Influence of *Listeria innocua* on the growth of *Listeria monocytogenes*

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A B S T R A C T

The growth of *Listeria monocytogenes* and *Listeria innocua* strains was monitored during this study: (i) in TSB–YE media and (ii) in a food matrix (pasteurized milk) according to the ISO 11290-1 methodology. Different inocula concentrations and mixtures were tested. The response was shown to be strain dependent. In TSB–YE the inhibition of a *L. monocytogenes* strain was observed in just one of the three mixtures (*L. monocytogenes_1340* with *L. innocua_11288*) showing a reduction of 1.37 log cfu/ml after 42.5 h and 1.85 log after 66.5 h of incubation. In pasteurized milk the inhibition of *L. monocytogenes* by *L. innocua* was always observed when *L. innocua* was present in higher concentrations than *L. monocytogenes*. The reverse was also observed but only in one mixture (cocktail of six *L. monocytogenes* with *L. innocua_2030c*) when the initial concentration of *L. monocytogenes* was 100 times higher than *L. innocua* suggesting the phenomenon of quorum sensing. Furthermore, inhibitory activity was not caused by bacteriocins, and no correlation between the growth rate and inhibition was demonstrated.

Introduction

Listeria monocytogenes is an important foodborne pathogen which causes listeriosis, a serious invasive illness in humans (Farber & Peterkin, 1991). Despite the low incidence, listeriosis is of considerable public health concern because it still represents a health risk due to its high mortality rate (30%) within the risk groups: neonates, elderly people, pregnant women and immunocompromised individuals (Siegman-Igra et al., 2002).

L. monocytogenes has an ubiquitous distribution and a great ability to grow in a wide range of conditions, such as refrigeration temperatures, low pH and high salt concentration (Seeliger & Jones, 1986; Grau & Vanderlinde, 1992), that enables it to survive and grow in foods and food-processing environments, and overcome the multiple hurdles employed in food preservation and safety, increasing the risk of food contamination. Detection of *L. monocytogenes* is crucial within the food industry because consumption of contaminated raw and/or processed food products such as meat, poultry, seafood, dairy products and vegetables, is the cause of 99% of all listeriosis cases (Mead et al., 1999; Schlech, 2000).

The detection of *L. monocytogenes* usually involves selective enrichment procedures due to the high levels of background microflora that are normally present in food matrices and also because the presence of this microorganism in food is generally low, which exacerbates further analysis (Norton et al., 2001).

Several research reports have demonstrated that the presence of *Listeria innocua* may mask *L. monocytogenes*, which could lead to a false negative result for the presence of *L. monocytogenes* (Cornu, Kalmokoff, & Flandrois, 2002; Curiale & Lewus, 1994; Petran & Swanson, 1993).

Different explanations for this have been proposed, such as a more rapid growth advantage of *L. innocua cf. L. monocytogenes* (Beumer, Giffel, Anthonie, & Cox, 1996; Curiale & Lewus 1994; Petran & Swanson 1993), in contrast to inhibitory interspecies interactions which have been attributed to the production of bacteriocin-like agents (Besse, Audinet, Kérouanton, Collin, & Kalmokoff, 2005; Cornu et al., 2002; Yokoyama, Maruyama, Katsube, & Mikami, 2005). At the present time, both explanations remain unclear.

The majority of inhibitors may correspond to defective bacteriophage particles, also referred to as monocins (Curtis & Mitchell, 1992; Zink, Loessner, & Scherer, 1994), listeriocins (Lebek, Teysseire, & Baumgartner, 1993; Ortel, 1989), or bacteriocin-like compounds (Curtis & Mitchell, 1992; Yokoyama et al., 2005). However, there remains some confusion regarding inhibitory activities resulting from the production of bacteriocins among *Listeria* isolates (Zink, Loessner, & Scherer, 1995).

