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Review

Wholegenome sequencing as the gold standard approach for control of *Listeria monocytogenes* in the food chain

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ABSTRACT

Listeria monocytogenes has been implicated in numerous outbreaks and related deaths of listeriosis. In food production, *L. monocytogenes* occurs in raw food material and above all, through postprocessing contamination. The use of next-generation sequencing technologies such as whole-genome sequencing (WGS) facilitates foodborne outbreak investigations, pathogen source tracking and tracing geographic distributions of different clonal complexes, routine microbiological/epidemiological surveillance of listeriosis, and quantitative microbial risk assessment. WGS can also be used to predict various genetic traits related to virulence, stress, or antimicrobial resistance, which can be of great benefit for improving food safety management as well as public health.

Contents

Listeria monocytogenes is heterogeneous species regarding virulence; its population structure is currently grouped into 14 different serotypes (including newly described hypervirulent serovar 4h) and four evolutionary lineages (I, II, III, and IV) that have been divided into multiple clonal complexes (CCs) and sequence types (STs) based on multilocus sequence typing (MLST) (Orsi et al., 2011; Ragon et al., 2008; Yin et al., 2019). *L. monocytogenes* CCs include (i) hypervirulent lineage I with representative CCs such as CC1, CC2, CC4, and CC6 isolated from clinical cases and nonfood contact surfaces, (ii) hypovirulent lineage II with representative CCs such as CC9 and CC121 that persist and colonize food contact surfaces, and (iii) intermediate isolates such as CC3, CC5, CC8 + CC16, CC37, and CC155 that are found in both clinical and food settings (Chen et al., 2016; Health Canada, 2011; Matle et al., 2020). Strains from lineages III and IV have demonstrated significant biodiversity and are mostly identified in animals (Kuenne et al., 2013; Ward et al., 2008, 2010; Wiedmann, 2002; Wiedmann, 2003). Although the CCs of *L. monocytogenes* differ in their virulence, current regulations presume that all strains are equally

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Table 1
Selected multistate (US) and international outbreaks of listeriosis identified using WGS

Year	Location	No. of Cases/No. of Deaths	Food Type	References
United States of America				
2020	Multistate	12/1	Deli meats	Centers for Disease Control and Prevention, 2020
2020	Multistate	36/4	Enoki Mushrooms	Centers for Disease Control and Prevention, 2020
2019	Multistate	8/1	Hard-boiled eggs	Centers for Disease Control and Prevention, 2019
2019	Multistate	10/1	Deli sliced meat and cheeses	Centers for Disease Control and Prevention, 2019
2018	Multistate	4/0	Pork products	Centers for Disease Control and Prevention, 2018
2018	Multistate	4/1	Deli Ham	Centers for Disease Control and Prevention, 2018
2016[a]	Multistate	9/3	Frozen vegetables	Centers for Disease Control and Prevention, 2016
2016	Multistate	2/1	Raw milk	Centers for Disease Control and Prevention, 2016
2016[a]	Multistate	19/1	Packaged salads	Centers for Disease Control and Prevention, 2016
2015[a]	Multistate	30/3	Soft cheese	Centers for Disease Control and Prevention., 2015
Europe				
2018/19	Germany	112/7	Blood Sausage	Halbedel et al., 2020
2019	Spain	200/3	Roasted pork meat product	World Health Organization (WHO), 2019
2017/19	Netherlands, Belgium	21/3	RTE meat products	European Centre for Disease Prevention and Control, European Food Safety Authority, 2019
2019	United Kingdom	9/7	RTE Sandwiches	Public Health England, 2020
2018	Austria	13/1	Liver paté	Cabal et al., 2019
2014/19	Multicountry	22/5	Cold smoked fish products	European Food Safety Authority and European Centre for Disease Prevention and Control, 2019
2015/18	Multicountry	47/9	Frozen corn	European Food Safety Authority, 2018
2014	Denmark	41/17	Deli meat	Kvistholm Jensen et al., 2016
2012/16[a]	Czech Republic	26/3	Turkey meat products	Gelbíčová et al., 2018
South Africa				
2017		1060/216	RTE Meats Polony	World Health Organization (WHO), 2018

[a] PFGE was also used.

pathogenic (French Agency for Food, Environmental and Occupational Health and Safety, 2020).

Although a rare disease, listeriosis causes a very high proportion of deaths and severe cases especially in elderly and immunocompromised persons, pregnant women, and infants. Listeriosis occurs after ingestion of *L. monocytogenes* via contaminated food. Centers for Disease Control and Prevention (U. S. CDC) estimates that the number of confirmed cases of listeriosis is approximately 1600 cases every year in the USA (Centers for Disease Control and Prevention, 2022) while the incidence rates of listeriosis vary by year in the EU (European Food Safety Authority and European Centre for Disease Prevention and Control, 2021). However, no statistically significant upward or downward trend regarding listeriosis was seen from 2016 to 2020 (European Food Safety Authority and European Centre for Disease Prevention and Control, 2021). In 2020, 27 EU countries reported 1876 listeriosis cases which included 16 outbreaks and 168 deaths (European Food Safety Authority and European Centre for Disease Prevention and Control, 2021). *L. monocytogenes* can be found in a wide range of ready-to-eat foods that do not undergo any kill step before consumption. Ingestion of even low numbers of *L. monocytogenes* in a food can produce listeriosis in vulnerable groups. The world's largest listeriosis outbreak occurred in South Africa from January 2017 to July 2018 with a total of 1060 cases and a 27% mortality rate. Ready-to-eat processed meat products were confirmed as the source of infection (Smith et al., 2019), and WGS is now increasingly being used in many jurisdictions to enhance the surveillance of listeriosis outbreaks. Selected multistate (US) and international outbreaks of listeriosis identified using WGS are presented in Table 1.

