Introduction

*Listeria monocytogenes* is a food-borne pathogen adapted to survive, grow and ultimately persist in different environments (Gray et al., 2006). In food processing plants, *L. monocytogenes* has been repeatedly isolated from food samples as well as food processing environment for months or years (Stasiewicz et al., 2015; Véghová et al., 2017; Leong et al., 2014). Through the contamination of food, *L. monocytogenes* can be transmitted to humans where it can switch from saprophyte to intracellular pathogen associated to approximately 2000 confirmed cases of Listeriosis each year in Europe, with a fatality rate of 17% (EFSA and ECDC, 2016).

Within *L. monocytogenes* biodiversity, isolates of lineage II and serotype 1/2a have been isolated from food and food processing plants more frequently than isolates belonging to lineage I (Orsi et al., 2011). Clonal complex (CC) 121 belonging to serotype 1/2a has been described as the most prevalent clone with a strong association to food origin. In particular, CC121 showed an overall prevalence of 17.6% over 6633 tested isolates of *L. monocytogenes* collected over nine years from food and clinical sources, with a statistical significant over-representation in food sources in comparison to clinical ones (92.9% vs 7.0%) (Maury et al., 2016). Comparable values of prevalence of human CC121 (11/116, 9.5%) were observed also within the Institute Pasteur *L. monocytogenes* database (http://bigdb.pasteur.fr/listeria/). The low frequency of *L. monocytogenes* in humans might be linked to the attenuated virulence of this CC. Premature Stop Codons (PMSC) in key virulence genes, such as *inlA* and *prfA*, as well as production of truncated InlA and PrfA proteins, were associated to attenuated virulence (Nightingale et al., 2005; Van Stelten et al., 2011; Cruz et al., 2014; Kanki et al., 2015). Compared to CC121, CC14 has been isolated rarely in food. Maury and colleagues found 92 isolates belonging to CC14 over 6633 tested isolates (1.4%) (Maury et al., 2016). Lower detection values were described also in 19 meat processing plants located in Northern Italy (5.7% over 69 tested isolates) in comparison to CC121 (23%) (Morganti et al., 2015). Besides a low prevalence, CC14 was described to be associated to higher infection rates. The clinical frequency of CC14 reached a not negligible 29.5% among isolates of clinical sources (Maury et al., 2016). Within CC14, a ST14 strain isolated from a case of invasive listeriosis was molecular characterised as belonging to epidemic clone (EC) III (corresponding to Multi-Virulence Locus Type 1 (VT1)) previously associated to a sporadic case occurred in United States in 1988, as well as a multi-state outbreak occurred in United States in 2000 (Mammina et al., 2013; Kathariou et al., 2002) (https://sites.google.com/site/mlstdatabase/protocol-for-mlst).

Whole Genome sequencing (WGS) based analyses have recently revealed a valuable potential in pathogen fingerprinting and identification of novel gene/features related to specific phenotypes. Based on the nucleotide sequence of the whole genome, an unprecedented discrimination power has been achieved by core genome Multi Locus Sequence Typing (cgMLST). This is particularly relevant in studies of repeatedly re-isolated strains showing high genetic similarity (same Pulsed Field Gel Electrophoresis (PFGE) profile or 7-locus Multi Locus Sequence Typing (7-locus MLST)) in which a superior discrimination...
power is required, especially to differentiate true persistent strains to sporadic strains as well as strains repeatedly reintroduced into the food processing plant through contaminated raw materials (Ferreira et al., 2014). Moreover, starting from the same sequence data, WGS offers the great potential for multiple investigations of novel genetic determinants as well as genetic determinants already known as linked to specific phenotypes (i.e. virulence).

