat, A., Shaker, R., & Holley, R. (2014). Occurrence and antibiotic susceptibility of *Listeria monocytogenes* isolated from raw and processed meat products in Amman, Jordan. *CytA – Journal of Food*, 13(3), 346–352. <https://doi.org/10.1080/19476337.2014.982191>
- Alonso-Hernando, A., Prieto, M., García-Fernández, C., Alonso-Calleja, C., & Capita, R. (2012). Increase over time in the prevalence of multiple antibiotic resistance among isolates of *Listeria monocytogenes* from poultry in Spain. *Food Control*, 23(1), 37–41. <https://doi.org/10.1016/j.foodcont.2011.06.006>
- Aminov, R. I., Garrigues-Jeanjean, N., & Mackie, R. I. (2001). Molecular ecology of tetracycline resistance: Development and validation of primers for detection of tetracycline resistance genes encoding ribosomal protection proteins. *Applied and Environmental Microbiology*, 67(1), 22–32. <https://doi.org/10.1128/AEM.67.1.22-32.2001>
- Arslan, S., & Özdemir, F. (2008). Prevalence and antimicrobial resistance of *Listeria* spp. in homemade white cheese. *Food Control*, 19(4), 360–363. <https://doi.org/10.1016/j.foodcont.2007.04.009>
- Badawy, B., Gwida, M., Sadat, A., El-Toukhy, M., Sayed-Ahmed, M., Alam, N., Ahmad, S., Ali, M. D. S., & Elafify, M. (2022). Prevalence and antimicrobial resistance of virulent *Listeria monocytogenes* and *Cronobacter sakazakii* in dairy cattle, the environment, and dried milk with the in vitro application of natural alternative control. *Antibiotics*, 11(8), 1087. <https://doi.org/10.3390/antibiotics11081087>
- Barker, C. R., Greig, D. R., Olonade, I., Swift, C., Crewdson, A., Painset, A., Pittock, N., Rajendram, D., Godbole, G., & Ribeca, P. (2025). Characterization of *Listeria monocytogenes* plasmid with antibiotic and stress resistance genes. *Microbial Genomics*, 11(1), e001445. <https://doi.org/10.1099/mgen.0.001445>
- Basu, S., Kundu, M., & Kumar, S. (2017). Antibiotic resistance patterns of *Listeria monocytogenes* isolated from food sources: A review. *Foodborne Pathogens and Disease*, 14(5), 252–261. <https://doi.org/10.1089/fpd.2016.2230>
- Beuls, E., Modrie, P., Deserranno, C., & Mahillon, J. (2012). High-salt stress conditions increase the pAW63 transfer frequency in *Bacillus thuringiensis*. *Applied and Environmental Microbiology*, 78(19), 7128–7131. <https://doi.org/10.1128/AEM.01105-12>
- Bille, J., Blanc, D. S., Schmid, H., Boubaker, K., Baumgartner, A., Siegrist, H. H., Tritten, M. L., Lienhard, R., Berner, D., Anderau, R., Treboux, M., Ducommun, J. M., Malinverni, R., Genné, D., Erard, P. H., & Waespi, U. (2006). Outbreak of human listeriosis associated with Tomme cheese in Northwest Switzerland. *Euro Surveillance*, 11(4–6), 91–93. PMID:16801693
- Borucki, M. K., Gay, C. C., Reynolds, J., McElwain, K. L., Kim, S. H., Call, D. R., & Knowles, D. P. (2005). Genetic diversity of *Listeria monocytogenes* strains from a high-prevalence dairy farm. *Applied and Environmental Microbiology*, 71(10), 5893–5899. <https://doi.org/10.1128/AEM.71.10.5893-5899.2005>
- Brito, J. R. F., Santos, E. M. P., Arcuri, E. F., Lange, C. C., Brito, M. A. V. P., Souza, G. N., Cerqueira, M. M. P. O., Beltran, J. M. S., Call, J. E., Liu, Y., Porto-Fett, A. C. S., & Luchansky, J. B. (2008). Retail survey of Brazilian milk and Minas Frescal cheese and a contaminated dairy plant to establish prevalence, relatedness, and sources of *Listeria monocytogenes* isolates. *Applied and Environmental Microbiology*, 74(15), 4954–4961. <https://doi.org/10.1128/AEM.01828-07>
- Buchanan, R. L., Gorris, L. G. M., Hayman, M. M., Jackson, T. C., & Whiting, R. C. (2017). A review of *Listeria monocytogenes*: An update on outbreaks, virulence, dose-response, ecology, and risk assessments. *Food Control*, 75,

- 1–13. <https://doi.org/10.1016/j.foodcont.2016.12.016>
- Bula, C. J., Bille, J., & Glauser, M. P. (1995). An epidemic of food-borne listeriosis in western Switzerland: Description of 57 cases involving adults. *Clinical Infectious Diseases*, 20(1), 66–72. <https://doi.org/10.1093/clinids/20.1.66>
- Çağrı-Mehmetoglu, A., Yaldirak, G., Bodur, T., Şimşek, M., Bozkir, H., & Eren, N. (2011). Incidence of *Listeria monocytogenes* and *Escherichia coli* O157:H7 in two Kasar Cheese processing environments. *Food Control*, 22, 762–766. <https://doi.org/10.1016/j.foodcont.2010.11.015>
- Carrique-Mas, J. J., Hokeberg, I., Andersson, Y., Arneborn, M., Tham, W., Danielsson-Tham, M. L., Osterman, B., Leffler, M., Steen, M., Eriksson, E., Hedin, G., & Giesecke, J. (2003). Febrile gastroenteritis after eating on-farm manufactured fresh cheese – An outbreak of listeriosis? *Epidemiology and Infection*, 130(1), 79–86. <https://doi.org/10.1017/s0950268802008014>
- Centers for Disease Control and Prevention. (2001). Outbreak of listeriosis associated with homemade Mexican-style cheese North Carolina, October 2000–January 2001. *Morbidity and Mortality Weekly Report*, 50(26), 560–562.