In response to recent technological advances in DNA sequencing technologies and the fact that PFGE is now abandoned by bioRad, public health laboratories in the EU/EEA are now transitioning from PFGE- to WGS-based typing methods. DNA sequencing can be conducted on various platforms including Roche 454 Life Sciences (short-read technologies which belong to second-generation sequencing but its role in surveillance of listeriosis has been minimal), Illumina, Ion Torrent (short-read third-generation sequencing technologies), PacBio, and Oxford Nanopore (long-read fourth-generation sequencing technologies). With long-read sequencing, the quality of assemblies can be improved and also time to obtain results decreases from 3 days (for Ilumina 2 × 300 bp) to 2 days (NextSeq) or 1.5 days or in urgent situations even to hours (Nanopore Sequencing).

WGS is increasingly being used as the primary epidemiological surveillance tool in national programs, outbreak investigations, and environmental monitoring programs for food-processing facilities to support food safety management systems and protect public health (European Centre for Disese Prevention and Control, 2020; Jackson, Tarr et al., 2016, Jackson, Stroika et al., 2016; Kwong et al. 2016; Schmid et al., 2014). There are different ways how the WGS data can be elaborated to deduce genetic relatedness between isolates such as single-nucleotide variants (SNP), gene-by-gene allelic profiling using core genome (cgMLST), or whole-genome multilocus sequence typing (wgMLST). The advantage of cgMLST approach is the stability of the scheme allowing an automated analysis workflow including an alert system. SNP analysis has the advantage of a slightly higher resolution, but the disadvantage to find suitable reference genomes makes automated workflows challenging and in general the entire SNP process more time consuming. Further, wgMLST can provide a higher resolution and can be a useful tool for comparing closely related isolates, where the probably missing targets (compared to cgMLST) are limited.

Benefits and future insights of WGS

The benefits of WGS-based strain characterization compared to traditional methods include speed, universality, robustness, superior discriminatory power, and the opportunity to gain new knowledge of both the geographic origin and evolutionary status of outbreak isolates (Jenkins et al., 2019; Ruppitsch et al., 2019). WGS also can lead to a

better understanding of the acquisition and evolution of virulence factors, stress, and antimicrobial resistance in *L. monocytogenes* (Franz et al., 2016). The intraspecific variation in different genetic traits and identification of biomarkers that predict microbial behavior can also be used to strengthen current quantitative microbiological risk assessments (QMRAs) (Lakicevic et al., 2022). QMRAs have been done for various pathogen/food product combinations with the exposure assessment and hazard characterization steps focused on pathogenic species as a whole (European Food Safety Authority, 2019; Tirloni et al., 2018; U.S. Food and Drug Administration and Department of Agriculture, 2003). Ongoing improvements in the field of omics technology are expanding our current understanding of intraspecific variability based on different and more accurate bioinformatics tools (Brul et al., 2012; Den Besten et al., 2018; Fritsch et al., 2019; Haddad et al., 2018; Njage et al., 2020; Rantsiou et al., 2018; Ruppitsch et al., 2019). These advances are also increasing our knowledge of pathogen strain/subtype risk ranking relative to their differences in virulence, stress robustness, fitness, and ability to reach the consumers (Chen et al., 2011; Collineau et al., 2019; Den Besten et al., 2018). The QMRA input parameters can be adjusted for each strain to fine-tune the QMRA output. Fritsch et al. (2018) demonstrated the potential of WGS to refine QMRA models when considering the pheno–genotype association of *L. monocytogenes*. The authors described the growth variability of *L. monocytogenes* at low temperatures and defined three groups for this pathogen based on differences in virulence. According to the QMRA output, the CCs that contribute the most to consumer exposure are not those that cause the most listeriosis cases. This could explain why a low number of sporadic listeriosis cases in France were associated with the consumption of crustaceans contaminated by hypovirulent lineage II clones such as CC121 and CC9 (European Food Safety Authority and European Centre for Disease Prevention and Control, 2018; Fritsch et al., 2018; Leclercq et al., 2020; Painset et al., 2019).

Drawbacks

Despite the proven superiority of WGS in outbreak investigations and the successful implementation of this new technology for surveillance in public health and food safety in several countries (Wang et al., 2016), its use remains challenging for many countries due to deficiencies in infrastructure and resources (Apruzzese et al., 2019; Grace, 2015), including functional surveillance systems to assemble isolates and metadata from clinical, food, and environmental samples (European Food Safety Authority Working Group on Developing Harmonised Schemes for Monitoring Antimicrobial Resistance in Zoonotic Agents, 2008; Food and Agriculture Organization of the United Nations, 2016). Implementation of WGS as a tool for surveillance and outbreak investigation also requires an appropriate IT infrastructure for interpretation, internet connection/speed, handling, storage, and sharing of WGS data (Bergholz et al., 2014). Additional hurdles to implementing WGS include cost, perception of cost, lack of trust for data sharing, sustainability (e.g., training course on WGS technique), and possible imbalanced trade opportunities (Food and Agriculture Organization of the United Nations, 2016). However, given the rapidly declining cost of this technology, WGS should become more attractive and soon be of benefit to many countries (Food and Agriculture Organization of the United Nations, 2016; Nastasijevic et al., 2017). Future challenges in food safety and public health will require global data sharing to identify and characterize foodborne pathogens in a standardized, harmonized workflow in real time (Taboada et al., 2017).

