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Inhibition of *Listeria monocytogenes* using biofilms of non-pathogenic soil bacteria (*Streptomyces* spp.) on stainless steel under desiccated condition

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ABSTRACT

Of the 1648 microbial isolates from 133 soil samples collected from 30 diverse locations in the Republic of Korea, two isolates exhibited strong antilisterial activity and ability to grow to high populations (> 8.0 log CFU/ml) in Bennett's broth. Isolates were identified as *Streptomyces lactacystinicus* (strain Samnamu 5–15) and *Streptomyces purpureus* (strain Chamnamu-sup 4–15). Both isolates formed biofilms on the surface of stainless steel coupons (SSCs) immersed in Bennett's broth within 24 h at 25 °C. Cells retained antilisterial activity after biofilm formation and showed significantly ($P \leq 0.05$) enhanced resistance against dry conditions (43% relative humidity [RH]) compared to the cells not in biofilm. An initial population (ca. 3.2 log CFU/cm^2) of *Listeria monocytogenes* inoculated on SSCs lacking *Streptomyces* biofilm decreased to 1.4 log CFU/cm^2 within 48 h at 25 °C and 43% RH. In contrast, *L. monocytogenes* (3.3 log CFU/cm^2) inoculated on SSCs containing *Streptomyces* biofilm decreased to populations below the theoretical detection limit (0.5 log CFU/cm^2) within 24 h. The results indicate that biofilms formed by the *Streptomyces* spp. inhibitory to *L. monocytogenes* showed enhanced resistance to desiccation condition (43% RH) and effectively inhibited the growth of *L. monocytogenes* on the surfaces of SSCs. Antilisterial biofilms developed in this study may be applicable on desiccated environmental surfaces in food related environments such as food storage, handling, and processing facilities to enhance the microbiological safety of foods.

1. Introduction

Listeria monocytogenes is a gram-positive rod-shaped bacterium known to cause foodborne disease (Buchanan et al., 2017; Swaminathan and Gerner-Smidt, 2007). Globally, it is estimated that *L. monocytogenes* is responsible for 23,150 illnesses and 5463 deaths annually (de Noordhout et al., 2014). Although less common than other foodborne illnesses, listeriosis is characterized by high mortality rates in high-risk groups such as the elderly, neonates, pregnant women, and immunocompromised populations, and may cause severe sequelae such as sepsis, meningitis, encephalitis, stillbirth, and abortion (de Noordhout et al., 2014).

L. monocytogenes is widespread in the environment and, due to its ubiquitous nature, the pathogen has been isolated not only from various foods but also from food production and processing environments (Leong et al., 2014). In recent years, raw vegetables and their production and processing environments have been increasingly recognized as sources of *L. monocytogenes* responsible for outbreaks of listeriosis (Zhu et al., 2017). It is estimated that approximately 5–9% of cultivated soils (Soni et al., 2014; Strawn et al., 2013) and 9.4% of environmental surfaces in vegetable processing facilities, including storage shelves, cutting areas, drains, and walls have been reported to be contaminated by *L. monocytogenes* (Leong et al., 2014). Thus, effective methods are needed to inactivate *L. monocytogenes* on environmental surfaces in food handling and processing facilities, thereby enhancing the microbiological safety of the foods produced in these environments.

Biofilms are defined as microbial cells enclosed in matrices that are adherent to each other and/or to surfaces (Costerton et al., 1995). The majorities of bacterial cells tend to live on surfaces rather than to grow planktonically (Cappitelli et al., 2014). One of the major advantage of biofilm formation for microorganisms is that the resistance of the cells to various environmental stresses and antimicrobial agents can be dramatically increased (Jefferson, 2004). Recently, bacterial biofilms have been used beneficially in some industries. For examples, biofilm formation by some fermentative bacteria have been used to biodegrade toxic compounds in wastewater or to produce beneficial by-products

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such as ethanol and organic acids (Ercan and Dermirci, 2015). In food industry, biofilms of lactic acid bacteria (LAB) inhibitory to foodborne pathogens have been investigated (Gómez et al., 2016). However, studies attempting to enhance the survival and persistence of bacteria inhibitory to foodborne pathogens by inducing biofilm formation on abiotic surfaces have received less research attention.