- Centers for Disease Control and Prevention. (2008). Outbreak of *Listeria monocytogenes* infections associated with pasteurized milk from a local dairy—Massachusetts, 2007. *Morbidity and Mortality Weekly Report*, 57(40), 1097–1100. <https://www.cdc.gov/mmwr/preview/mmwrhtml/mm5026a2.htm>
- Centers for Disease Control and Prevention. (2014, December 4). *Oasis Brands, Inc. cheese recalls and investigation of human listeriosis cases*. <https://www.cdc.gov/listeria/outbreaks/cheese-10-14/index.htm>
- Centers for Disease Control and Prevention. (2011). Multistate outbreak of listeriosis associated with Jensen Farms cantaloupe United States, August–September 2011. *Morbidity and Mortality Weekly Report*, 60(39), 1357–1358. <https://www.cdc.gov/mmwr/preview/mmwrhtml/mm6039a6.htm>
- Centers for Disease Control and Prevention. (2021). Multistate outbreak of listeriosis linked to Hispanic style soft cheeses United States. <https://www.cdc.gov/listeria/outbreaks/hispanic-cheese-21/index.html>
- Centers for Disease Control and Prevention. (2022). *Listeria* outbreaks linked to ice cream products Florida, USA. <https://www.cdc.gov/listeria/outbreaks/ice-cream-22/index.html>
- Centers for Disease Control and Prevention. (2022). Listeriosis linked to brie and camembert style cheese Multistate, USA. <https://www.cdc.gov/listeria/outbreaks/brie-camembert-22/index.html>
- Centers for Disease Control and Prevention. (2024). Listeriosis associated with cottage cheese and dairy desserts United States. <https://www.cdc.gov/listeria/outbreaks/cottage-cheese-24/index.html>
- Charpentier, E., & Courvalin, P. (1999). Antibiotic resistance in *Listeria* spp. *Antimicrobial Agents and Chemotherapy*, 43(9), 2103–2108. <https://doi.org/10.1128/AAC.43.9.2103>
- Choi, M. H., Park, Y. J., Kim, M., Seo, Y. H., & Lee, K. (2018). Increasing incidence of listeriosis and infection-associated clinical outcomes. *Annals of Laboratory Medicine*, 38(2), 102–109. <https://doi.org/10.3343/alm.2018.38.2.102>
- Cocolin, L., Nucera, D., Alessandria, V., Rantsiou, K., Dolci, P., Grassi, M. A., Lomonaco, S., & Civera, T. (2009). Microbial ecology of Gorgonzola rinds and occurrence of different biotypes of *Listeria monocytogenes*. *International Journal of Food Microbiology*, 133(1–2), 200–205. <https://doi.org/10.1016/j.ijfoodmicro.2009.05.003>
- Conter, M., Paludi, D., Zanardi, E., Ghidini, S., Vergara, A., & Ianieri, A. (2009). Characterization of antimicrobial resistance of foodborne *Listeria monocytogenes*. *International Journal of Food Microbiology*, 128(3), 497–500. <https://doi.org/10.1016/j.ijfoodmicro.2008.10.018>
- Dalton, C. B., Austin, C. C., Sobel, J., Hayes, P. S., Bibb, W. F., Graves, L. M., Swaminathan, B., Proctor, M. E., & Griffin, P. M. (1997). An outbreak of gastroenteritis and fever due to *Listeria monocytogenes* in milk. *New England Journal of Medicine*, 336(2), 100–105. <https://doi.org/10.1056/NEJM199701093360204>
- de la Fuente-Núñez, C., Refeuville, F., Fernández, L., & Hancock, R. E. (2013). Bacterial biofilm development as a multicellular adaptation: Antibiotic resistance and new therapeutic strategies. *Current Opinion in Microbiology*, 16(5), 580–589. <https://doi.org/10.1016/j.mib.2013.06.013>
- Díaz-Martínez, A., et al. (2024). Exploring the antibiotic resistance of *Listeria monocytogenes* in food environments: A review. *Critical Reviews in Microbiology*.
- Disson, O., & Lecuit, M. (2012). Targeting of the central nervous system by *Listeria monocytogenes*. *Virulence*, 3(3), 213–221. <https://doi.org/10.4161/viru.19586>
- Dortet, L., Veiga-Chacon, E., & Cossart, P. (2009). *Listeria monocytogenes*. In *Encyclopedia of Microbiology* (pp. 182–198). <https://doi.org/10.1016/b978-012373944-5.00217-0>
- European Food Safety Authority & European Centre for Disease Prevention and Control. (2023). *Listeria monocytogenes outbreaks in raw milk soft cheeses—Europe*. <https://www.efsa.europa.eu/en/topics/topic/listeria>
- Evans, R. P., & Macrina, F. L. (1983). Streptococcal R plasmid pIP501: Endonuclease site map, resistance determinant location, and construction of novel derivatives. *Journal of Bacteriology*, 154(4), 1347–1355. <https://doi.org/10.1128/jb.154.3.1347-1355.1983>
- Faezi Ghasemi, M., & Kazemi, S. (2015). Effect of sub-lethal environmental stresses on the cell survival and antibacterial susceptibility of *Listeria monocytogenes* PTCC1297. *Zahedan Journal of Research in Medical Sciences*, 17(1), e1915.