In a previous study on prevalence of *L. monocytogenes* in four Italian rabbit meat processing plants (A, B, C, D), isolates sharing the same 7-locus MLST (ST), Multi Locus Tandem Repeat Analysis (MLVA) and *Apa*I-PFGE profiles were repeatedly collected over time from carcasses, meat cuts, meat products and the food processing environment (De Cesare et al., 2017). This study provided an interesting dataset to investigate further specific ST-types over time. For this purpose, a specific focus was put on ST14 (belonging to CC14) and ST121 (belonging to CC121) isolates, repeatedly collected over one year and six month, respectively, from different rabbit meat and environmental sources of the same processing plant (A). The aims of the present study were: 1) to evaluate the discriminatory power of cgMLST in comparison to molecular typing methods; 2) to characterize the virulence potential of ST14 and ST121 sequenced isolates by comparative genomic analyses.

### Materials and Methods

*L. monocytogenes* isolates included in the present study are a subset of isolates collected over one year within a previous study on prevalence of *L. monocytogenes* in rabbit meat processing plants (De Cesare et al., 2017). In particular, isolates sharing the same genotype and collected more than six times over a period of more than six months from different sources (rabbit carcasses, rabbit meat cuts, rabbit meat products and food processing environment) in the same plant were considered as potentially persistent. With this definition, 33 isolates of *L. monocytogenes* isolates of lineage II, serotype 1/2a and belonging to two 7-locus Multi Locus Sequence Types (MLST) ST14 and ST121 were selected as potentially persistent. An additional sporadic isolate, belonging to lineage I, serotype 1/2b, ST224 was also included for backward comparability. Isolates sharing the same 7-locus MLST were indistinguishable also by *Apa*I-PFGE, automated ribotyping and Multi Locus Variable number tandem repeat Analysis (MLVA) (De Cesare et al., 2017).

Whole-genomic DNA was extracted using the MagAttract HMW DNA Kit (Qiagen, Hilden, Germany). The purified DNA concentration and the quality parameter ratio 260/280 were measured by BioSpectrometer fluorescence (Eppendorf). The whole genome of selected 34 *L. mono-

| Isolate ID | ST | No. of contigs | N50 | Genome size (bp) | Fold coverage |
|------------|----|---------------|-----|------------------|---------------|
| LM1        | 14 | 13            | 579785 | 3022050          | 84,03         |
| LM2        | 14 | 14            | 456298 | 3022428          | 41,78         |
| LM3        | 14 | 13            | 580466 | 3022420          | 114,86        |
| LM5        | 14 | 15            | 579913 | 3022168          | 57,83         |
| LM8        | 14 | 14            | 580478 | 3023685          | 176,68        |
| LM9        | 14 | 13            | 580478 | 3023308          | 121,54        |
| LM10       | 14 | 14            | 580478 | 3023687          | 167,18        |
| LM11       | 224| 13            | 511384 | 2925197          | 159           |
| LM15       | 14 | 13            | 580472 | 3022932          | 146,98        |
| LM16       | 14 | 14            | 580454 | 2986892          | 131,2         |
| LM17       | 14 | 14            | 580454 | 2986900          | 140,23        |
| LM18       | 14 | 14            | 580454 | 2986900          | 187,12        |
| LM19       | 14 | 15            | 580471 | 3023022          | 172,15        |
| LM22       | 14 | 13            | 580454 | 3022659          | 79,03         |
| LM27       | 121| 26            | 529438 | 3060499          | 120,24        |
| LM29       | 121| 28            | 530140 | 3061007          | 131,41        |
| LM31       | 121| 25            | 530140 | 3060579          | 127,78        |
| LM35       | 14 | 13            | 580472 | 3022414          | 106,18        |
| LM39       | 14 | 15            | 580604 | 3022475          | 120,54        |
| LM41       | 14 | 13            | 580472 | 3022475          | 126,39        |
| LM44       | 14 | 13            | 580478 | 3022308          | 144,31        |
| LM46       | 14 | 13            | 580478 | 3022405          | 85,42         |
| LM47       | 14 | 13            | 580478 | 3022625          | 106,27        |
| LM50       | 121| 24            | 530364 | 3068560          | 111,58        |
| LM51       | 121| 25            | 530139 | 3060573          | 137,29        |
| LM53       | 121| 21            | 530354 | 3062194          | 139,38        |
| LM54       | 14 | 13            | 580472 | 3022424          | 150,5         |
| LM55       | 14 | 13            | 580478 | 3022427          | 142,63        |
| LM56       | 14 | 13            | 580478 | 3022415          | 121,34        |
| LM57       | 14 | 13            | 580478 | 3022426          | 134,73        |
| LM58       | 14 | 13            | 580478 | 3022498          | 123,61        |
| LM59       | 14 | 13            | 580478 | 3022821          | 135,9         |
| LM60       | 14 | 13            | 580472 | 3022629          | 132,49        |
| LM61       | 14 | 13            | 580478 | 3022408          | 108,5         |