Bacteriocin production within *Listeria* spp. may be important because the accompanying resistance phenotype could influence the susceptibility of these isolates to the presence of added or produced LAB bacteriocins (Eijsink, Skeie, Middelhoven, Brurberg, & Nes, 1998; Song & Richard, 1997). They could also indirectly enhance pathogenicity by allowing the competition and establishment of bacteriocin-producing isolates within mixed flora food systems. Moreover, if bacteriocins are produced among *Listeria* spp., these may represent new anti-*Listeria* inhibitors with poten-

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tial applications in food products. Therefore, there is currently much interest in the application of bacteriocins that demonstrate anti-*Listeria* properties for the inhibition of this pathogen in a variety of food products either through bacteriocin-producing cultures (Albano et al., 2008; Eppert, Valdés-Stauber, Götz, Busse, & Scherer, 1997; Muriana, 1996; Winkowski, Crandall, & Montville, 1993), or by the addition of pure or semi-pure bacteriocins (Davies, Bevis, & Delves-Broughton, 1997; Muriana, 1996; Vigonolo et al., 1998; Albano et al., 2008).

The aim of this study was to evaluate the influence of *L. innocua* on the growth of *L. monocytogenes* determined by; (i) growth of these two species when grown individually and concurrently in a non-selective *Listeria* culture medium (TSB–YE); (ii) determination of *L. monocytogenes* recovery in the enrichment procedure according to ISO 11290-1 reference method in a food matrix, namely pasteurized milk; both systems were inoculated with different concentrations of both species and evaluated the impact of strain over-growth during each step of the enrichment process; and (iii) detection of any inhibitory activity produced by *L. innocua* against *L. monocytogenes*.

Materials and methods

Cultures and preparation of inocula

Different *L. monocytogenes* and *L. innocua* strains were used during this study: *L. monocytogenes* 1339, 1340, 1334, 1792, 999, 1336 (all from ESB, UCP culture collection) and *L. innocua_2030c* (Public Health Laboratory Services, London) and 11288 (National Collection of Type Cultures, UK; NCTC). Stock cultures were kept in Tryptone Soya broth with Yeast Extract 0.6% w/v (TSB–YE, Lab M, UK) supplemented with 30% (w/v) of glycerol at −80 °C. Working cultures were sub-cultured twice in TSB–YE (1% v/v) incubated at 37 °C for 24 h, before use.

Monitoring growth of L. monocytogenes and L. innocua strains individually

For each culture, growth was determined using the Microplate Method. To each well of a sterile 96-well microtiter plate (Orange Scientific, Belgium), 200 μL of TSB–YE were added and inoculated with 1% (v/v) of each cell suspension obtained as described above, previously diluted in sterile Ringer solution to 10^4 cfu/ml (for all the tested strains growth curves were previously determined, O.D. vs. cfu/ml; data not shown). Microplates were incubated at 30 °C for 24 h and the Optical Density (O.D.) at 665 nm was registered at 30 min intervals by the Microplate Reader (Model 680, Bio-Rad). Three independent replicates of these assays were performed.

Monitoring growth of L. monocytogenes strains in the presence of L. innocua

The growth of different isolates of *L. monocytogenes* in the presence of *L. innocua* was evaluated during this study in different co-cultures as described in Table 1. In all the experiments, a positive control of each isolate was performed.

In non-selective medium

TSB–YE was inoculated with 1% (v/v) of each mixture (see Table 1) with an initial cell concentration of 10^4 cfu/ml and incubated in a water bath (Julabo SW22, Germany) with agitation (70 rpm) for 72 h at 30 °C. At defined intervals aliquots of 1 ml were collected for further enumeration. Two independent replicates of this assay were performed.

In food matrix artificially contaminated undergoing enrichment culturing

Pasteurized milk obtained from a retail establishment was artificially contaminated with strains of *L. monocytogenes*, *L. innocua* or both (1% v/v); cultures were grown at 37 °C for 24 h in TSB–YE and suitably diluted as described in Table 2. The subsequent analysis of the inoculated milk was performed according to the ISO 11290-1 method for enumeration of *L. monocytogenes* (Anonymous, 2004). At each defined interval, aliquots were taken for enumeration, such as immediately after the addition of Half Fraser broth (Merck, Germany) to the inoculated milk; after 24 h at 30 °C in Half Fraser broth, and after a further 24 h and 48 h in Fraser broth (Merck) at 37 °C. Two independent replicates of this assay were performed.