- Flamm, R. K., Hinrichs, D. J., & Thomashow, M. F. (1984). Introduction of pAM beta 1 into *Listeria monocytogenes* by conjugation and homology between native *L. monocytogenes* plasmids. *Infection and Immunity*, 44(1), 157–161. <https://doi.org/10.1128/iai.44.1.157-161.1984>
- Fleming, D. W., Cochi, S. L., MacDonald, K. L., Brondum, J., Hayes, P. S., Plikaytis, B. D., Holmes, M. B., Audurier, A., Broome, C. V., & Reingold, A. L. (1985). Pasteurized milk as a vehicle of infection in an outbreak of listeriosis. *New England Journal of Medicine*, 312(7), 404–407. <https://doi.org/10.1056/NEJM198502143120704>

- FAO/WHO. (2016). *The FAO action plan on antimicrobial resistance 2016–2020*. Food and Agriculture Organization of the United Nations & World Health Organization. <https://www.fao.org/3/i5996e/i5996e.pdf>.
- FAO/WHO. (2019). *Expert meeting on microbiological risk assessment of Listeria monocytogenes in ready-to-eat foods*. Food and Agriculture Organization of the United Nations & World Health Organization. <https://www.fao.org/3/ca4468en/ca4468en.pdf>
- FAO/WHO. (2020). *Joint FAO/WHO expert consultation on foodborne antimicrobial resistance: Guidance for risk management and surveillance*. Rome, Italy: Food and Agriculture Organization of the United Nations & World Health Organization. <https://www.fao.org/3/ca9505en/CA9505EN.pdf>
- FAO/WHO. (2021). *One Health approach for integrated surveillance of antimicrobial resistance in humans, animals, and food*. Rome, Italy: Food and Agriculture Organization of the United Nations & World Health Organization. <https://www.fao.org/3/cb4567en/CB4567EN.pdf>
- FAO. (2022). *Antimicrobial resistance in the food chain: Guidance for policy and action*. Food and Agriculture Organization of the United Nations. <https://www.fao.org/3/cb9728en/CB9728EN.pdf>
- Frieri, M., Kumar, K., & Boutin, A. (2017). Antibiotic resistance. *Journal of Infection and Public Health*, 10(4), 369–378. <https://doi.org/10.1016/j.jiph.2016.08.007>
- Gaulin, C., Ramsay, D., Ringuette, L., & Ismail, J. (2003). First documented outbreak of *Listeria monocytogenes* in Quebec, 2002. *Canada Communicable Disease Report*, 29(21), 181–186. <https://doi.org/10.17795/zjrms-1915>
- Gartley, S., Anderson-Coughlin, B., Sharma, M., & Kniel, K. E. (2022). *Listeria monocytogenes* in irrigation water: An assessment of outbreaks, sources, prevalence, and persistence. *Microorganisms*, 10, 1319. <https://doi.org/10.3390/microorganisms10071319>
- Gilmour, M. W., Graham, M., Van Domselaar, G., Tyler, S., Kent, H., Trout-Yakel, K. M., Larios, O., Allen, V., Lee, B., & Nadon, C. (2010). High-throughput genome sequencing of two *Listeria monocytogenes* clinical isolates during a large foodborne outbreak. *BMC Genomics*, 11(120), 1471–2164. <https://doi.org/10.1186/1471-2164-11-120>
- Godreuil, S., Galimand, M., Gerbaud, G., Jacquet, C., & Courvalin, P. (2003). Efflux pump Lde is associated with fluoroquinolone resistance in *Listeria monocytogenes*. *Antimicrobial Agents and Chemotherapy*, 47(2), 704–708. <https://doi.org/10.1128/AAC.47.2.704-708.2003>
- Goulet, V., Jacquet, C., Vaillant, V., Rebiere, I., Mouret, E., Lorente, C., Maillot, E., Stainer, F., & Rocourt, J. (1995). Listeriosis from consumption of raw-milk cheese. *Lancet*, 345(8964), 1581–1582. [https://doi.org/10.1016/S0140-6736\(95\)91077-7](https://doi.org/10.1016/S0140-6736(95)91077-7)
- Greenwood, M. H., Roberts, D., & Burden, P. (1991). The occurrence of *Listeria* species in milk and dairy products: A national survey in England and Wales. *International Journal of Food Microbiology*, 12(2–3), 197–206. [https://doi.org/10.1016/0168-1605\(91\)90070-6](https://doi.org/10.1016/0168-1605(91)90070-6)
- Gulel, G. T., Gucukoglu, A., Cadirci, Ö., Saka, E., & Alisarli, M. (2020). Serotyping and antibiotic resistance of *Listeria monocytogenes* isolated from raw water buffalo milk and milk products. *Journal of Food Science*, 85(9), 2889–2895. <https://doi.org/10.1111/1750-3841.15376>
