



## Review

# Growth, detection and virulence of *Listeria monocytogenes* in the presence of other microorganisms: microbial interactions from species to strain level

Evangelia A. Zilelidou, Panagiotis N. Skandamis\*

Agricultural University of Athens, Department of Food Science and Human Nutrition, Laboratory of Food Quality Control and Hygiene, Iera odos 75, 11855 Athens, Greece

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## ABSTRACT

Like with all food microorganisms, many basic aspects of *L. monocytogenes* life are likely to be influenced by its interactions with bacteria living in close proximity. This pathogenic bacterium is a major concern both for the food industry and health organizations since it is ubiquitous and able to withstand harsh environmental conditions. Due to the ubiquity of *Listeria monocytogenes*, various strains may contaminate foods at different stages of the supply chain. Consequently, simultaneous exposure of consumers to multiple strains is also possible. In this context even strain-to-strain interactions of *L. monocytogenes* play a significant role in fundamental processes for the life of the pathogen, such as growth or virulence, and subsequently compromise food safety, affect the evolution of a potential infection, or even introduce bias in the detection by classical enrichment techniques. This article summarizes the impact of microbial interactions on the growth and detection of *L. monocytogenes* primarily in foods and food-associated environments. Furthermore it provides an overview of *L. monocytogenes* virulence in the presence of other microorganisms.

## 1. Introduction

Most microorganisms all over the planet exist in communities and engage in networks of beneficial or detrimental relationships. The mere presence of a species in a microbial ecosystem might substantially affect the abundance or behavior of a second species without directly interacting with this species (Matsui et al., 2000; Wootton, 1994). Evidently, all types of interactions (direct or indirect) are driven by evolution and natural selection, which will determine the existence of bacteria in time and space.

In foods, microbial interactions, either specific or nonspecific, may have a great influence on the fate of pathogenic species contaminating foods (Gram et al., 2002; Haruta et al., 2009). *Listeria monocytogenes*, a Gram-positive pathogenic bacterium of major concern for food safety, thrives in a wide range of environments which are inhabited by an abundance of bacterial species (Adams and Moss, 2007; Farber and Peterkin, 1991). Due to its ubiquitous distribution, contamination of foods and/or raw materials is not only very common (Fenlon et al., 1996; Ferreira et al., 2014) but may also involve more than one strain of the microorganism (Danielsson-Tham et al., 1993; Navas et al., 2007). Thus, different *L. monocytogenes* strains may occur in foods potentially interacting with each other and with various other microorganisms. In foods, the ability of *L. monocytogenes* strains to survive processing and

even proliferate during storage is attributable to the innate potential of this organism to withstand extremely adverse conditions (Gandhi and Chikindas, 2007). Once ingested, the capacity to overcome stressful challenges associated with the gastrointestinal passage allows *L. monocytogenes* to infect the host (Gahan and Hill, 2014, 2005). Throughout these different stages of *L. monocytogenes* life (from saprophyte and food contaminant to intracellular pathogen) the responses of *L. monocytogenes* in order to promote its survival and growth may be related to inter- and intra-species interactions. For instance, the expression pattern of antibiotic-resistance related genes of *L. monocytogenes*, changes in the presence of *Bacillus subtilis* compared to the mono-culture state (Tirumalai and Prakash, 2012). Likewise, other physiological responses of *L. monocytogenes* also may be governed by community-wise interactions with close neighbors.

Studies on *L. monocytogenes* interactions can offer new insights on the different activities of the microorganism from proliferation and metabolism to pathogenicity and virulence. This, from a food safety perspective, can contribute to more accurate risk assessments and development of effective strategies to eliminate this particular pathogen. Taking the above into consideration, this review will summarize the knowledge on the growth, detection and virulence of *L. monocytogenes* as influenced by the interactions of the microorganism with special focus on strain-to-strain ('inter-strain') interactions. Throughout the

\* Corresponding author at: Laboratory of Food Quality Control & Hygiene, Department of Food Science & Technology, Agricultural University of Athens, Iera Odos 75, 11855 Athens, Greece.