ST, sequence type.

| Typing method | N profiles | Simpson’s ID | CI (95%) |
|---------------|------------|--------------|----------|
| cgMLST         | 5         | 0.439       | (0.253-0.624) |
| Ribotyping     | 2         | 0.214       | (0.045-0.383) |
| *Apa*I-PFGE    | 3         | 0.348       | (0.170-0.525) |
| MLST           | 3         | 0.348       | (0.170-0.525) |
| MLVA           | 3         | 0.348       | (0.170-0.525) |

CI, confidence interval; MLST, multilocus sequence typing; MLVA, multiple-locus variable number tandem repeat analysis.
cytogenes isolates was sequenced using Illumina MiSeq platform (TrueSeq library, paired-end reads). Reads were quality checked and \textit{de novo} assembled using the INNUca pipeline (https://github.com/INNUENDOCON/INNUca).

Briefly, INNUca calculates if the sample raw data fulfill the expected coverage (minimum default 15X). Then, after a read quality analysis using FASTQC and trimming using TRIMMOMATIC, the \textit{de novo} draft genome assembly is performed with SPAdes, which is subsequently improved using PILON to correct bases and fix misassemblies.

Core genome Multi Locus Sequence Typing (cgMLST) was inferred based on \textit{in silico} sequence alignment of 1748 loci of corresponding core genes. Briefly, after alignment, similarly to 7-locus MLST, an allele number is assigned to each locus. A cluster type, representative of all allele numbers, is then assigned (Moura et al., 2016).

The Multi Virulence Locus Sequence Type (MVLST) was inferred based on \textit{in silico} sequence alignment of seven virulence determinant gene loci: \textit{clpP}, \textit{dal}, \textit{inlB}, \textit{inlC}, \textit{lisR}, \textit{prfA} (https://sites.google.com/site/mvlstdatabase) (Zhang et al., 2004).

Analyses of virulence was performed using VirulenceFinder 1.5 (https://cge.cbs.dtu.dk/services/VirulenceFinder) (Joensen et al., 2014). With this tool a BLAST search of a database of 82 \textit{L. monocytogenes} virulence determinant genes was applied to all ST14 and ST121 draft genomes included in the present study, as well as to 23 publicly available genomes of \textit{L. monocytogenes} belonging to ST14 and ST121 and isolated from humans or food processing plants. Publicly available genome of EGD-e (Genbank accession number NC_003210.1) was included as reference. The default parameters used were 90\% ID threshold and 60\% of minimum length. Upon detection of no gene the analysis was repeated with 85\% ID threshold and 20\% minimum length. Alignment of \textit{inlA} and \textit{prfA} genes was performed by Clustal Omega (http://www.ebi.ac.uk/Tools/msa/clustalo).

The discriminatory power of each typing method was assessed by the Simpson’s Index of Diversity (ID). ID values with $P<0.05$ were considered statistical significantly different (Hunter and Gaston, 1988).

Results

Thirty four isolates of \textit{L. monocytogenes} of ST14, ST121 and ST224 collected over one year of sampling in a rabbit meat processing plant from environment, meat cuts and meat products were sequenced and \textit{de novo} assembled. Extracted DNA had a yield ranging from 14.2 to 81.3 µg/mL and a 260/280 ratio ranging from 1.81 to 1.88. The generated draft whole genomes sizes ranged from 2,925,197 to 3,068,560 bp. Draft genomes included a number of contigs ranging from 13 to 28 and N50 ranging from 456298 to 580604. Finally, coverage ranged from 42 to 187X (Table 1).