- Guérin, F., Galimand, M., Tuambilangana, F., Courvalin, P., & Cattoir, V. (2014). Overexpression of the novel MATE fluoroquinolone efflux pump FepA in *Listeria monocytogenes* is driven by inactivation of its local repressor FepR. *PLoS ONE*, 9(9), e106340. <https://doi.org/10.1371/journal.pone.0106340>
- Haase, J. K., Didelot, X., Lecuit, M., & Kuroda, M. (2014). Antimicrobial susceptibility of *Listeria monocytogenes* isolates and genomic insights into resistance mechanisms. *Journal of Antimicrobial Chemotherapy*, 69(8), 2125–2134. <https://doi.org/10.1093/jac/dku109>
- Harakeh, S., Saleh, I., Zouhairi, O., et al. (2009). Antimicrobial resistance of *Listeria monocytogenes* isolated from dairy-based food products. *Science of the Total Environment*, 407(13), 4022–4027. <https://doi.org/10.1155/2022/1351983>
- Harshani, H. B. C., Halmillawewa, A. P., & Wijendra, R. R. A. S. W. (2022). Phenotypic and genotypic characterization of antibiotic resistance of *Listeria monocytogenes* isolated from raw milk samples collected from Polonnaruwa, Sri Lanka. *Emirates Journal of Food and Agriculture*, 34(1), 74–81. <https://doi.org/10.9755/ejfa.2022.v34.i1.2809>
- Harshani, H. B. C., Balasuriya, D. K., Kaushalya, A. G. G., & Wijendra, W. A. S. (2024). Assessment of *Listeria monocytogenes* contamination and antibiotic resistance in raw milk samples collected from Colombo district, Sri Lanka. *Journal of Microbiology and Infectious Diseases*, 14(2), 67–79. <https://doi.org/10.5455/JMID.2024.v14.i2.5>
- Haubert, L., Mendonça, M., Lopes, G. V., de Itapema Cardoso, M. R., & da Silva, W. P. (2016). *Listeria monocytogenes* isolates from food and food environment harbouring tetM and ermB resistance genes. *Letters in Applied Microbiology*, 62(1), 23–29. <https://doi.org/10.1111/lam.12516>
- He, Y., Zhang, L., Li, X., Wang, J., Chen, H., Liu, Y., & Zhao, X. (2025). Lactic acid bacteria-derived antimicrobial metabolites and their role in food preservation and pathogen inhibition. *Frontiers in Microbiology*. <https://doi.org/10.3389/fmicb.2025.1663475>
- Hilliard, A., Leong, D., O'Callaghan, A., Culligan, E. P., Morgan, C. A., DeLappe, N., Hill, C., Jordan, K., Cormican, M., & Gahan, C. G. M. (2018). Genomic Characterization of *Listeria monocytogenes* Isolates Associated with Clinical Listeriosis and the Food Production Environment in Ireland. *Genes*, 9(3), 171. <https://doi.org/10.3390/genes9030171>
- Ho, J. L., Shands, K. N., Friedland, G., Eckind, P., & Fraser, D. W. (1986). An outbreak of type 4b *Listeria monocytogenes* infection involving patients from eight Boston hospitals. *Archives of Internal Medicine*, 146(3), 520–524. <https://doi.org/10.1001/archinte.1986.00360150066009>
- Iwu, C. D., Korsten, L., & Okoh, A. I. (2020). The incidence of antibiotic resistance within and beyond the agricultural

- ecosystem: A concern for public health. *MicrobiologyOpen*, 9(9), e1035. <https://doi.org/10.1002/mbo3.1035>
- Jacquet, C., Saint-Clément, C., Brouille, F., Catimel, B., & Rocourt, J. (1998). La listériose humaine en France en 1997. Données du Centre National de Référence des *Listeria*. *Bulletin Épidémiologique Hebdomadaire*, 33, 142–143. [https://doi.org/10.1016/S0987-7983\(99\)80232-1](https://doi.org/10.1016/S0987-7983(99)80232-1)
- Jahid, I. K., et al. (2013). Influence of glucose concentrations on biofilm formation, motility, exoprotease production, and quorum sensing in *Aeromonas hydrophila*. *Journal of Food Protection*, 76, 239–247. <https://doi.org/10.4315/0362-028X.JFP-12-321>
- Jensen, A., Frederiksen, W., & Gerner-Smidt, P. (1994). Risk factors for listeriosis in Denmark, 1989–1990. *Scandinavian Journal of Infectious Diseases*, 26(2), 171–178. <https://doi.org/10.3109/00365549409011781>
- Jordan, K., Hunt, K., & Dalmaso, M. (2016). *Listeria monocytogenes* in milk products [PDF]. Teagasc Agriculture and Food Development Authority. <https://t-stor.teagasc.ie/bitstreams/download>
- Kayode, A. J., & Okoh, A. I. (2022). Assessment of multidrug-resistant *Listeria monocytogenes* in milk and milk product and One Health perspective. *PloS ONE*, 17(7), e0270993. <https://doi.org/10.1371/journal.pone.0270993>