E-mail address: [pskan@aua.gr](mailto:pskan@aua.gr) (P.N. Skandamis).

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paper, the term interactions refers to all types of direct or indirect effects between *L. monocytogenes* and other microorganisms. Hence, the review describes the responses/phenotypes observed for *L. monocytogenes* as a result of being in the same microenvironment with other microorganisms. In certain sections (e.g. Section 4) attention is given to the outcome of this simultaneous presence and not solely and strictly to the strength and type of microbial interactions.

## 2. *L. monocytogenes* and microbial interactions in the natural environment

Prior to contamination of food-processing environments and foods and infection of humans *L. monocytogenes* may exist in natural environments. Soil and decaying plants are considered as important habitats in the saprophytic life of *L. monocytogenes* (Freitag et al., 2009; Ivanek et al., 2006; Linke et al., 2014). Many studies have investigated the occurrence and potential of *L. monocytogenes* to survive in soil. Early, in the 1960 Welshimer (1960) demonstrated that *L. monocytogenes* could survive in soil for a period of at least 295 days. However, even today, elucidating the environmental factors that drive *L. monocytogenes* survival in soil is extremely hard as these factors are intimately linked to each other (Vivant et al., 2013b). Physicochemical properties of soil such as the pH, the saturation of basic cationic ratio or the soil texture may affect the survival of *L. monocytogenes* in this habitat. Soil microbiota strongly interacts with these factors generating a particularly competitive environment and regulating the fate of the microorganism in soil (Vivant et al., 2013b). Sidhu et al. (2001), illustrated that the indigenous microorganisms in composted biosolids – commonly used in agriculture as soil amendments – had a more profound impact on the survival of *Salmonella* than nutrient bio-availability in the compost. Accordingly, in several studies, exclusion of native soil microbiota via sterilization of soil led to enhanced survival of *L. monocytogenes*. For instance, McLaughlin et al. (2011) observed a decrease of *L. monocytogenes* EGDe population in non-sterile soil within 6 days. In contrast a slight increase of the microorganism was detected in autoclaved soil. In line with this, Locatelli et al. (2013) found a strong suppression of *L. monocytogenes* in non-autoclaved soils with a pH above 7. As suggested by Hartman et al. (2008), bacterial diversity increases in soils with high pH compared to acidic soils and can act as a barrier against invasion of pathogenic microorganisms such as *L. monocytogenes*. Vivant et al. (2013a), also proposed that the antagonistic effect of indigenous soil microbiota against *L. monocytogenes* decreased with loss of bio-diversity. According to Pietronave et al. (2004), the suppression of *Salmonella* and *Escherichia coli* in finished compost was not dependent on a single group of microorganisms, but was related to the concentration and diversity of the indigenous microbial community. In fact, even for the same level of bacterial diversity, the phylogenetic composition and microbial interactions taking place in soil may determine the survival of pathogenic species such as *L. monocytogenes* (Vivant et al., 2013a). Therefore, further investigation is necessary to reveal the microbial species, which play a fundamental role in the fate of *L. monocytogenes* in soil.

A detailed review of *L. monocytogenes* interactions with soil microorganisms is beyond the scope of this review. However, it was considered important to refer to these interactions, acknowledging their indirect, yet critical role in food safety. The interactions between *L. monocytogenes* and soil microorganisms may promote the development of traits such as antibiotic resistance (Linke et al., 2014). Furthermore the strategies that *L. monocytogenes* adopts in order to respond to microbial competition in soil may in turn affect growth in foods or/and pathogenicity (Baumgardner, 2012). Eventually, since *L. monocytogenes* may habituate to soil prior to food contamination, the biotic pressure and interactions with the soil community may be related to the survival and selection of strains, which will be subsequently introduced into the food-chain (McLaughlin et al., 2011).