Persistence and distribution of different CCs in food

L. monocytogenes can persist in difficult-to-remove biofilms on abiotic surfaces and can be isolated from equipment, floors, and cold storage areas over long periods of time (Lakicevic and Nastasijevic, 2017). Persistence of *L. monocytogenes* in specific environmental 'niches' (i.e., slicing machine) may lead to continued microbial cross-contamination of retail products (EFSA Panel on Biological Hazards et al., 2018). Numerous studies have confirmed that slicers can serve as a vehicle for cross-contamination of deli foods with different foodborne pathogens (Crandall et al., 2012; Vorst et al., 2006). To decrease cross-contamination from deli slicers, the U.S. FDA 2013 Food Code requires that slicers be cleaned and sanitized at least every four hours (U.S. Food and Drug Administration, 2013). In studies involving retail deli environments, the prevalence of *L. monocytogenes* ranged from 0 to more than 30% (Etter et al., 2017; Hammons et al., 2017; Hoelzer et al., 2011; Sauders et al., 2009; Simmons et al., 2014).

Some researchers suggest that persistence is the result of complex interactions between *L. monocytogenes* and the environment (Luque-Sastre et al., 2018; Taylor and Stasiewicz, 2019). Although the exact persistence mechanisms are still unclear, the key contributors to *L. monocytogenes* persistence in food-processing facilities include enhanced biofilm formation and resistance to sanitizers (Aase et al., 2000; Borucki et al., 2003; Heir et al., 2004; Lourenço et al., 2009; Lundén et al., 2000, 2003; Norwood and Gilmour, 1999; Pan et al., 2006). Importantly, lineage II hypovirulent clones of *L. monocytogenes*, CC9 and CC121, were found to create more biofilm and grow better than lineage I hypervirulent clones (CC1, CC2, CC4, and CC6) in the presence of low levels of benzalkonium chloride (BC) (Maury et al., 2019). CC8/VT59, associated with previous Canadian outbreaks (Knabel et al., 2012), possess a strong capacity for biofilm formation, which may support persistence in food production environments and subsequent contamination of foods (Verghese et al., 2011). In addition, Pérez-Baltar et al. (2021) found that ST121 (CC121) strains are strong biofilm producers, with some of these strains containing the transposon Tn6188, associated with enhanced tolerance toward quaternary ammonium compounds (QACs). Along with Tn6188, *L. monocytogenes* possesses some other BC-tolerant determinants such as the *bcrABC* cassette and *emrE* detected on mobile genetic elements (MGEs) that are primarily present among CCs within lineage II (Dutta et al., 2013; Kovacevic et al., 2016). A recent publication by Castro et al. (2021) suggested that MGEs aid in the persistence of *L. monocytogenes* on dairy farms and can be spread via the food industry. MGEs are thought to be critical in increasing the antimicrobial resistance of *L. monocytogenes* strains and in creating new resistant phenotypes through horizontal gene transfer between *Listeria* and some other species. Another recent study (Palaiodimou et al., 2021) using WGS also showed that nonpathogenic *L. innocua* and *L. welshimeri* carried the *bcrABC* cassette and *qacH*, suggesting that these strains may be the reservoirs of BC determinants.

Based on long-term surveillance data, both raw and processed foods can become contaminated with *L. monocytogenes* throughout food production (Gómez et al., 2015; Thimothe et al., 2002; Wijnands et al., 2014), with certain food categories more often contaminated (Wagner et al., 2007), including dairy (Linan et al., 1988), meat (Borovic et al., 2014; Olsen et al., 2005), seafood (Acciari et al., 2017), and mixed ready-to-eat products (Soderqvist et al., 2016). Some CCs appear to have a predisposition for certain food types, for example hypervirulent clones (e.g., CC1 and CC87) for dairy products and raw seafood, and hypovirulent clones (e.g., CC9 and CC121) for meat and fish products (Maury et al., 2019; Painset et al., 2019; Zhang et al., 2020). A link between ST121 and fish products has been reported in the study conducted by Knudsen et al. (2017) while ST155 of lineage II was isolated from leafy vegetables in Nigeria (Nwaiwu et al., 2017). In addition, food-related hypovirulent clones can still cause listeriosis in immunocompromised hosts (Maury et al., 2016). Such low virulence may be due to a loss-of-function mutation in virulence genes such as *inlA* (Fagerlund et al., 2016; Maury et al., 2019). Maury et al. (2016) demonstrated increased invasion of the CNS and placenta by the hypervirulent clone CC4. Another epidemic

clone, CC1, is also associated with more severe invasive (systemic) forms of listeriosis, and its prevalence was remarkably higher in ruminants than in human infection (Dreyer et al., 2016).

Sources of *L. monocytogenes* and control measures

Several possible mechanisms throughout the farm-to-table chain can lead to the contamination of food products with *Listeria*. *L. monocytogenes* may be introduced into or spread elsewhere within a facility via employees, transport equipment, tools, animals or pests, and raw materials or ingredients (Anonymous, 2017; Ivanek et al., 2005). Incoming raw materials contaminated during growing and harvesting can also lead to contamination of food-processing equipment if appropriate controls are not in place (Ministry for Primary Industries, 2017). Although *L. monocytogenes* can be inactivated during thermal processing, the risk of postprocessing contamination of products from the facility environment and equipment continues to challenge the food industry. This is especially critical for RTE foods that support the growth of *L. monocytogenes* and have extended shelf-lives (Food and Drug Administration and Center for Food Safety and Applied Nutrition, 2017; Health Canada, 2011; U.S. Department of Agriculture Food Safety and Inspection Service, 2012). Therefore, an integrated approach for the control of *L. monocytogenes* should be applied along the farm-to-fork continuum. These control measures should be appropriately designed and synergistically implemented at multiple steps in the food chain and be based on the scientific literature including predictive microbiology and validation studies. Other studies could provide scientific proof that antilisterial control measures can reduce the levels of *Listeria* in foods and environmental samples.