- Turner, N. (2007). Risky trade: Infectious disease in the era of global trade. *Journal of Epidemiology and Community Health*, 61(10), 926. <https://doi.org/10.1136/jech.2007.059659>
- Li, Y., & Hu, C. (2021). Biogeographical patterns and mechanisms of microbial community assembly that underlie successional biocrusts across northern China. *NPJ Biofilms & Microbiomes*, 7(15). <https://doi.org/10.1038/s41522-021-00188-6>
- Linnan, M. J., Mascola, L., Lou, X. D., Goulet, V., May, S., Salminen, C., ... Weaver, R. (1988). Epidemic listeriosis associated with Mexican-style cheese. *The New England Journal of Medicine*, 319(13), 823–828. <https://doi.org/10.1056/NEJM198809293191303>
- Little, C. L., Rhoades, J. R., Sagoo, S. K., Harris, J., Greenwood, M., Mithani, V., ... McLauchlin, J. (2008). Microbiological quality of retail cheeses made from raw, thermized or pasteurized milk in the UK. *Food Microbiology*, 25(2), 304–312. <https://doi.org/10.1016/j.fm.2007.10.007>
- Lundén, J., Tolvanen, R., & Korkeala, H. (2004). Human listeriosis outbreaks linked to dairy products in Europe. *Journal of Dairy Science*, 87(E. Suppl.), E6–E11. [https://doi.org/10.3168/jds.S0022-0302\(04\)70056-9](https://doi.org/10.3168/jds.S0022-0302(04)70056-9)
- Lyon, S. A., Berrang, M. E., Fedorka-Cray, P. J., Fletcher, D. L., & Meinersmann, R. J. (2008). Antimicrobial resistance of *Listeria monocytogenes* isolated from a poultry further processing plant. *Foodborne Pathogens and Disease*, 5(4), 253–259. <https://doi.org/10.1089/fpd.2007.0070>
- Lyytiäinen, O., Autio, T., Rantala, L., Aalto, T., Korkeala, H., Siitonen, A., Majjala, R., Ruutu, P., Honkanen-Buzalski, T., Miettinen, M., Hatakka, M., Mikkola, J., Anttila, V.-J., & Johansson, T. (2000). An outbreak of *Listeria monocytogenes* serotype 3a infections from butter in Finland. *Journal of Infectious Diseases*, 181(5), 1838–1841. <https://doi.org/10.1086/315453>
- MacDonald, P. D. M., Whitwam, R. E., Boggs, J. D., MacCormack, J. N., Anderson, K. L., Reardon, J. W., Saah, J. R., Graves, L. M., Hunter, S. B., & Sobel, J. (2005). Outbreak of listeriosis among Mexican immigrants as a result of consumption of illicitly produced Mexican-style cheese. *Clinical Infectious Diseases*, 40(5), 677–682. <https://doi.org/10.1086/427803>
- Mahmoodi, M. M. (2010). Occurrence of *Listeria monocytogenes* in raw milk and dairy products in Noorabad, Iran. *Journal of Animal and Veterinary Advances*, 9(1), 16–19. <https://doi.org/10.3923/javaa.2010.16.19>
- Makino, S. I., Kawamoto, K., Takeshi, K., Okada, Y., Yamasaki, M., Yamamoto, S., & Igimi, S. (2005). An outbreak of food-borne listeriosis due to cheese in Japan, during 2001. *International Journal of Food Microbiology*, 104(2), 189–196. <https://doi.org/10.1016/j.ijfoodmicro.2005.02.009>
- Marshall, B. M., & Levy, S. B. (2011). Food animals and antimicrobials: Impacts on human health. *Clinical Microbiology Reviews*, 24(4), 718–733. <https://doi.org/10.1128/CMR.00002-11>
- Massa, S., Cesaroni, D., Poda, G., & Trovatielli, L. D. (1990). The incidence of *Listeria* spp. in soft cheeses, butter and raw milk in the province of Bologna. *Journal of Applied Bacteriology*, 68(2), 153–156. <https://doi.org/10.1111/j.1365-2672.1990.tb02560.x>
- Mendonça, A. F., Romero, M. G., Lihono, M. A., Nannapaneni, R., & Johnson, M. G. (2004). Radiation resistance and virulence of *Listeria monocytogenes* Scott A following starvation in physiological saline. *Journal of Food Protection*, 67(3), 470–474. <https://doi.org/10.4315/0362-028x-67.3.470>
- Mohamed, H. M. A., Katreen, K. G., Abd Al-Azeem, M. W., Wasel, F. A., & Abd-Eldayem, A. M. (2022). Molecular detection of *Listeria* species isolated from raw milk with special reference to virulence determinants and antimicrobial resistance in *Listeria monocytogenes*. *Journal of Animal Health and Production*, 10(4), 492–505. <http://dx.doi.org/10.17582/journal.jahp/2022/10.4.492.505>
