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Research Article

Changes in antibiotic susceptibility of *Salmonella* Typhimurium and *Listeria monocytogenes* under conditions of biofilm formation and freezing stress in meat juice model

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Abstract

The aim of this study was to investigate the changes in antibiotic susceptibility /resistance of bacteria isolated from biofilms in the presence of freezing stress in different meat juices (beef, mutton and goat). Gram-positive and Gram-negative bacteria of food origin (*Listeria monocytogenes* and *Salmonella enterica* ser. Typhimurium) were selected. Meat juice model was selected as a nutritious and complex environment containing a wide range of different compounds. Biofilms were studied in 96-well microplates and disk diffusion method was used to measure the antibiotic susceptibility. The results showed that the bacteria isolated from biofilms in meat juice models and freezing conditions exhibited significant changes in their antibiotic susceptibility. Long-term freezing (3 weeks and 1 month) significantly increased the antibiotic resistance. Both bacteria became resistant to chloramphenicol. The results indicated that foods should not be subjected to long-term freezing conditions so that existing pathogens do not acquire the ability to resist antibiotics.

Keywords: Antibiotic resistance, Food processing, Meat, Zoonoses.

Introduction

Food-borne pathogens are the leading causes of human illness and death in the world (Di Stasi et al., 2025). Most microbial pathogens are zoonotic in nature, and healthy food animals are reservoirs of many foodborne pathogens. In humans, the consumption of foods of animal origin is a major source of exposure to food-borne pathogens. Thus, people are at risk of being infected with pathogens from repository animals through the food chain (Abebe et al., 2023). Foodborne bacterial outbreaks, particularly those involving *Salmonella* spp. and *Listeria monocytogenes*, are related to poor hygiene of food contact surfaces, equipment, and processing settings (Fliss et al., 2025). In the presence of moisture, improperly maintained surfaces promote soil accumulation, leading to the growth of bacterial biofilms that may contain dangerous pathogens. Cross-contamination occurs when food comes into contact with contaminated surfaces or contaminated airborne particles or surface condensation. The type of food, contact surface, and topography play a major role in the failure to clean a surface (Kaboudari and Aliakbarlu, 2025; Sauer et al., 2022). *Listeria* spp. and other foodborne pathogens may be present in the food processing area as biofilm, and they are primarily resistant to disinfectants. Foodborne bacteria on food matrices or industrial equipment

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may develop bacterial biofilms and can lead to human infection. Toxins produced by microbial flora in food processing facilities can contaminate food products leading to disease outbreaks. Such bacteria are mainly observed in dairy farms and beverage processing facilities (Kostoglou et al., 2025; Bombelli et al., 2025).

Biofilms represent a complex microbial ecosystem dependent on multiple factors. Biofilm matrix protects the resident microflora from external environmental stresses (Manafi et al., 2020). The survival of bacteria in different food environments is a prominent factor associated with meat spoilage. Biofilms are matrices containing multiple microorganisms in a microenvironment that adhere strongly to a surface (Sutton et al., 2025). Biofilms contribute to physicochemical tolerance and show high resistance to disinfection and cleaning techniques. In addition, different bacteria may be present in a mixed species biofilm. This increases the structure, activity and tolerance of the biofilm. Consequently, the removal or inactivation of biofilms produced by foodborne pathogens in industrial environments is challenging. This challenge is further complicated by the requirement to maintain the taste, texture, and quality of red meat during the treatment process (Kaboudari and Aliakbarlu, 2025; Manafi et al., 2023).