Examples of contamination routes

WGS-based typing methods are important and powerful tools for source tracking in the food industry. A proof of concept on the practical use of WGS to define the entry and contamination routes of *L. monocytogenes* in a meat establishment has been described by Nastasijevic et al. (2017). In this study, WGS was used to characterize eight environmental isolates of *L. monocytogenes* (out of 53 *Listeria* spp.-positive samples) from various locations in a pork-processing facility including the slaughter line, chilling chamber, deboning equipment, modified atmosphere packaging (MAP) equipment, and dispatch. WGS grouped these eight isolates into 1/2a, 1/2c, and 4b serotypes and three clonal complexes and sequence types - ST26, ST9, and ST1. The isolates of *L. monocytogenes* originated from MAP, chilling chamber, and dispatch units were genetically similar and/or the same as isolates from the slaughter line. Accordingly, the authors concluded that contamination originated from the slaughter line and highlighted WGS as a strong supporter of food safety management/-surveillance systems in meat establishments. Based on the research conducted by Demaître et al. (2021); WGS revealed that the hypovirulent CC9 clone persisted in the carcass splitter for more than a year.

Using WGS, transient and resident strains with unique or even closely related profiles can be differentiated, which will facilitate the implementation of control measures in food industry (Brown et al., 2019). Also, this will lead to a better understanding of contamination routes along with potentially new pathways of contamination. This information can be shared not only within the facilities involved in contamination event but within the whole food sector (Jagadeesan et al., 2019). Further, it will lead to a reduction in costs associated with recalls of contaminated food products. However, many processors remain reluctant to speciate or further characterize *Listeria* isolates by WGS due to regulatory implications, complexity of analysis, costs, and time to obtain results. For example, in-house sequencing by food manufacturers and food testing laboratories will only be cost effective if a large number of strains are sequenced simultaneously and if WGS equipment is used for multiple applications (WGS of pathogenic and spoilage microorganisms, starter cultures, and metagenomics) (Nastasijevic et al., 2017). Additionally, the infrastructure should not be underestimated as huge amounts of data produced by WGS need to be transferred through the internet to be available and useful to the global community (Food and Agriculture Organization of the United Nations., 2016).

Infectious routes and WGS-based outbreak investigations

In one prolonged listeriosis outbreak involving L. monocytogenes 4b ST6 CT7448, WGS was used to match clinical isolates to a cheese sample and to samples from diverse sites within the production environment (Nüesch-Inderbinen et al., 2021). *Listeria* persistence in the factory may be related to the enhanced acid tolerance of 4b strains. *ORF2110*, which encodes a putative serine protease, was identified as a potentially associated molecular marker and contributes to survival during environmental stress (Van Der Veen et al., 2008). In 2014, a multistate listeriosis outbreak affecting 35 people across the United States and one individual in Canada was linked to caramel-coated apples -a previously unreported vehicle for *L. monocytogenes* (Centers for Disease Control and Prevention, 2015). The flesh of these apples had a pH < 4, and the a_w of the caramel was < 0.80. However, Glass et al. (2015) hypothesized that stick insertion could make a film of apple juice between the caramel and apple surface, creating a niche that may then become more favorable for *Listeria* growth than either component alone.

In 2014, WGS data collected and analyzed by the U.S. CDC by whole-genome multilocus sequence typing (wgMLST) identified a restaurant in Rhode Island as the likely source of a small outbreak and also linked the establishment to a prior listeriosis case in 2013 (Berkley et al., 2014). Namely, WGS analysis gave adequate resolution to establish a clear link between the 2014 outbreak cases, 2013 clinical isolate, and restaurant food (sliced prosciutto). Based on wgMLST analysis, the prosciutto isolate differed by 0–5 alleles from the 2014 clinical samples as well as by 0–11 alleles from the 2013 clinical isolate (Berkley et al., 2014). In another outbreak connected to two Blue Bell Creamery production facilities, ice cream was likely contaminated from the plant environment (Centers for Disease Control and Prevention, 2015). This was both a complex and unusual outbreak since ten cases from four different states were detected from 2010 to 2015. Additionally, this product which does not support the growth of *L. monocytogenes* contained extremely low levels of contamination (Chen et al., 2016). The first case was identified in one Kansas hospital over one year (Centers for Disease Control and Prevention, 2015). Only two of the five patient isolates had the same PFGE pattern, suggesting different sources. However, wgMLST analyses showed that four of the isolates were closely related not only to each other but also to ice cream isolates from a production facility in Texas. This led to sampling in a third facility located in Oklahoma where the *L. monocytogenes* was also found in ice cream products. The cases in Texas and Arizona were subsequently linked to ice cream manufactured in the Oklahoma facility. All outbreak-associated isolates were grouped into two clusters (delineated as Cluster I and II) which was not possible through PFGE typing (Centers for Disease Control and Prevention, 2015). In another US outbreak linked to soft cheese in 2015, 30 people across ten states were sickened and three deaths were reported from California and Ohio (Centers for Disease Control and Prevention, 2016). In this outbreak, WGS analysis did not only improve cluster identification that was not possible through PFGE typing but also facilitated retroactive inclusion of an earlier undetermined cluster from 2013 into the outbreak and trace back to the contaminated soft cheese (Centers for Disease Control and Prevention, 2015). Analogously, PulseNet identified an outbreak cluster of *L. monocytogenes* clinical iso-