The objective of the study presented here was to develop non-pathogenic, desiccation-resistant, and antilisterial biofilms of *Streptomyces* spp. on stainless steel surfaces. To achieve this goal, we isolated and identified bacteria exhibiting strong antilisterial activities and ability to grow to high populations in a laboratory medium. We examined their biofilm-forming abilities on stainless steel surfaces, evaluated desiccation-resistance of cells in biofilms, and confirmed the antilisterial activities of the biofilms.

2. Materials and methods

2.1. L. monocytogenes strains and preparation of inoculum

Five strains of *L. monocytogenes* (KCTC 3569 [serotype 1/2a, isolated from poultry], Scott A [serotype 4b, isolated from a patient in a milk-associated outbreak], 12443 [serotype 1/2a, monkey clinical isolate], 101M [serotype 4b, isolated from beef and pork sausage], and G1091 [serotype 4b, isolated from a patient in a coleslaw-associated outbreak]) were used. Cryopreserved *L. monocytogenes* cells were activated in tryptic soy broth (TSB; BBL/Difco, Sparks, MD, USA) at 37 °C for 24 h. After three consecutive transfers of each strain in TSB at 24-h intervals, 10 ml of a five-strain cocktail was prepared by combining 2 ml of each culture. The *L. monocytogenes* cocktail was centrifuged at 2000 × *g* for 15 min at room temperature (22 ± 2 °C) and the pelleted cells were resuspended in sterile 0.1% peptone water (PW) or TSB, depending on the experiment to be performed. The cells were washed again, and the suspensions were serially diluted in 0.1% PW or TSB to prepare two concentrations (ca. 7 and 5 log CFU/ml) of *L. monocytogenes* inocula.

2.2. Isolation and identification of bacteria inhibitory to L. monocytogenes

Bacteria tested for antilisterial activity were isolated from soil following the procedures described by Kim et al. (2011). Briefly, 133 soil samples (10 g each) collected from 30 diverse locations in the Republic of Korea were suspended in 100 ml of sterile distilled water (DW). The slurry (0.1 ml) of soil and water was spread-plated on humic acid vitamin agar (pH 7.2; humic acid 1.0 g, Na_2HPO_4 0.5 g, KCl 1.71 g, $MgSO_4{\cdot}7H_2O$ 0.05 g, $FeSO_4{\cdot}7H_2O$ 0.01 g, $CaCO_3$ 0.02 g, thiamin-HCl 0.5 mg, riboflavin 0.5 mg, niacin 0.5 mg, pyridoxine-HCl 0.5 mg, inositol 0.5 mg, calcium pantothenate 0.5 mg, *p*-aminobenzoic acid 0.5 mg, biotin 0.25 mg, cycloheximide 50 mg, and agar 15 g in 1 L of H_2O) and incubated at 28 °C for 3–14 days. After incubation, cells from selected colonies were streaked on Bennett's agar and incubated at 25 °C for 6 days. Cells from colonies were transferred to 50-ml conical tubes containing 10 ml of Bennett's broth and 5 g of sterile glass beads (1 mm, Glass beads 1; Glastechnique Mfg., Germany), followed by incubation at 25 °C for at least 3 days with shaking at 200 rpm before being used in experiments.

A double-layer assay (Kim et al., 2018; Zhao et al., 2004) was used to screen for soil isolates exhibiting a strong inhibitory activity against *L. monocytogenes*. Isolate suspensions (10 μl) prepared as described above were spot-inoculated (spot diameter ca. 7 mm) on tryptic soy agar (TSA; BBL/Difco) plates, followed by incubation at 25 °C for 24 h. Molten TSA (10 ml) containing *L. monocytogenes* (ca. 5 log CFU/ml) was poured onto the surface of spot-inoculated TSA, and the plates were incubated at 37 °C for up to 24 h. The antilisterial activity of isolates was evaluated by measuring diameters of zones of inhibition surrounding colonies formed by the test isolates.

Among the isolates possessing strong antilisterial activity, those with an ability to grow to high populations were selected for the further investigation. Isolates were inoculated in Bennett's broth and incubated for 0, 24, 48, 72, 96, or 120 h at 25 °C. Cultures were serially diluted in PW, and diluted suspensions (0.1 ml in duplicate) were surface-plated on Bennett's agar and incubated at 25 °C for 72 h before the colonies were counted.