Enumeration

Aliquots obtained as described above were serially diluted and plated using the drop counting technique onto the Agar Listeria Ottaviani Agosti plates (ALOA, AES Laboratories, France) and incubated at 37 °C for 18–48 h. The differentiation of *L. monocytogenes* and *L. innocua* was performed according to the presence of characteristic colonies in ALOA, namely blue green with halo in the case of *L. monocytogenes* and blue green without halo in the case of *L. innocua*.

Detection of inhibitory activity produced by Listeria strains

Listeria isolates were screened for the production of inhibitory activity such as bacteriocins, by the spot-on-lawn method. The cultures of *L. innocua* and *L. monocytogenes* obtained as described above, were evenly spread on plates of TSA-YE (Tryptone Soya Agar with Yeast Extract 0.6% w/v) and drops (10 μl) of the other species, respectively, were spotted on the lawns and incubated at 30 °C for 24–48 h. Inhibition was considered positive if a translucent halo was observed around the spot.

Statistical analysis

All the experiments were repeated at least three times. An analysis of variance (one-way ANOVA) was performed to test significant effects of: (i) the survival of *L. monocytogenes* when *L. innocua* is present (ii) the survival of *L. innocua* when *L. monocytogenes* is present and (iii) the inoculum concentration of each *Listeria* strain in the mixture. All calculations were carried out using the software Kaleidagraph (version 4.04, Synergy Software, Reading, USA).

Table 1
Mixtures of *Listeria monocytogenes* and *Listeria innocua* strains.

Mixture	
1	Six strains of *L. monocytogenes* (1339, 1340, 1334, 1792, 999, 1336) and *L. innocua_2030c*
2	*L. monocytogenes_1339* and *L. innocua_11288*
3	*L. monocytogenes_1340* and *L. innocua_11288*

Table 2
Conditions used for artificial contamination of pasteurized milk.

Conditions	Inoculum
1	*L. monocytogenes* (10^2 cfu/ml) and *L. innocua* (10^2 cfu/ml)
2	*L. monocytogenes* (10^4 cfu/ml) and *L. innocua* (10^4 cfu/ml)
3	*L. monocytogenes* (10^4 cfu/ml) and *L. innocua* (10^2 cfu/ml)
4	*L. monocytogenes* (10^2 cfu/ml) and *L. innocua* (10^4 cfu/ml)

Results and discussion

Monitoring growth of L. monocytogenes and L. innocua strains individualy

The growth kinetics of all *L. monocytogenes* and *L. innocua* strains were previously evaluated by the microplate method. In fact, other authors have already described the success of the microplate method for studying growth kinetics compared to standard cultivation methods (Horáková, Greifová, Seemannová, Gondová, & Wyatt, 2004).

Results were compared and analyzed according to the generation time, growth rate, lag and exponential phase duration and by the comparison of the differences between the initial and final O.D. of the growth curve (data not shown). According to our results, the growth rate varied according to the tested strain. Furthermore, *L. monocytogenes_1339* showed the shortest generation time (119 min) followed by *L. innocua_11288* (124 min), *L. monocytogenes_1340* (130 min) and *L. innocua_2030c* (167 min). Within these results, the mixtures of *L. monocytogenes* and *L. innocua* were selected for further studies.

Curiale and Lewus (1994) verified that in TSB–YE the generation times of *L. innocua* were longer than *L. monocytogenes*. However, they only used a single strain from each species and ignored the inter-strain variability. The work performed by Petran and Swanson (1993) and MacDonald and Sutherland (1994), used a range of strains; however, they did not find significant differences between the two species.

Monitoring growth of L. monocytogenes strains in the presence of L. innocua

Table 1 describes the three different mixture conditions that were selected to evaluate the growth of *L. monocytogenes* in the presence of *L. innocua*. One of those conditions was performed with all the *L. monocytogenes* isolates since frequently the food products are contaminated with more than one strain of this pathogen (mixture 3, Table 1). The strains' behaviours were evaluated in a non-selective medium and in artificially contaminated milk, as discussed below.