Table 2
Selected outbreaks of listeriosis with maximum number of allele differences between outbreak-related isolates (Median)

Year	Location	No. of Cases/ Deaths	Vehicle of infection	Max. No. of allele difference by wgMLST (Median)*	References
2013 2014	Rhode Island	4/2	contamination at restaurant	11 (4) 5 (3)	Berkley et al., 2014
2010/ 2015	Multistate	10/3	production facility 1 production facility 2	30 (15) 32 (15)	Centers for Disease Control and Prevention., 2015
2015	Multistate	30/3	Soft cheese	26 (13)	Centers for Disease Control and Prevention., 2015
2015/ 2016	Multistate	16/1	Packaged salads	16 (10)**	Self et al., 2016

* Whole-genome multilocus sequence typing.
** Enviromental samples not tested.

lates associated with packaged salad, indistinguishable by two-enzyme PFGE but highly related genetically by WGS (Table 2) (Self et al., 2016). In general, WGS has enhanced listeriosis outbreak detection and investigation in at least six key ways which was described in detail by Jackson, Tarr et al. (2016).

In a report dated April 2020, FDA and CDC investigated a multistate outbreak of 36 cases with four deaths traced to *L. monocytogenes*-contaminated enoki mushrooms imported from Korea (Centers for Disease Control and Prevention, 2020). Other reports include a 2018 multistate listeriosis outbreak from pork products and an outbreak linked to hard-boiled eggs where the environmental and clinical *L. monocytogenes* isolates were closely related genetically (Centers for Disease Control and Prevention, 2018, 2019). Lastly, in the multistate outbreak reported in October 2020 deli meats were considered as the source, however, the specific type of deli meat and supplier was never identified (Centers for Disease Control and Prevention, 2020). In all of these outbreaks, WGS was used to assess the degree of genetic relatedness among clinical isolates and those suspected as a source of infection. On January 15, 2018, PulseNet officially replaced PFGE with WGS (Kubota et al., 2019).

In Denmark, WGS was able to link the deaths of seven adults and one stillborn baby to the consumption of smoked fish (Lassen et al., 2016). In addition to smoked fish, ready-to-eat salmon products were the likely source of two multicountry outbreaks caused by *L. monocytogenes* ST8 and ST1247 that affected Germany (ST8), France (ST8 and ST1247), Denmark (ST8 and ST1247), Estonia (ST1247), Finland (ST1247), and Sweden (ST1247), respectively (European Food Safety Authority and European Centre for Disease Prevention and Control, 2018, 2019). In late December 2018, the use of epidemiological data and WGS-based typing confirmed liver pâté as the likely vehicle in an outbreak of listeriosis due to *L. monocytogenes* IVb-CC4-ST4-CT7652, a strain, not previously detected in Austria or elsewhere (Cabal et al., 2019). Lüth et al. (2020) described a multiclonal *L. monocytogenes* outbreak linked to meat products from a single producer which involved 83 cases of invasive listeriosis between 2013 and 2018. One multicountry outbreak in five European countries (Austria, Denmark, Finland, Sweden, and the United Kingdom) and another in the Czech Republic, likely associated with frozen corn and turkey meat, have shown the importance of WGS-based methods, as the source of contamination probably would not have been detected using PFGE or other former typing methods (European Food Safety Authority and European Centre for Disease Prevention and Control, 2018; Gelbíčová et al., 2018). Using cgMLST, *L. monocytogenes* isolates originating from human and nonhuman samples showed up to 1, 3, 7, 8, and 18 allelic differences (Table 3).

All of the above reports indicate that the WGS-based typing methods are an important tool for epidemiological investigations and source tracking in the food industry as well as in discovering new food vehicles (such as caramel-coated apples and ice cream). Also, WGS has improved the ability to distinguish between outbreak-associated and sporadic cases, linked sporadic cases to specific food products, animal sources, and geographical regions, and identified root causes of contamination. As reported by Leclercq et al. (2020), people at a highest risk of contracting invasive listeriosis are those suffering from an immunocompromising disease. Using meta-analysis, the same authors identified consumption of RTE food categories such as milk, fish, and meat products as other major risk factors. Another study using WGS reported that various source attribution models applied on a collection of human sporadic strains tended to place bovine products, and thus cheese, as the leading cause of human listeriosis (Møller Nielsen et al., 2017). This difference could be explained by the fact that there

Table 3
Selected outbreaks of listeriosis with maximum number of allele differences between human and nonhuman isolates

Year	Location	No. of human isolates	No. of nonhuman isolates	Max. No. of allele difference by cgMLST*	References
2015/ 18	Multicountry	47	25	7	European Food Safety Authority, 2018
2012/ 16	Czech Republic	25	4	7	Gelbíčová et al., 2018
2013/ 18	Germany	77	235	18** 8***	Lüth et al., 2020
2017/ 19	Netherlands, Belgium	21	9	3	European Centre for Disease Prevention and Control, European Food Safety Authority, 2019
2018/ 20	Switzerland	34	6	8	Nüesch-Inderbinen et al., 2021
2018	Austria	19	73	1	Cabal et al., 2019

* Core genome multilocus sequence typing.
** Cluster 1.
*** Cluster 2.

is intraspecies virulence variability which consequently should change the contribution of that food type (Leclercq et al., 2020).