The genus and species of two isolates with strong antilisterial activity (> 2.0-cm diameter of inhibition zone) and ability to grow to high populations (> 8.0 log CFU/ml) in Bennett's broth were identified using 16S rRNA sequence analysis (Macrogen, http://www.macrogen.co.kr, Seoul, Republic of Korea). The 16S rRNA gene sequences were analyzed using BLAST software available online at the National Center for Biotechnology Information (NCBI) website (http://www.ncbi.nlm.nih.gov/, USA). A neighbor-joining phylogenetic tree was constructed using distances corrected according to the Kimura two-parameter model with the Mega software version 5.05. Bootstrap values are expressed as percentages of 1000 replications.

2.3. Biofilm formation of antilisterial bacteria on SSCs

The two antilisterial isolates identified as described above were separately attached to the surface of stainless steel coupons (SSCs; Type 304, 5 × 2 cm, no. 4 finished) using procedures described by Kim et al. (2018) and induced to form biofilms. Briefly, suspensions of the two isolates were serially diluted in phosphate-buffered saline (PBS, pH 7.4) to a population of ca. 5 log CFU/ml and deposited in a sterile sprayer (50 ml, code 654447641; Iple, Incheon, Republic of Korea). Sterile SSCs were placed in polystyrene dishes (diameter 60 mm; height 8 mm), and 1 ml of the bacterial suspension was sprayed perpendicularly to the surface of the SSC at a distance of 5 cm. Cells were attached to the surface of SSCs by drying in a laminar flow biosafety hood at room temperature (22 ± 2 °C) for 1 h, and loosely attached cells on SSCs were removed by washing the SSCs in sterile DW. Bennett's broth (4 ml) was deposited on SSCs containing the attached cells, and the SSCs were incubated at 25 °C for 0, 24, 48, 72, 96, or 120 h. After incubation, SSCs were washed in sterile DW to remove poorly adhered cells and transferred to 50-ml conical tubes containing 3 g of glass beads (425–600 μm; Sigma-Aldrich, St. Louis, MO, USA) and 30 ml of Bennett's broth. The mixtures of SSCs, glass beads, and Bennett's broth were vortexed at maximum speed for 1 min, and the suspensions were serially diluted in PW. Undiluted (0.25 ml in quadruplicate and 0.1 ml in duplicate) and serially diluted (0.1 ml in duplicate) suspensions were surface-plated on Bennett's agar and the plates were incubated at 25 °C for 72 h before the colonies were counted. The theoretical detection limit for direct plating was ca. 0.5 log CFU/cm^2.

2.4. Survival of antilisterial bacteria in desiccated biofilms

To simulate typical desiccated conditions in some food production and processing environments, the atmosphere surrounding Petri dishes was adjusted to 43% relative humidity (RH) by exposure to a saturated potassium carbonate solution (a_w 0.430 ± 0.005; Daejung, Siheung, Republic of Korea) for at least 24 h at 25 °C before initiating experiments. Bacterial suspensions (ca. 9.0 log CFU/ml) of the two antilisterial isolates were used to induce high attachment level. Biofilms of antilisterial isolates on SSCs were prepared by following the procedure as described above (section 2.3.). SSCs with attached antilisterial bacteria or SSCs with antilisterial biofilms were then placed in the Petri dishes and sealed with Parafilm (Bemis, Neenah, WI, USA), followed by incubating at 25 °C and 43% RH for 0, 24, 48, 72, 96, or 120 h. After incubation, SSCs were transferred to 50-ml conical tubes containing 3 g of glass beads and 30 ml of Bennett's broth. The mixtures of SSCs, glass beads, and Bennett's broth were vortexed at maximum speed for 1 min, and the suspensions were serially diluted in PW. Undiluted (0.25 ml in quadruplicate and 0.1 ml in duplicate) and serially diluted (0.1 ml in duplicate) suspensions were surface-plated on Bennett's agar and

incubated at 25 °C for 72 h before the colonies were counted. The remaining mixtures of SSCs, glass beads, and Bennett's broth were incubated at 25 °C for 72 h for enrichment. When no colonies of antagonistic bacteria were formed on Bennett's agar, the enriched suspensions were streaked on Bennett's agar followed by incubation at 25 °C for 72 h to determine their presence or absence. The theoretical detection limits for direct plating and enrichment were ca. 0.5 and −1.0 log CFU/cm^2, respectively.