- Morvan, A., Moubareck, C., Leclercq, A., Hervé-Bazin, M., Bremont, S., Lecuit, M., Courvalin, P., & Le Monnier, A. (2010). Antimicrobial resistance of *Listeria monocytogenes* strains isolated from humans in France. *Antimicrobial agents and chemotherapy*, 54(6), 2728–2731. <https://doi.org/10.1128/AAC.01557-09>
- Nichols, M., Conrad, A., Whitlock, L., Stroika, S., Strain, E., Weltman, A., Johnson, L., DeMent, J., Reporter, R., & Williams, I. (2020). Multistate outbreak of *Listeria monocytogenes* infections retrospectively linked to unpasteurized milk using whole-genome sequencing. *Journal of Dairy Science*, 103(1), 176–178. <https://doi.org/10.3168/jds.2019-16703>
- Noll, M., Kleta, S., & Al Dahouk, S. (2018). Antibiotic susceptibility of 259 *Listeria monocytogenes* strains isolated from food, food-processing plants and human samples in Germany. *Journal of Infection and Public Health*, 11(4), 572–577. <https://doi.org/10.1016/j.jiph.2017.12.007>
- Obaidat, M. M., & Stringer, A. P. (2019). Prevalence, molecular

- characterization, and antimicrobial resistance profiles of *Listeria monocytogenes*, *Salmonella enterica*, and *Escherichia coli* O157:H7 on dairy cattle farms in Jordan. *Journal of Dairy Science*, 102(10), 8710–8720. <https://doi.org/10.3168/jds.2019-16461>
- O'Brien, M., Hunt, K., McSweeney, S., & Jordan, K. (2009). Occurrence of foodborne pathogens in Irish farmhouse cheese. *Food Microbiology*, 26(8), 910–914. <https://doi.org/10.1016/j.fm.2009.06.009>
- Olaimat, A. N., Al-Holy, M. A., Shahbaz, H. M., Al-Nabulsi, A. A., Abu Ghoush, M. H., Osaili, T. M., Ayyash, M. M., & Holley, R. A. (2018). Emergence of antibiotic resistance in *Listeria monocytogenes* isolated from food products: A comprehensive review. *Comprehensive Reviews in Food Science and Food Safety*, 17(5), 1277–1292. <https://doi.org/10.1111/1541-4337.12387>
- O'Neill, J. (2016). *Tackling drug-resistant infections globally: Final report and recommendations*. Review on Antimicrobial Resistance. https://amr-review.org/sites/default/files/160525_Final%20paper_with%20cover.pdf
- Osaili, T. M., Al-Nabulsi, A. A., Taha, M. H., Al-Holy, M. A., Alaboudi, A. R., Al-Rousan, W. M., & Shaker, R. R. (2012). Occurrence and antimicrobial susceptibility of *Listeria monocytogenes* isolated from brined white cheese in Jordan. *Journal of Food Science*, 77(9), M528–M532. <https://doi.org/10.1111/j.1750-3841.2012.02877.x>
- Osman, K. M., Samir, A., Abo-Shama, U. H., Orabi, A., & Zolnikov, T. (2016). Determination of virulence and antibiotic resistance pattern of biofilm producing *Listeria* species isolated from retail raw milk. *BMC Microbiology*, 16, 263. <https://doi.org/10.1186/s12866-016-0880-7>
- Oussalah, M., Caillet, S., Saucier, L., & Lacroix, M. (2005). Antimicrobial effects of selected plant essential oils on *Listeria monocytogenes*. *Food Control*, 16(6), 529–540. <https://doi.org/10.1016/j.foodcont.2004.06.010>
- Ramatla, T., Khasapane, G., Achilonu, C. C., Tshikantwa, T. S., Nkhebenyane, J., Lekota, K. E., & Thekisoe, O. (2026). “One Health” perspective on the prevalence of *Listeria monocytogenes* and its antibiotic resistance profiles in South Africa: a comprehensive systematic review and meta-analysis. *Scientific reports*, 16(1), 7680. <https://doi.org/10.1038/s41598-025-34005-3>
- Roberts, B. N., Chakravarty, D., Gardner, J. C., III, Ricke, S. C., & Donaldson, J. R. (2020). *Listeria monocytogenes* Response to Anaerobic Environments. *Pathogens*, 9(3), 210. <https://doi.org/10.3390/pathogens9030210>
- Robinson, E., Travanut, M., Fabre, L., Larréché, S., Ramelli, L., Pascal, L., Guinard, A., Vincent, N., Calba, C., Meurice, L., Le Thien, M. A., Fourgere, E., Jones, G., Fournet, N., Smith-Palmer, A., Brown, D., Le Hello, S., Pardos de la Gandara, M., Weill, F. X., & Jourdan-Da Silva, N. (2020). Outbreak of *Salmonella* Newport associated with internationally distributed raw goats' milk cheese, France, 2018. *Epidemiology and infection*, 148, e180. <https://doi.org/10.1017/S0950268820000904>
- Pagotto, F., Ng, L. K., Clark, C., & Farber, J. (2006). Canadian listeriosis reference service. *Foodborne Pathogens and Disease*, 3(1), 132–137.