It is widely accepted that *L. innocua* has an advantage over *L. monocytogenes* during enrichment culturing due to faster growth rates (Beumer et al., 1996; Curiale and Lewus, 1994) however, our results demonstrated that there were no absolute correlations between growth rates or inhibitory activity in terms of strain evolution during enrichment (data not shown).

In non-selective medium

In the case of mixtures 1 and 3, strains of *L. innocua* had no influence on the growth of *L. monocytogenes* (data not shown). Concerning the mixture 2, a cell reduction of *L. monocytogenes_1340* was observed when *L. innocua_11288* was present (1.37 log after 42.5 h and 1.85 log after 66.5 h of incubation) suggesting *L. monocytogenes* inhibition (Fig. 1). Besides the same initial numbers of both strains, the preferential growth of *L. innocua*, in our case, was not consistent with differences in generation times and growth rate. At the end of the normal enrichment period, the number of *L. innocua* cells exceeded the number of *L. monocytogenes* cells by at least 10-fold.

Other studies, also evaluated the influence of *L. innocua* on the growth of *L. monocytogenes*; however, these studies were performed after the enrichment step described in the ISO methodology (Anonymous, 2004; Besse et al., 2005; Cornu et al., 2002; Yokoyama et al., 2005).

In the present study, it was demonstrated that even in a non-selective medium i.e. TSB–YE, it is possible to observe the inhibition of *L. monocytogenes* when *L. innocua* is present.

In a food matrix artificially contaminated undergoing enrichment culturing

Previously, Cornu et al. (2002) studied the influence of *L. innocua* in the growth of *L. monocytogenes*; however, an initially high cell number (10^7 cells/ml) was used and that is not likely to occur in naturally contaminated food samples. Other authors, however, studied lower initial contamination levels but with the same inocula concentrations of *L. monocytogenes* and *L. innocua* (Besse et al., 2005; Yokoyama et al., 2005). The challenge of the current study is to evaluate the impact of lower initial contamination levels on inter-strain interaction when both strains are or not in the same cellular concentration.

Cocktail of six strains of L. monocytogenes with L. innocua_2030c.

At the same inoculum concentration (conditions 1 and 2, Table 2) there were no significant differences ($P > 0.05$) in the growth of the cocktail of *L. monocytogenes* when *L. innocua_2030c* was present and *vice versa* (Fig. 2). When different inoculum concentrations were tested, two situations were observed; (i) inhibition of the *L. monocytogenes* cocktail (decrease of 3.21 log after 72 h) when *L. innocua* was present in higher concentration ($P < 0.05$) and (ii) inhibition of *L. innocua* (decrease of 3.32 log after 72 h) when *L. monocytogenes* cocktail was present in higher cell numbers ($P < 0.05$) (Fig. 2).

In the literature, only the inhibition of *L. monocytogenes* by *L. innocua* is discussed. However, in the present study the contrary was also demonstrated. A possible explanation could be 'quorum sensing' (QS), that is a regulation of gene expression in response to cell population density, in this case resulting in an inhibition of growth of a population of bacteria when a certain number are present, usually *ca.* 10^6 cfu/ml. QS occurs by recognition of a concentration of a 'quorum compound' in pure cultures and in mixed cultures of similar organisms (e.g. *E. coli* and *Salmonella* spp.), and a

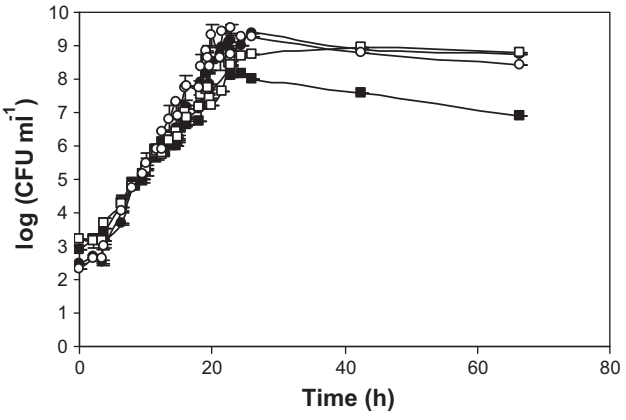

Fig. 1. Growth curves in TSB–YE of *L. monocytogenes_1340* with *L. innocua_11288*. Error bars indicate variability between assays (●-*L. innocua* in mixture; ○-control of *L. innocua*; ■-*L. monocytogenes* in mixture; □-control of *L. monocytogenes*).