The cgMLST showed a superior discriminatory power in comparison to ribotyping, 7-loci MLST and MLVA (0.439 vs 0.214, 0.348 and 0.348 respectively) although statistically significant only in comparison to ribotyping ($P=0.01$) (Table 2, Figure 1). In particular, by WGS based method, ST14 isolates were differentiated in three clusters, whereas the same isolates were indistinguishable by \textit{ApaI}-PFGE, automated ribotyping and MLVA (De Cesare et al., 2017). According to cgMLST results, one cluster gathered the majority of putative persistent ST14 sequenced \textit{L. monocytogenes} isolates (CT1701). The other two clusters (CT1702 and CT1703) included only one isolate each (LM15, Article Figure 1. Whole Genome Sequencing-based analysis of the 34 sequenced \textit{Listeria monocytogenes} isolates.

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virulence genes were found in relation to type 6 which was specifically associated to length InlA of 800 aa (Figure 2). This mutation inlA protein of 492 aa instead of the full-length virulence genes carried 82, 80 and 80 virulence genes VT94. Regarding virulence type VT107, whereas all ST121 to ST14 isolates belonged to virulence type VT107, whereas all ST121 to ST14 isolates were confirmed to belong to the same persistent event. Two cgMLST clusters included only one isolate each, suggesting the detection of these two isolates as a sporadic event in the rabbit-meat processing plant.

Persisting L. monocytogenes isolates collected in food processing plants represent a public health concern, due to their potential transfer to humans via the food chain. In order to investigate the virulence potential of sequenced ST14 and ST121 L. monocytogenes isolates, MLST as well as an in silico detection of 82 virulence determinant genes was carried out. All ST14 belonged to VT107. This VT is particularly interesting since the concatenated sequence of the 7 virulence loci differs to VT1 (Epidemic Clone III) for only 4 nucleotides, suggesting the high similarity of sequenced ST14 isolates to this epidemic clone (Murugesan et al., 2015). Interestingly, three years after sampling of the rabbit-meat processing plant, a case of invasive Listeriosis in the North of Italy associated to ST14 strain belonging to VT1 has been described (Mammina et al., 2013).

Eighty out of 82 virulence determinant genes were found in the 57 L. monocytogenes genotypes analyzed. This finding suggests that the presence/absence of these 82 genes can hardly explain the high diversity between ST14 and ST121 which have been shown to occur with a high and low frequency respectively in clinical samples (Maury et al., 2016; Morganti et al., 2015). The genes infI and lmo2026 were not detected. The gene infI belongs to the internalin family, which includes genes exclusive of the genus Listeria and associated to the adhesion and invasion of host cells (Vázquez-Boland et al., 2001). The gene lmo2026 was recently identified as an internalin gene, infI, associated to biofilm formation and adhesion to mucin (Popowska et al., 2017). Besides presence/absence of virulence genes the regulation of expression as well as the presence of truncated genes or the presence of mutations leading to truncated versions of their translated proteins might have a crucial role in the virulence potential of ST14 and ST121. Regarding truncated virulence genes, the genes inlI, actA and ami were found truncated. The gene inlI belongs to the internalin family (Vázquez-Boland et al., 2001; Sabet et al., 2008). The actA gene found truncated in all ST121 genomes, encodes the surface protein ActA, the factor responsible for actin-based motility and cell-to-cell spread (Smith and Portnoy, 1997). The gene ami codes for a autolysin which contributes to the adhesion of L. monocytogenes to eukaryotic cells by anchoring its cell wall (Milohanic et al., 2001). Regarding point mutations, a premature stop codon (PMSC), already described as associated to attenuated virulence of ST121, was detected in all sequenced ST121 genomes (Van Stelten et al., 2010). The attenuated virulence potential of sequenced ST121 isolates is also supported by the detection of a truncated version of the gene actA, which was described as indispensable for L. monocytogenes pathogenicity (Smith and Portnoy, 1997). An attenuated virulence of ST121 might explain the low frequency of its corresponding clonal complex CC in clinical samples (Maury et al., 2016).