## 3. Survival and growth of *L. monocytogenes* in food and food processing environments in the presence of other microorganisms

Numerous studies (Aspridou et al., 2014; Bae et al., 2012; Meldrum et al., 2003; Poimenidou et al., 2016; Schwartzman et al., 2011; Tienungoon et al., 2000; Vermeulen et al., 2007) have investigated or reviewed the potential of *L. monocytogenes* to grow under diverse conditions, (e.g. of acidity, salinity, nutrient content or viscosity, emulsification etc.) which reproduce habitats encountered by the microorganism in food or food processing environments. However, for realistic food safety risk assessment, the growth of *L. monocytogenes* cannot be considered only as a result of foods physicochemical parameters but also as a function of the microbial consortia residing in foods and food-associated environments (Powell et al., 2004). Considering the growth of *L. monocytogenes* in the presence of other organisms is of paramount importance from a food safety perspective as it potentially affects the numbers of *L. monocytogenes* found in different foods and subsequently consumer exposure. The infectious dose of *L. monocytogenes* is considered to be high but still even relatively low levels of the organism might infect and cause disease to impaired hosts (Lianou and Sofos, 2007; McLaughlin, 1996; McLaughlin et al., 2004). To assess the risk of a food product to support growth of *L. monocytogenes*, it is very important to evaluate whether the microbiota of foods may inhibit, allow or enhance survival and growth of *L. monocytogenes*. For instance the absence of food microbiota leads to fast proliferation of *L. monocytogenes* in hot-smoked fish products (Lianou and Sofos, 2007). A number of studies developing mathematical models for the prediction of *L. monocytogenes* behaviour in different foods have incorporated microbial interactions in predictive models; these interactions are regarded as a factor influencing the growth of *L. monocytogenes* and particularly the growth rate ( $\mu_{max}$ ) and the maximum population density (MPD) (Blanco-Lizarazo et al., 2016; Cornu et al., 2011; Giménez and Dalgaard, 2004; Guillier et al., 2008; Koseki et al., 2011; Mejlholm and Dalgaard, 2015; Østergaard et al., 2014; Ye et al., 2014). The aforementioned models are usually simple, based on well-established (historical) concepts such as the Jameson effect, which assumes simultaneous growth deceleration and cessation of competing microorganisms, or the Lotka-Volterra equation, a general competition model. These models have been used in predictive microbiology to include interactions of *L. monocytogenes* and natural food microbiota (Guillier et al., 2008; Koseki et al., 2011), and particularly the inhibitory effect of lactic acid bacteria (LAB) on the growth of *L. monocytogenes* (Blanco-Lizarazo et al., 2016; Cornu et al., 2011; Giménez and Dalgaard, 2004; Mejlholm and Dalgaard, 2015; Østergaard et al., 2014; Ye et al., 2014). For instance, Blanco-Lizarazo et al. (2016), modelled the simultaneous growth of *L. monocytogenes*, *L. sakei*, and *S. carnosus* in co-cultures and their microbial interactions based on the Jameson effect and found a significantly higher  $\mu_{max}$  for *L. monocytogenes* in monoculture ( $1.060 \pm 0.11$ ) compared to the co-culture ( $0.462 \pm 0.02$ ). On the other hand, Cornu et al. (2011), used a case study regarding the growth of *L. monocytogenes* in cooked and smoked diced bacon to show that the simple Jameson effect and Lotka-Volterra model over- or underpredicted, respectively, the fate of *L. monocytogenes*. However, even though these models can be sometimes too simplistic and need further improvement, predictions for the growth of *L. monocytogenes* can be invalid if microbial interactions are not taken into consideration (Augustin et al., 2005). In fact, Guillier et al. (2008) observed growth arrest of *L. monocytogenes* on smear cheese wooden shelves when the natural biofilm microbiota stopped increasing; they confirmed that the physicochemical parameters of foods (e.g. pH and  $a_w$ ) were not sufficient to describe *L. monocytogenes* inhibition by existing growth/no growth models, resulting in inaccurate predictions. Evidently, understanding these interactions plays a pivotal role to the control of the microorganism. Several studies have been conducted to investigate the behaviour of *L. monocytogenes* in the presence of food-related microorganisms. Tables 1 and 2 list a number of such studies describing

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