2.5. Antilisterial activity of antagonistic bacterial biofilms on SSCs

The antilisterial activity of biofilms formed by *Streptomyces lactacystinicus* or *Streptomyces purpureus* biofilms formed on SSCs was determined. *L. monocytogenes* suspensions (100 μl; 5 log CFU/ml) were inoculated (18 ± 2 spots) on the surface of sterile SSCs (control) or SSCs containing *Streptomyces* spp. biofilms. The spot-inoculated SSCs were placed in a Petri dish with internal atmosphere adjusted to 43% RH as described above, sealed with Parafilm, and incubated at 25 °C for 0, 3, 6, 12, 24, or 48 h. After incubation, the SSCs were transferred to 50-ml conical tubes containing 3 g of glass beads and 30 ml of TSB, and the mixtures were vortexed at maximum speed for 1 min. The suspension was serially diluted in PW and surface-plated on Oxford agar (Oxoid Ltd, Wade Road, Hants, UK). Plates were incubated at 37 °C for 24 h before *L. monocytogenes* colonies (black colonies with black halos) were counted. The remaining mixtures of SSCs, glass beads, and TSB were incubated at 37 °C for 24 h for enrichment. If no presumptive *L. monocytogenes* colonies were formed on Oxford agar plates, enriched suspensions were streaked on Oxford agar and incubated at 37 °C for 24 h to determine the presence or absence of *L. monocytogenes*. The theoretical detection limits for direct plating and enrichment were 0.5 and −1.0 log CFU/cm^2, respectively.

2.6. Statistical analysis

All experiments were performed at least three times and data were analyzed using a general linear model with Statistical Analysis System software (SAS 9.3; SAS Institute, Cary, NC, USA). The ability of antilisterial bacteria to form biofilms on the surface of SSCs, the desiccation resistance of cells attached to and in biofilms on SSCs, and the antilisterial effects of SSCs with and without biofilms of antilisterial bacteria were analyzed by SAS proc *t*-test or analysis of variance (ANOVA) with Fisher's least significant difference (LSD) test ($P \leq 0.05$).

3. Results and discussion

3.1. Isolation and identification of bacteria inhibitory to L. monocytogenes

In total, 1648 microorganisms were isolated from 133 soil samples. Among them, 117 isolates showed antagonistic activity against *L. monocytogenes*; 14 isolates showed strong antilisterial activity (diameter of inhibition zone ≥ 2.0-cm) (Supplementary Fig. 1). When 14 isolates with strong antilisterial activity were cultured in Bennett's broth at 25 °C for up to 120 h, populations of two isolates designated as Samnamu 5–15 and Chamnamu-sup 4–15 reached ≥8.1 log CFU/ml, while populations of the other isolates reached ≤6.5 log CFU/ml (data not shown). Based on these results, two isolates (Samnamu 5–15 and Chamnamu-sup 4–15) exhibiting both strong antilisterial activity and the ability to grow to high populations in Bennett's broth were selected for the further investigation.

The Samnamu 5–15 and Chamnamu-sup 4–15 isolates were identified as *Streptomyces* spp. using 16S rRNA sequence analysis and BLAST software provided by the NCBI. By constructing a neighbor-joining phylogenetic tree, these isolates were designated as *St. lactacystinicus* strain Samnamu 5–15 and *St. purpureus* strain Chamnamu-sup 4–15 (Supplementary Fig. 2). *Streptomyces* is one of the largest antibiotic-producing bacterial genera and is known to be abundant in terrestrial environments (Také et al., 2015; Isnaeni et al., 2017). It has been reported that *St. lactacystinicus* and *St. purpureus* are capable of producing lactacystin and viomycin, respectively, as secondary antibiotic metabolites (Také et al., 2015; Waksman, 1959). Although antimicrobial activity of *St. purpureus* against methicillin-resistant *S. aureus* has been described (Isnaeni et al., 2017), the antilisterial activities of *St. lactacystinicus* or *St. purpureus* grown in biofilms on abiotic surfaces have not been reported.