Conclusions
Although not yet fully standardized, Whole genome Sequencing (WGS) can be applied for multiple investigations, such as typing and prediction of virulence. In the present study, WGS-based analyses revealed higher discriminatory power in comparison to molecular typing methods, although significant only in comparison to ribotyping, on 34 L. monocytogenes isolates collected over one year in a rabbit meat processing plant. In particular 25 ST14 and 6 ST121 isolates were confirmed to belong to two different genotypes, although based on the same genome sequence used for typing purposes, in silico analyses were useful to predict the potential virulence of L. monocytogenes isolates. Multi Virulence Locus Sequence typing (MVLSST) results, as well as analysis of virulence genes, suggest a higher virulence potential of ST14 sequenced isolates in comparison to ST121. Additional in vitro investigations should be performed.

Discussion
Whole-genome based analyses have recently revealed an unprecedented potential as a powerful tool for multiple analyses, including typing and gene characterization of food-borne pathogens. In the present study, WGS revealed its great potential as a one-serve-all approach. Based on the same genome sequence data, cgMLST typing, in silico MLST and in silico detection of 82 virulence genes were performed in parallel. However, it must be noted that, in comparison to standard molecular techniques, this approach requires great bioinformatics skills, standardized protocols, agreed cut off and parameter values in order to obtain robust and comparable results.

The cgMLST revealed a superior discriminatory power in comparison to molecular tools, although significant only in comparison to ribotyping. The cgMLST confirmed only in part results of molecular typing, suggesting that most, but not all, of the ST14 isolates, collected over one year in the same rabbit-meat processing plant, belonged to the same persistent event. Two cgMLST clusters included only one isolate each, suggesting the detection of these two isolates as a sporadic event in the rabbit-meat processing plant.

LM10). Out of the 1748 loci of the cgMLST scheme, these two singletons carried 12 and 11 different loci respectively in comparison to CT1701. This finding suggests that three ST14 strains circulated in the rabbit-meat processing plant during the time of sampling: one persistent strain and two sporadic ones. All ST121 isolates were indistinguishable by cgMLST, confirming the high similarity of these isolates already suggested by molecular typing methods.

In order to investigate the virulence potential of 33 ST14 and ST121 isolates, repeatedly isolated over one year and six months, respectively, in a rabbit meat processing plant, MLST was assessed along with the in silico detection of 82 Listeria virulence genes. In order to investigate potential associations of presence/absence of genes with STs or origin, virulence genes were additionally investigated in the reference genome EGD-e as well as in 23 publicly available genomes of L. monocytogenes belonging to ST14 and ST121 and isolated from humans or food processing environment. Regarding MLST results, all sequenced ST14 isolates belonged to virulence type VT107, whereas all ST121 to VT94. Regarding in silico detection of virulence genes, the reference genome EGD-e and the analyzed ST14 and ST121 genomes carried 82, 80 and 80 virulence genes respectively indicating that those genes are core virulence genes of L. monocytogenes. The genes infI and lmo2026 were not detected in any of the 56 ST14 and ST121 genomes analyzed. The gene inlI was not found or found truncated in all 56 genomes analyzed. All ST14 carried a full-length version of the gene actA (1920 nucleotides), which was detected truncated in all the ST121 genomes. The gene ami was detected in a truncated version in some ST14 and ST121 genomes.

No mutations were found in prfA genes of all sequenced genomes as well as of inlA of ST14 genomes. In contrast, the inlA gene of all ST121 genomes showed a mutation leading to a premature stop codon (PMSC) predicting the translation of a truncated InlA protein of 492 aa instead of the full-length InlA of 800 aa (Figure 2). This mutation has been already described as PMSC of type 6 which was specifically associated to attenuated virulence of L. monocytogenes (Van Stelten et al., 2010).

No relevant differences in carriage of virulence genes were found in relation to food or human origin.
performed to confirm the virulence of ST14 and ST121 isolates.

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Figure 2. Predicted amino acid sequence alignment of InlA in ST121 Listeria monocytogenes isolates and EGD-e (GenBank accession number NC_003210.1). The mutation leading to the truncated InlA protein is highlighted in bold.
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