- Palmer, M. E., Chaturongakul, S., Wiedmann, M., & Boor, K. J. (2011). The *Listeria monocytogenes* σ B regulon and its virulence-associated functions are inhibited by a small molecule. *mBio*, 2(6), e00241-11. <https://doi.org/10.1128/mBio.00241-11>
- Parra-Flores, J., Holý, O., Bustamante, F., Lepuschitz, S., Pietzka, A., Contreras-Fernández, A., ... Ruppitsch, W. (2022). Virulence and antibiotic resistance genes in *Listeria monocytogenes* strains isolated from ready-to-eat foods in Chile. *Frontiers in Microbiology*, 12, 796040. <https://doi.org/10.3389/fmicb.2021.796040>
- Parussolo, L., Sfaciotte, R. A. P., Dalmina, K. A., Melo, F. D., Costa, U. M., & Ferraz, S. M. (2021). Detection of virulence genes and antimicrobial susceptibility profile of *Listeria monocytogenes* isolates recovered from artisanal cheese produced in the southern region of Brazil. *Anais da Academia Brasileira de Ciências*, 93, e20190200. <https://doi.org/10.1590/0001-3765202120190200>
- Périchon, B., & Courvalin, P. (2009). VanA-type vancomycin-resistant *Staphylococcus aureus*. *Antimicrobial Agents and Chemotherapy*, 53(11), 4580–4587. <https://doi.org/10.1128/AAC.00346-09>
- Poyart-Salmeron, C. (1990). Transferable plasmid-mediated antibiotic resistance in *Listeria monocytogenes*. *The Lancet*, 335(8703), 1422–1426. [https://doi.org/10.1016/0140-6736\(90\)91447-1](https://doi.org/10.1016/0140-6736(90)91447-1)
- Rahimi, E., Ameri, M., & Momtaz, H. (2010). Prevalence and antimicrobial resistance of *Listeria* species isolated from milk and dairy products in Iran. *Food Control*, 21(11), 1448–1452. <https://doi.org/10.1016/j.foodcont.2010.03.014>
- Ramaswamy, V., Cresence, V. M., Rejitha, J. S., Lekshmi, M. U., Dharsana, K. S., Prasad, S. P., & Vijila, H. M. (2007). *Listeria*—Review of epidemiology and pathogenesis. *Journal of Microbiology, Immunology and Infection*, 40(1), 4–13.
- Reda, W. W., Abdel-Moein, K., Hegazi, A., et al. (2016). *Listeria monocytogenes*: An emerging food-borne pathogen and its public health implications. *Journal of Infection in Developing Countries*, 10(2), 149–154. <https://doi.org/10.3855/jidc.6616>
- Rhoades, J. R., Duffy, G., & Koutsoumanis, K. (2009). Prevalence and concentration of verocytotoxigenic *Escherichia coli*, *Salmonella enterica* and *Listeria monocytogenes* in the beef production chain: A review. *Food Microbiology*, 26(4), 357–376. <https://doi.org/10.1016/j.fm.2008.10.012>
- Romanova, N., Wolffs, P., Brovko, L., & Griffiths, M. (2006). Role of efflux pumps in adaptation and resistance of *Listeria monocytogenes* to benzalkonium chloride. *Applied and Environmental Microbiology*, 72(5), 3498–3503. <https://doi.org/10.1128/AEM.72.5.3498-3503.2006>
- Schwartz, B., Hexter, D., Broome, C. V., Hightower, A. W., Hirschhorn, R. B., Porter, J. D., Hayes, P. S., Bibb, W. F., Lorber, B., & Faris, D. G. (1989). Investigation of an outbreak of *Listeriosis*: New hypotheses for the etiology of epidemic *Listeria monocytogenes* infections. *The Journal of Infectious Diseases*, 159(4), 680–685. <https://doi.org/10.1093/infdis/159.4.680>

- org/10.1093/infdis/159.4.680
- Serhan, M., & Mattar, J. (2013). Characterization of four Lebanese artisanal goat milk cheeses: Darfiyeh, Aricheh, Shankleesh, and Serdale by physico-chemical, microbiological, and sensory analyses. *Journal of Food, Agriculture & Environment*, 11(4), 97–101. <https://scholarhub.balamand.edu.lb/handle/uob/1723>
- Shamloo, E., Hosseini, H., Abdi Moghadam, Z., Halberg Larsen, M., Haslberger, A., & Alebouyeh, M. (2019). Importance of *Listeria monocytogenes* in food safety: A review of its prevalence, detection, and antibiotic resistance. *Iranian Journal of Veterinary Research*, 20(4), 241–254. <https://doi.org/10.22099/IJVR.2019.31560.2642>
- Shin, J. H., Kim, J., Kim, S. M., Kim, S., Lee, J. C., Ahn, J. M., & Cho, J. Y. (2010). Sigma B dependent protein induction in *Listeria monocytogenes* during vancomycin stress. *FEMS Microbiology Letters*, 308, 94–100. <https://doi.org/10.1111/j.1574-6968.2010.01998.x>
- Smith, B. (2008). *Listeriosis in the Rio Grande Valley 2003–2008*. United States–Mexico Border Health Commission. Retrieved October 15, 2023.