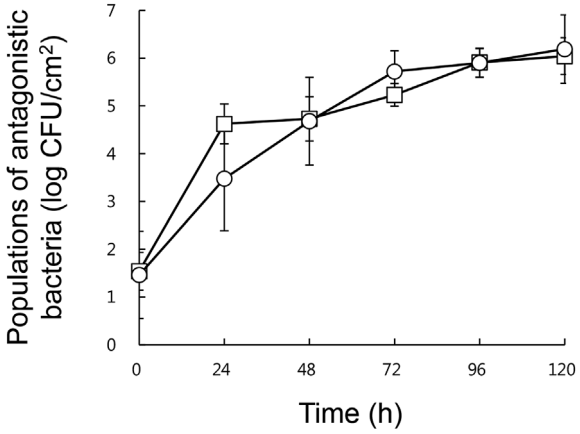

Fig. 1. Biofilm maturation curves of *Streptomyces lactacystinicus* strain Samnamu 5–15 (○) and *Streptomyces purpureus* strain Chamnamu-sup 4–15 (□) on SSCs. Cells were attached to SSCs at 25 °C for 1 h, and the SSCs with attached cells were immersed in Bennett's broth at 25 °C for 120 h. Bars indicate the mean ± standard deviation (SD) of multiple replicates.

3.2. Biofilm formation of antilisterial bacteria on SSCs

Fig. 1 shows biofilm maturation curves for *St. lactacystinicus* strain Samnamu 5–15 and *St. purpureus* strain Chamnamu-sup 4–15 on SSCs immersed in Bennett's broth at 25 °C for up to 120 h. Populations of the two antilisterial bacteria attached to the surface of SSCs (ca. 1.5 log CFU/cm^2) increased significantly ($P \leq 0.05$) to 3.5–4.6 log CFU/cm^2 within 24 h and 6.0–6.2 log CFU/cm^2 within 120 h. This shows that both bacteria can form biofilms on the surface of SSCs. The biofilm-forming abilities of other *Streptomyces* spp. on stainless steel surfaces have been described by others. Cherif-Antar et al. (2016) described the biofilm-forming ability of *Streptomyces* spp. on the surface of stainless steel pipes in a milk-processing diary plant. Son et al. (2016) demonstrated the ability of *Streptomyces spororaveus* to form biofilm on stainless steel surfaces, and more recently, Kim et al. (2018) described conditions resulting in biofilm formation by *Streptomyces cirratus* on SSCs. However, this is the first report describing biofilm-forming abilities of *St. lactacystinicus* and *St. purpureus* on stainless steel.

3.3. Survival of antilisterial bacteria in desiccated biofilms

Fig. 2 shows the survival of *St. lactacystinicus* strain Samnamu 5–15 and *St. purpureus* strain Chamnamu-sup 4–15 attached to and in biofilms on SSCs exposed to 43% RH at 25 °C for up to 120 h. The number of culturable cells of *St. lactacystinicus* strain Samnamu 5–15 and *St. purpureus* strain Chamnamu-sup 4–15 attached to SSCs (ca. 5.9 log CFU/cm^2) decreased to populations below the theoretical detection limit (0.5 log CFU/cm^2) within 24–48 h, and culturable cells were not detected after 96–120 h. In contrast, *St. lactacystinicus* strain Samnamu 5–15 and *St. purpureus* strain Chamnamu-sup 4–15 cells in biofilms decreased to ca. 4.4 and 2.5 log CFU/cm^2, respectively, after 120 h of exposure to 43% RH. This indicates that resistance of the antilisterial bacteria to inactivation by desiccation increased significantly ($P \leq 0.05$) as a result of biofilm formation. The enhanced desiccation resistance of *Streptomyces* spp. by forming biofilms has been reported by