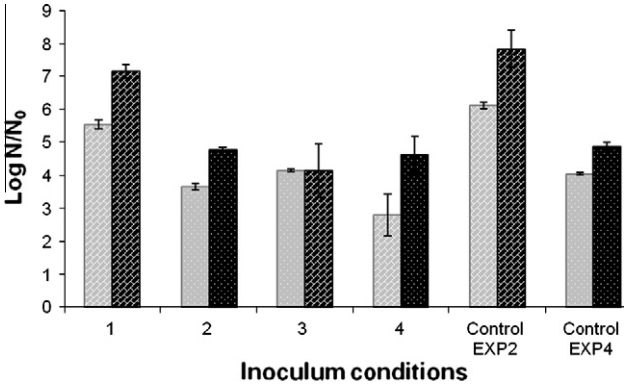

Fig. 2. Monitoring the number of viable cells in pasteurized milk: combination of all six strains of *L. monocytogenes* with *L innocua_2030c*. *L. monocytogenes* (10^2 cfu/ml); *L. monocytogenes* (10^4 cfu/ml); *L. innocua* (10^2 cfu/ml); *L. innocua* (10^4 cfu/ml).

similar phenomenon (QS cross-talk) may be occurring in mixed cultures of *Listeria* spp., although probably by a different type of quorum compound (<http://www.nottingham.ac.uk/quorum>/; accessed 15/04/09).

Nevertheless, it would also be important to evaluate the growth of each strain of *L. monocytogenes* in the presence of *L. innocua_2030c* to improve knowledge of this inhibitory effect.

L. monocytogenes_1339 with L. innocua_11288. In all the cases (mixture 2), no significant differences in the cell number of *L. innocua_11288* was observed when *L. monocytogenes_1339* was present ($P > 0.05$; Fig. 3). Except in the condition 5 (10^4 *L. monocytogenes*:10^2 *L. innocua*), *L. monocytogenes_1339* was significantly inhibited in the presence of *L. innocua* ($P < 0.05$; Fig. 3). The higher reduction rate (5.69 log) was shown when the initial concentrations of *L. innocua_11288* and *L. monocytogenes_1339* were 10^4 cfu/ml and 10^2 cfu/ml respectively (condition 3), Thereby, the inhibition of *L. monocytogenes_1339* was dependent on the initial concentration of *L. innocua_11288*.

L. monocytogenes_1340 with L. innocua_11288. The significant inhibition of *L. monocytogenes_1340* in the presence of *L. innocua_11288* was only observed when its initial concentration was lower than the initial concentration of *L. innocua_11288* (condition 4), with a final reduction of 5.01 log ($P < 0.05$; Fig. 4).

Again, no significant differences in the cell numbers of *L. innocua_11288* were observed when *L. monocytogenes_1340* was present ($P > 0.05$; Fig. 4).

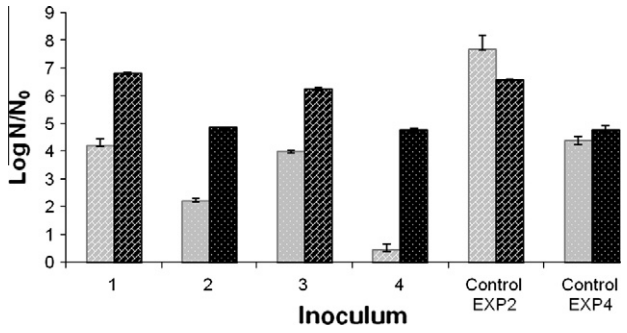

Fig. 3. Monitoring the number of viable cells in pasteurized milk: *L. monocytogenes_1339* with *L. innocua_11288*. *L. monocytogenes* (10^2 cfu/ml); *L. monocytogenes* (10^4 cfu/ml); *L. innocua* (10^2 cfu/ml); *L. innocua* (10^4 cfu/ml).