- Spitzer, P. G., Hammer, S. M., & Karchmer, A. W. (1986). Treatment of *Listeria monocytogenes* infection with trimethoprim-sulfamethoxazole: Case report and review of the literature. *Clinical Infectious Diseases*, 8(3), 427–430. <https://doi.org/10.1093/clinids/8.3.427>
- Srinivasan, V., Nam, H. M., Nguyen, L. T., Tamilselvam, B., Murinda, S. E., & Oliver, S. P. (2005). Prevalence of antimicrobial resistance genes in *Listeria monocytogenes* isolated from dairy farms. *Foodborne Pathogens and Disease*, 2(3), 201–211. <https://doi.org/10.1089/fpd.2005.2.201>
- Suryawanshi, R. D., Patil, M. D., Shinde, O. N., Jogdand, A. A., Bhosle, P. D., Deshmukh, O. N., & Babar, A. Y. (2023). The *Listeria monocytogenes* isolated from raw milk: Phenotypic and molecular characterization, pathogenicity testing, and multidrug resistance profiling. *Indian Journal of Dairy Science*, 76(6). <https://epubs.icar.org.in/index.php/IJDS/article/view/134469>
- Swaminathan, B., & Gerner-Smidt, P. (2007). The epidemiology of human listeriosis. *Microbes and Infection*, 9(10), 1236–1243. <https://doi.org/10.1016/j.micinf.2007.05.011>
- Tahoun, A. B. M. B., Abou Elez, R. M. M., Abdelfatah, E. N., Elsohaby, I., El Gedawy, A. A., & Elmoslemay, A. M. (2017). *Listeria monocytogenes* in raw milk, milking equipment, and dairy workers: Molecular characterization and antimicrobial resistance patterns. *Journal of Global Antimicrobial Resistance*, 10, 264–270. <https://doi.org/10.1016/j.jgar.2017.07.008>
- Tayeb, B. A., Mohamed-Sharif, Y. H., Choli, F. R., Haji, S. S., Ibrahim, M. M., Haji, S. K., Rasheed, M. J., & Mustafa, N. A. (2023). Antimicrobial susceptibility profile of *Listeria monocytogenes* isolated from meat products: A systematic review and meta-analysis. *Foodborne Pathogens and Disease*, 20(8), 315–333. <https://doi.org/10.1089/fpd.2023.0004>
- U.S. Food and Drug Administration. (2003). *Listeria monocytogenes risk assessment: II. Hazard identification*. <https://www.fda.gov/media/73648/download>
- Ulusoy, B. H., & Chirkena, K. (2019). Two perspectives of *Listeria monocytogenes* hazards in dairy products: The prevalence and the antibiotic resistance. *Food Quality and Safety*, 3(4), 233–241. <https://doi.org/10.1093/fqsafe/fyz035>
- Unal Turhan, E. (2019). The presence of pathogenic bacteria in traditional cheese sold in the local market in Hatay province, Turkey. *Applied Ecology and Environmental Research*, 17(3), 7135–7145. https://doi.org/10.15666/aer/1703_71357145
- Van Boeckel, T. P., Brower, C., Gilbert, M., Grenfell, B. T., Levin, S. A., Robinson, T. P., et al. (2015). Global trends in antimicrobial use in food animals. *Proceedings of the National Academy of Sciences*, 112(18), 5649–5654. <https://doi.org/10.1073/pnas.1503141112>
- Vázquez-Boland, J. A., Kuhn, M., Berche, P., Chakraborty, T., Domínguez-Bernal, G., Goebel, W., González-Zorn, B., Wehland, J., & Kreft, J. (2001). *Listeria* pathogenesis and molecular virulence determinants. *Clinical Microbiology Reviews*, 14(3), 584–640. <https://doi.org/10.1128/cmr.14.3.584-640.2001>
- Vicente, M. F., Baquero, F., & Pérez-Díaz, J. C. (1988). Antibiotic resistance in *Listeria monocytogenes*. *Antimicrobial Agents and Chemotherapy*, 32(5), 644–646. <https://doi.org/10.1128/AAC.32.5.644>
- Walsh, D., Duffy, G., Sheridan, J. J., Blair, I. S., & McDowell, D. A. (2001). Antibiotic resistance among *Listeria*, including *Listeria monocytogenes*, in retail foods. *Journal of Applied Microbiology*, 90(3), 517–522. <https://doi.org/10.1046/j.1365-2672.2001.01273.x>
- Wesche, A. M., Gurtler, J. B., Marks, B. P., & Ryser, E. T. (2009). Stress, sublethal injury, resuscitation, and virulence of bacterial foodborne pathogens. *Journal of Food Protection*, 72(5), 1121–1138. <https://doi.org/10.4315/0362-028X-72.5.1121>
- Wiktorczyk-Kapischke, N., Skowron, K., & Walecka-Zacharska, E. (2023). Genomic and pathogenicity islands of *Listeria monocytogenes*-Overview of selected aspects. *Frontiers in Molecular Biosciences*, 10, 1161486. <https://doi.org/10.3389/fmolb.2023.1161486>
- Wijendra, W. A. S., Kulathunga, K. A. C., & Ramesh, R. (2014). First report of *Listeria monocytogenes* serotypes detected from milk and milk products in Sri Lanka. *Advances in Animal and Veterinary Sciences*, 2(5S), 11–16. <http://dx.doi.org/10.14737/journal.aavs/Year/2.5s.11.16>
- Wilson, A., Gray, J., Chandry, P., & Fox, E. (2018). Phenotypic and genotypic analysis of antimicrobial resistance among *Listeria monocytogenes* isolated from Australian food production chains. *Genes*, 9, 80. <https://doi.org/10.3390/genes9020080>
- World Health Organization. (2017). *WHO guidelines on use of medically important antimicrobials in food-producing animals*. Geneva: World Health Organization.
- Yde, M., & Genicot, A. (2004). Use of PFGE to characterize clonal relationships among Belgian clinical isolates of *Listeria monocytogenes*. *Journal of Medical Microbiology*, 53(5), 399–402. <https://doi.org/10.1099/jmm.0.05408-0>

Zanini, S. F., Silva-Angulo, A. B., Rosenthal, A., Rodrigo, D., & Martínez, A. (2014). Effect of citral and carvacrol on the susceptibility of *Listeria monocytogenes* and *Listeria*

innocua to antibiotics. *Letters in Applied Microbiology*, 58(5), 486–492. <https://doi.org/10.1111/lam.12218>