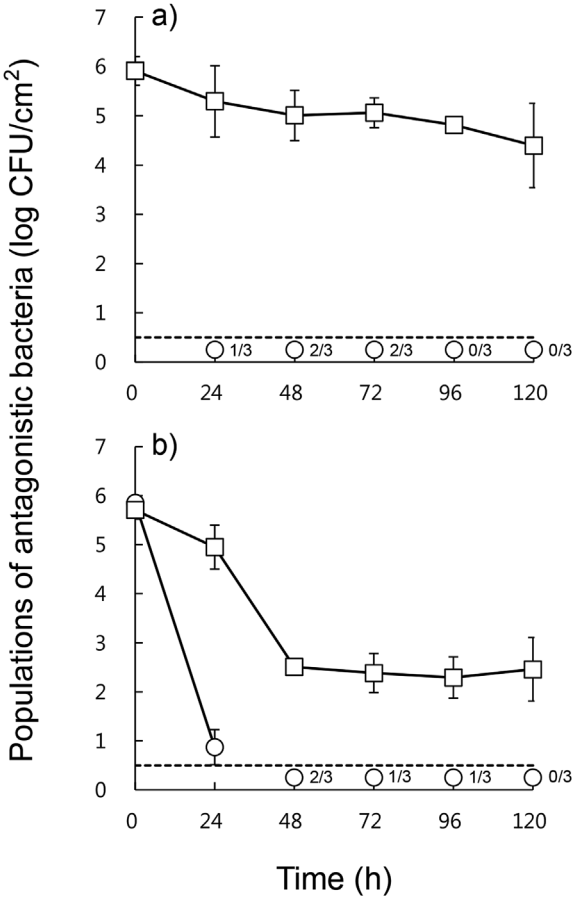

Fig. 2. Survival of (a) *Streptomyces lactacystinicus* strain Samnamu 5–15 and (b) *Streptomyces purpureus* strain Chamnamu-sup 4–15 attached to SSCs (○) and in biofilms on SSCs (□) under a desiccation condition (43% RH) at 25 °C for 5 days. The detection limits by direct plating (dashed line) and enrichment were 0.5 and −1.0 log CFU/cm^2, respectively. Bars indicate the mean ± SD of multiple replicates. Values shown below the detection limit by direct plating indicate the number of enriched SSCs positive for attached cells out of the number of SSCs analyzed.

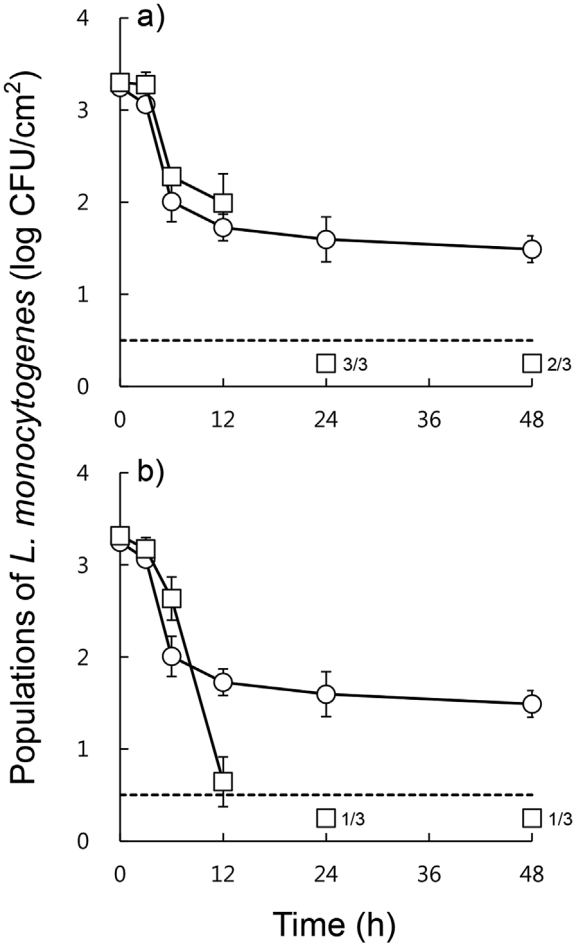

Fig. 3. Changes in populations of *Listeria monocytogenes* on SSCs without (○) or with (□) biofilms of (a) *Streptomyces lactacystinicus* strain Samnamu 5–15 and (b) *Streptomyces purpureus* strain Chamnamu-sup 4–15 at 25 °C and 43% RH for 48 h. The detection limits by direct plating (dashed line) and enrichment were 0.5 and −1.0 log CFU/cm^2, respectively. Bars indicate the mean ± SD of multiple replicates. Values shown below the detection limit by direct plating indicate the number of enriched SSCs positive for *L. monocytogenes* out of the number of SSCs analyzed.