WGS is being adopted by different competent authorities

In 2019, European Centre for Disease Prevention and Control and European Food Safety Authority (ECDC-EFSA) recommended routine WGS of human and nonhuman *L. monocytogenes* isolates (European Centre for Disease Control et al., 2019) to generate a European-wide molecular typing database (Møller Nielsen et al., 2017). Four *L. monocytogenes* species-specific core genome MLST schemes have been developed (Chen et al., 2016; Moura et al., 2016; Pightling et al., 2015; Ruppitsch et al., 2015). A cut-off of ≤10 alleles (of 1701 alleles, implemented in the SeqSphere+ software, RIDOM, Münster, Germany) or ≤7 alleles (of 1748 alleles, developed at Institut Pasteur and implemented in both BIGSdb-Listeria and BioNumerics software, Applied Maths, Sint-Martens-Latem, Belgium) has been proposed to distinguish (separate) strains associated to different outbreaks based on the cgMLST schemes of Ruppitsch et al. (2015) and Moura et al. (2016), respectively. The CDC, USDA-FSIS, and FDA began using WGS as a tool for improved outbreak identification and investigation in 2013. Jackson, Tarr et al. (2016) demonstrated the impact of WGS on the annual incidence of listeriosis with more clusters and outbreaks of foodborne listeriosis identified and solved after (19 outbreaks) as compared to before the implementation of WGS (two outbreaks). The same authors suggested that isolates with <10 wgMLST allele difference should be considered epidemiologically linked, whereas those in the 10–30 range and >30 are frequently and occasionally linked.

In 2010, Gilmour et al. (2010) showed that two closely related *L. monocytogenes* strains were responsible for a Canadian listeriosis outbreak using high-throughput genome sequencing. This foodborne outbreak demonstrated the need for enhanced listeriosis surveillance as well as adequate control of *L. monocytogenes* in establishments manufacturing RTE foods (Currie et al., 2015). In January 2017, WGS was implemented across Canada as the primary typing tool for routine sequencing of human *Listeria* isolates and shortly thereafter, FoodNet Canada started to work with Public Health Agency of Canada's (PHAC) National Microbiology Laboratory (NML) to sequence and match *Listeria* isolates from both retail meat samples and human isolates (Public Health Agency of Canada, 2019).

In Australia, the Public Health Laboratory Network has suggested some recommendations for incorporating WGS in public health microbial surveillance but most laboratories within PHAC do not perform WGS for routine purposes (Department of Health, 2015).

The setup of open accessible databases allows the comparison and sharing of data between public health laboratories worldwide and facilitates as well as international source tracking and multinational outbreak investigations (Nadon et al., 2017; Schjørring et al., 2017). It is important that food safety competent authorities jointly cooperate with national partners in independent sectors, the Food and Agricultural Organization of the United Nation (FAO), World Health Organization (WHO), and World Organization for Animal Health (OIE) to promote cross-sectoral cooperation through the One Health concept (Food and Agriculture Organization of the United Nations, 2016).

WGS-Based geographical distribution of different CCs of *L. monocytogenes*

Work has shown that multilocus sequence typing (MLST) and multivirulence locus sequence typing (MVLST) can be effective in tracing the geographic distribution of different CCs and in linking these CCs to specific listeriosis outbreaks (Yin et al., 2015). Strains belonging to CC1 are distributed globally, with listeriosis cases caused by serotype 4b strains of CC1 identified in North America, Europe, Africa, Asia, and Oceania (Yin et al., 2015). Using MLST, CC1 and CC2 (significantly associated with food) (Lee et al., 2018) were also shown to predominate except for CC1 in northern Africa (Chenal-Francisque et al., 2011). CC3 ranked among the four most common clones in all regions, whereas CC9 ranked third in Europe and the Western Hemisphere (Chenal-Francisque et al., 2011). Using WGS, Zhang et al. (2020) and Yin et al. (2020) showed that CC8, CC9, and CC87 predominated in China. Particularly, CC87 was the predominant CC among foodborne and clinical isolates in China with its high prevalence in raw seafood implying this food type as a high risk to human health. Importantly, hypovirulent ST121 (strongly associated with food and overrepresented in processing environments in many different European countries) showed a high prevalence among Norwegian clinical isolates (Fagerlund et al., 2022). This could be explained by the fact that ingestion of high numbers of hypovirulent *L. monocytogenes* has occurred among high-risk groups. Furthermore, ST21 was found in vegetable products (Cabal et al., 2019; Maćkiw et al., 2021) and in Montenegrin dry pork sausage, Prosciutto, and environmental swabs during 2011 and 2013 (Toledo et al., 2018). CC8, belonging to lineage II, is globally distributed and the second most frequent in Austria in 2017 (Cabal et al., 2019). However, WGS can further delineate the geographical distribution within the same CC. For example, CC8 isolates originating from both China and Canada differed but were closely related to the European CC8 isolates (Italian and Switzerland) (Shi et al., 2021).