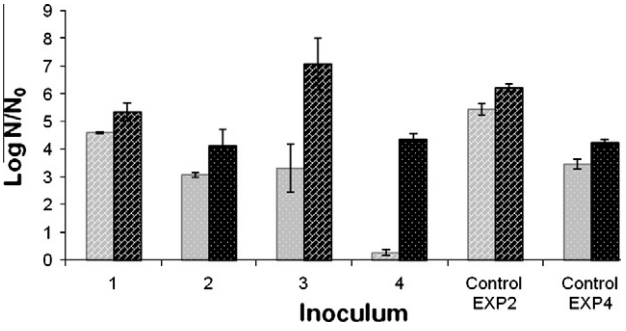

Fig. 4. Monitoring the number of viable cells in pasteurized milk: *L. monocytogenes_1340* with *L. innocua_11288*. *L. monocytogenes* (10^2 cfu/ml); *L. monocytogenes* (10^4 cfu/ml); *L. innocua* (10^2 cfu/ml); *L. innocua* (10^4 cfu/ml).

The inhibition of *L. monocytogenes* by *L. innocua* undergoing enrichment culture as well as in growth in TSB–YE, only occurred after 24 h because following this time microorganisms are in more hostile conditions and consequently cells become more sensitive and easily inhibited. However, in TSB–YE only *L. monocytogenes_1339* was inhibited by *L. innocua_11288*. This is a non-selective medium and consequently more favourable to growth than a selective medium.

Besse et al. (2005) concluded that 24 h of incubation in Fraser broth was sufficient to attain the maximum population level in contrast to the current practice of 48 h and this suggested that Fraser enrichment can be reduced by 24 h in order to decrease the effected inhibition by *L. innocua* of some strains of *L. monocytogenes*. In fact, some of our results show a significant reduction in viable numbers of *L. monocytogenes* after 24 h of growth in Fraser broth in the presence of *L. innocua,* which could result in difficulties in detecting the presence of the pathogen. However, when levels of contamination are lower than the tested concentrations, 24 h in Fraser enrichment might not be long enough to reach the maximum population level which could lead to a false negative result for *L. monocytogenes* presence, since enrichment favours the non-pathogenic *L. innocua*. Therefore, it would be important to evaluate lower levels of contamination to improve knowledge about this possibility.

Detection of inhibitory activity produced by Listeria strains

Many authors (Besse et al., 2005; Kalmokoff, Daley, Austin, & Farber, 1999; Yokoyama et al., 2005) demonstrated that *Listeria* species may produce inhibitory compounds such as bacteriocins that are active against other *Listeria* isolates. However in this study no inhibitory activity of *L. innocua* against *L. monocytogenes* or *L. monocytogenes* against *L. innocua* was observed in the spot-on-lawn assays. These results can be explained because the majority of inhibitors represent defective bacteriophage particles. Therefore, production of bacteriocins was not the factor that explains the inhibition.

Conclusion

A relatively few mixtures of strains were tested, but it was enough to conclude that there was a high heterogeneity in the strains' behaviours. Overall, the inhibition of *L. monocytogenes* by *L. innocua* was always observed when the first one was initially present in lower concentration numbers. However it was also possible to observe the inhibition of *L. innocua* when a cocktail of *L. monocytogenes* was present in higher inoculum concentration. A possible explanation for this could be the phenomenon of quorum sensing. Growth inhibition by quorum sensing molecules has been

reported for several organisms (<http://www.nottingham.ac.uk/quorum>/; accessed 15/04/09).

The inhibition of *L. monocytogenes* by *L. innocua* is frequently related to the decrease in the growth rate of the strain inhibited or to the inhibitory activity caused by bacteriocins. In this study, however, these possible causes were not verified. Other explanations previously described, such as production of bacteriophages (Cornu et al., 2002; Kalmokoff et al., 1999), defective bacteriophage particles (Curtis & Mitchell, 1992; Zink et al., 1995), or possession of a prophage (rendering the 'infected' strain 'immune' to a lytic phage), or a higher degree of fitness of one strain (Curiale & Lewus, 1994; Beumer et al., 1996), were not investigated but could explain the results obtained.

Further experiments with a much broader number of isolates are required to better characterize these interactions, and also to determine the causes of inhibition of some strains by others.

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