several researchers. Son et al. (2016) reported that the resistance of *St. sporoaveus* cells in biofilms exposed to 43% RH was significantly ($P \leq 0.05$) higher than that of cells attached to SSCs. Similarly, Kim et al. (2018) reported that *St. cirratus* cells in biofilms exposed to 43% RH showed significantly ($P \leq 0.05$) higher resistance than did attached cells. However, this study is the first to demonstrate the retention of viability of *St. lactacystinicus* and *St. purpureus* in desiccated biofilms.

3.4. Antilisterial activity of antagonistic bacterial biofilms on SSCs

Fig. 3 shows changes in populations of *L. monocytogenes* inoculated on the surface of SSCs, with or without antilisterial *Streptomyces* biofilms, during incubation at 25 °C and 43% RH for 0, 3, 6, 12, 24, or 48 h. In this study, we used *L. monocytogenes* cocktail culture (5 strains) to avoid strain-dependent results, and the interactions between *L. monocytogenes* strains in the cocktail culture were not considered. The initial number of *L. monocytogenes* (ca. 3.2 log CFU/cm^2) inoculated on the SSCs without biofilms (control) decreased to ca. 1.5 log CFU/cm^2 within 48 h, while the number of *L. monocytogenes* (ca. 3.3 log CFU/cm^2) inoculated on SSCs containing *St. lactacystinicus* or *St. purpureus* biofilms decreased to below the theoretical detection limit (0.5 log CFU/cm^2) within 24 h. This indicates that antilisterial activity of the two *Streptomyces* spp. persists in biofilms.

Antilisterial biofilms of *Streptomyces* spp. isolated from soil have not been described before. However, research describing inhibition of growth of *L. monocytogenes* on abiotic surfaces which contain biofilms of LAB has been reported. Guerrieri et al. (2009) inhibited the growth of planktonic and adherent cells of *L. monocytogenes* using *Lactobacillus plantarum*, *Enterococcus casseliflavus*, and *Enterococcus faecalis* biofilms formed on the surfaces of 12-well microtiter plates. They observed that antimicrobial activity of LAB biofilms persisted for extended periods as a result of continuous metabolism of the cells. Similarly, Turhan et al. (2017) reported that the number of planktonic and adherent cells of *L. monocytogenes* inoculated on the surface of 12-well microtiter plates containing *Lactobacillus casei* and *Lactobacillus rhamnosus* biofilms decreased within 24 h. They concluded that the number of LAB in biofilms was influenced by the concentration of ingredients in culture media, and that antilisterial activity of biofilms varied among different strains of LAB in the biofilm. However, to our knowledge, this is the first study to demonstrate and quantify antilisterial activities in desiccated biofilms of antagonistic *Streptomyces* spp.

In the present study, the antilisterial biofilm was developed to apply for the surfaces which are not in direct contact with foods such as surfaces in storage rooms, floors, transportation vehicles, etc. to minimize the adverse effects of antagonistic bacteria on foods. However, in future studies, the possibilities of *Streptomyces* cells to sporulate in biofilms, and the influence of the vegetative and/or sporulated

Streptomyces cells on foods should be further determined. In addition, possibilities of emergence of *L. monocytogenes* resistant to *Streptomyces* spp., and their interactions with antagonistic biofilms should be investigated. Since the antilisterial activities of biofilms would be affected by the structure and components of biofilm, the microscopic observation for the biofilm structure should be conducted and the distribution and composition of microorganisms (including viable but non-culturable cells) should be studied. Finally, the influence of different environmental conditions such as high relative humidity (wet-condition), incubation time, and temperature on the antilisterial activities of the biofilms, and the mechanisms of antilisterial activities of *Streptomyces* spp. should be elucidated.

Acknowledgments

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fm.2018.11.007.

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