WGS-based investigations of some virulence, stress response, and antimicrobial resistance genes

The growing volume of WGS data for *L. monocytogenes* is now allowing the simultaneous identification of other genetic elements, i.e., accessory genes that are associated with virulent, stress-resistant, and antimicrobial-resistant phenotypes (Bergholz et al., 2018). Some clones carry genes in *Listeria* pathogenicity islands LIPI-3 and LIPI-4 that confer higher virulence (Cotter et al., 2008; Maury et al., 2016), whereas others may carry genes conferring better environmental survival (Chen et al., 2020; Harter et al., 2017; Ryan et al., 2010). SSI-1 aids in *Listeria* survival under suboptimal conditions, including high salt and low pH while SSI-2 is helpful for survival under alkaline and oxidative stresses (Gelbíčová et al., 2021). Wieczorek et al. (2020) identified all SSI-1 islet genes in lineage II strains of *L. monocytogenes* belonging to serotype 1/2a: CC7, CC8, CC31, and CC155. Besides these four CCs, SSI-1 is also present in *L. monocytogenes* strains belonging to both lineages I and II such as CC1, CC3, CC5, CC9, CC18, CC31, CC88, CC155, CC191, CC199, CC204, CC224, CC315, CC321, CC379, CC403, CC489, and CC1041 (Alvarez-Molina et al., 2021; Centorotola et al., 2021; Chen et al., 2020; Hingston et al., 2017; Lachtara et al., 2022; Mafuna et al., 2021; Palaiodimou et al., 2021; Roedel et al., 2019; Toledo et al., 2018; Wieczorek et al., 2020). Importantly, strains from serotype 1/2b, the majority of which contained SSI-1 (such as CC3 and CC5), created the strongest biofilms, while serotype 4b strains, the majority of which do not contain SSI-1 (such as CC2 and CC6), formed the weakest biofilms (Keeney et al., 2018). In a study of *L. monocytogenes* strains isolated over 20 years from food-processing plants, SSI-1 in CC7 and CC8 strains was associated with long-term persistence (Knudsen et al., 2017). Extended survival in food-processing environments was also described for ST121 strains of lineage II that carried SSI-2 (Centorotola et al., 2021; Chen et al., 2020; Guidi et al., 2021; Matle et al., 2019; Toledo et al., 2018).

Regarding virulence genes, Møller Nielsen et al. (2017) confirmed by WGS that the LIPI-3 genes and the gene for the virulence protein Vip were more likely present in clinical and/or lineage I isolates. According to Painset et al. (2019) and Tan et al. (2015), virulence surface protein Vip was found across all isolates in lineage I, but only in 70% of lineage II isolates (absent in CC204, CC21, CC31, and CC37,

Table 4
Genetic diversity and presence of stress survival and virulence determinants among *L. monocytogenes* strains

Key factors	*L. monocytogenes* lineage I	*L. monocytogenes* lineage II	*L. monocytogenes* lineage III and IV
SSI-1	+	+	nf
SSI-2	+	mostly present in CC 121	+
LIPI-1*	+	+	+
inlA/B locus*	+	harbor a truncated *inlA*	+
LIPI-2	−	hypervirulent serovar 4h carries a truncated LIPI-2	−
LIPI-3*	+	−	−
LIPI-4*	mostly present in CC4 and CC87	−	−
Virulence	+ + + overrepresented among clinical cases and NFCSs	+ overrepresented among food and food-processing environments	+ mostly identified in animals

nf – not found.
NFCSs – nonfood contact surfaces.
* Some atypical hemolytic *L. innocua* strains also harbor LIPI-1, LIPI-3, LIPI-4, and functional *inlA* genes.

and 1/43 of CC7 isolates and 3/98 CC8 isolates). More recently, Wang et al. (2021) confirmed the absence of Vip in CC8 but reported this gene missing in some other CCs such as CC11 and CC619. The presence of LIPI-3 has been proven by WGS in the following CCs of lineage I: CC1, CC2, CC3, CC4, CC6, CC155, CC191, CC228, and CC288 (Centorotola et al., 2021; Fox et al., 2016; Matle et al., 2020; Palaiodimou et al., 2021; Roedel et al., 2019; Shi et al., 2021; Toledo et al., 2018; Wieczorek et al., 2020). LIPI-3 genes (*llsAGHXBYDP*) are well conserved in ST1 (CC1), while in other STs of lineage I such as ST3, ST218, and ST288, a number of single-nucleotide polymorphisms have been found (Tavares et al., 2020). In the studies by Maury et al. (2016) and Hilliard et al. (2018), LIPI-4 was unique to CC4 strains of *L. monocytogenes* and closely linked to hypervirulence in CNS and maternal-neonatal listeriosis. In agreement with these findings, Painset et al. (2019) and Roedel et al. (2019) detected LIPI-4 in all isolates belonging to CC4 as well as those of CC87. However, the authors (Painset et al., 2019) highlighted that pathogenicity is a multifactorial process that is not merely derived from the presence or absence of virulence genes. Additionally, LIPI-1 is found in all *L. monocytogenes* strains whereas LIPI-2 is present in *L. ivanovii* and involved in phagosome disruption (Domínguez-Bernal et al., 2006). Using WGS, a truncated LIPI-2 was detected in hypervirulent serovar 4h strains of *L. monocytogenes* belonging to hybrid sublineage II whereas pathogenicity islands LIPI-3 and LIPI-4 were absent (Yin et al., 2019) (Table 4).

Regarding other types of resistance, some BC-tolerant determinants such as BC efflux pumps *qac* (above-mentioned Tn6188) (Moura et al., 2016; Müller et al., 2014, 2013; Ortiz et al., 2016; Zuber et al., 2019); *bcrABC* (Dutta et al., 2013), *emrC* (Kremer et al., 2017), and *emrE* (Kovacevic et al., 2016), have been detected in different *L. monocytogenes* strains, but with the existence of genomic variation within the identical CCs. Namely, some authors (Chen et al., 2020; Hurley et al., 2019) did not observe *emrC* in ST6, despite Kremer et al. (2017) and Roedel et al. (2019) finding it in ST6. Also, the three-gene cassette (*bcrABC*) was identified using WGS in *L. monocytogenes* strains belonging to CC5, CC9, CC88, CC155, CC199, CC204, CC321, CC1041, but literature data are sometimes inconsistent and not always related among all isolates of a particular CC within the same and between different studies (Chen et al., 2020; Cooper et al., 2021; Fox et al., 2016; Gelbíčová et al., 2021; Palaiodimou et al., 2021; Roedel et al., 2019; Stoller et al., 2019; Wagner et al., 2020).

Resistance to cadmium is frequently seen in *Listeria*, with several major outbreaks of listeriosis involving cadmium-resistant *L. monocytogenes* isolates (Elhanafi et al., 2010). The same plasmid that carries *bcrABC* also harbors the cadmium efflux determinant *cadA2*, and in addition, resistance to Cd is also conferred by plasmid-borne *cadA1* and chromosomal *cadA3* members of the *cadAC* efflux system (Katharios-Lanwermeyer et al., 2012; Lee et al., 2013). The recently described *cadA4* determinant has been identified in the Arsenic-resistance island LGI2 of *L. monocytogenes* human strain Scott A and other *L. monocytogenes* serotype 4b strains as well as in a few persistent strains belonging to CC14 and CC204 of lineage II (Fox et al., 2016; Parsons et al., 2017; Pasquali et al., 2018). Chen et al. (2020) also identified LGI2 in isolates belonging to CC4, CC1, and CC155. The presence of *cadA4* could be associated with the ability of *Listeria* to form biofilms (Parsons et al., 2017).

An earlier study suggested that the *comK* – prophage in *L. monocytogenes* may represent a rapid adaptation island (RAI) that contributes to the rapid adaption to different foods and environments as well as biofilm formation in specific niches within food-processing facilities (Verghese et al., 2011). Highly conserved *comK* – prophage was identified using WGS in all persistent clones (CC7, CC204, CC101, and CC155) analyzed by Palma et al. (2020). Also, Fagerlund et al. (2016) found *comK* gene in a persistent CC8 strain of *L. monocytogenes* recovered from a poultry processing environment.

Antibiotic target-modifying enzymes (*mprF* and *fosX*) also have been recognized in clonal complexes belonging to lineage I (CC1, CC2, and CC619) and lineage II (CC8, CC9, CC11, CC21, CC121, CC155, and CC204), whereas complexes CC8 and CC1 particularly harbored *mprF* that affects cell wall charge (Wang et al., 2021; Wieczorek et al., 2020; Zuber et al., 2019). However, Alvarez-Molina et al. (2021) found these two antibiotic-resistant genes in all CCs of lineage II, some of which coincided with the previous study. Shi et al. (2021) detected *fosX* in the following CCs from different regions: CC1 (Canada), CC3 (China), CC4 (Switzerland), CC6 (Italy), CC7 (Canada and China), CC8 (Italy, Switzerland, China, and Canada), and CC87 (China) while Roedel et al. (2019) reported the fosfomycin resistance gene in all tested strains belonging to different lineages. Importantly, CC6 from the USA did not harbor *fosX,* suggesting that intracomplex variation is most likely due to geographical origin. The presence of fosfomycin intrinsic resistance is epistatically canceled by virulence determinants present in *L. monocytogenes,* and this impact is manifested only during infection when virulent determinants are triggered within the host. This would help to explain why *L. monocytogenes* may become sensitive to fosfomycin and also support its use in the treatment of listeriosis (Scortti et al., 2018). It should be emphasized that most studies did not analyze all currently known *L. monocytogenes* lineages and genotypic subgroups (CCs). Therefore, a more holistic experimental approach is needed to better assess intraspecies variation by WGS (Lakicevic et al., 2022).

In terms of QMRAs, all CCs of *L. monocytogenes* are not assumed to be equally pathogenic, thus, risk assessments should be refined to help feed the modification of current regulations. Hypervirulent CCs, known as host-associated clones, better colonize the intestine and cause listeriosis in healthy hosts representing the largest impact on public health (Maury et al., 2019). In this regard, WGS data could help support the ranking of subtypes according to their level of virulence

and association to food (Lakicevic et al., 2022). Given our better understanding, foods contaminated with low numbers of hypervirulent strains should not meet food safety requirements. Additionally, high-risk populations should avoid certain foods likely to contain high numbers of *L. monocytogenes*. Consideration of intraspecies variability is crucial for fine-tuning risk assessments and decreasing the incidence of listeriosis in both humans and animals (Lakicevic et al., 2022).

The utilization of an efficient WGS-based surveillance system for human, food, and environmental isolates of *L. monocytogenes* will aid in faster implementation of interventions to better protect public health, inform risk assessment, and facilitate the management of national and international foodborne outbreaks (Matle et al., 2020; Ruppitsch et al., 2019). These outbreak investigations rely on close collaboration between clinicians, epidemiologists, microbiologists, and bioinformaticians (Cabal et al., 2019; Pietzka et al., 2019). Also, WGS has now become a critically important tool for tracking and tracing the source and geographic distribution of different clonal complexes as well as targeting known biomarkers associated with virulence, stress, and antimicrobial resistance. Although WGS has many benefits, the most important of which is high discriminatory power, easing the tension surrounding strain typing between food manufacturers and public health/food agencies remains a major challenge.

Conflict of Interest Statement

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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