Most foodborne pathogens cause various food safety problems to human health by forming biofilms. Food shortages have been a major challenge since the 21st century. Foods are not only threatened by pests, but also by pathogens, including bacteria and fungi. Eradication of these pathogenic microbes is difficult due to the protection provided by their biofilms. Furthermore, pathogenic biofilms pose challenges in clinical treatment due to their antibiotic resistance. Antibiotics can easily eliminate symptoms caused by pathogenic microbes, but they cannot do so as easily for the non-motile cells embedded in biofilms. Furthermore, bacterial contamination affects the production of meat and dairy products through lipolysis by heat-resistant enzymes secreted in biofilms (Flint et al., 2020; Alvarez- Ordóñez et al., 2019). During food processing stages, foodborne bacteria may encounter a variety of conditions that may cause chemical or physical stresses. When bacteria are exposed to mild forms of these stresses, opportunity is provided for them to improve their ability to adapt and become resistant to subsequent more extreme exposures through physiological adjustment, enabling reproduction. Furthermore, the adaptive responses to these stresses may enhance resistance to others such as exposure to antibiotics and lead to what is termed “cross-protection” (Al-Nabulsi et al., 2015).

Biofilm formation has been thoroughly investigated in various studies, but the molecular mechanisms, environmental influences, genotypic and phenotypic characteristics of microorganisms, cellular differentiation, and environmental response have not been clearly explained. However, there is still a long way to go in the field of biofilm from the laboratory to the industry. Considering the conducted studies (Kaboudari and Mehdizadeh, 2025; Li et al., 2022; Giacometti et al., 2021; Woode et al., 2020; Li et al., 2014) and the importance of finding a relationship between changes in antibiotic sensitivity/resistance and the ability to form biofilms in foodborne pathogens, in this study, the effect of biofilm formation under freezing stress conditions in meat juice environments was investigated. The aim of this study was to determine whether the presence of bacteria in enriched environments, together with freezing stress and subsequent biofilm formation, has an effect on antibiotic susceptibility of the selected bacteria.

Materials and Methods

Bacterial strains

L. monocytogenes ATCC19115 and *Salmonella enterica* ser. Typhimurium ATCC14028 were purchased from the microbial collection of the Iranian Research Organization for Science and Technology (Tehran, Iran). The bacteria were cultured twice in tryptic soy broth (TSB) medium (Quelab, Canada) and incubated at 37 °C for 24 h.

Preparing of meat juices

A frozen-thaw method was used to prepare the meat juices. The fresh meat (beef, mutton, and goat) was purchased from local market in Urmia, West Azarbaijan province, Iran. The meat samples were transferred to the food microbiology laboratory under refrigerated conditions after purchasing. Next, the meat samples were chopped (1.5 × 1.5 × 1.5 cm) by a cutter and frozen in a -20 °C freezer. After that, the frozen samples were thawed at 4 °C for 24 h, and the exudates were collected and centrifuged (3,000 rpm for 10 min) to remove the large particles. The supernatants were sterilized using a 0.22 μm filters, and then stored at -80 °C. Before each experiment, the frozen meat juice samples were thawed overnight at 4 °C (Li et al., 2022).

Exposure to stresses and forming biofilm

L. monocytogenes and *S.* Typhimurium were inoculated in different meat juice model types (beef, mutton, goat juices), and then stored at -20 °C for 30 days. To do this, the overnight bacterial culture was centrifuged (4000 rpm for 10 min), and the bacterial pellet was washed twice with phosphate buffer saline (PBS, pH 7.4). Then, the pellet was re-suspended in the buffer, and the bacterial concentration was adjusted to 1×10^8 CFU/mL using a spectrophotometer (Novaspec II; Pharmacia LKB, Uppsala, Sweden). Meat juice samples (beef, mutton, and goat juices) were poured into capped tubes, then, the bacteria (1×10^8 CFU/mL) were added to each tube. After that, the tubes were stored at -20 °C for 30 days. In parallel, the control group (TSB media inoculated with the bacteria without any juices) was also prepared. At each sampling day (2, 3, 4, 7, 14, 21 and 30), the frozen samples were thawed overnight at 4 °C, and used for forming biofilm (in polystyrene surface) for 48 h (Kaboudari et al., 2024a).

Table 1. Changes in antibiotic susceptibility (diameter of the inhibition zone ± standard deviation) of *Salmonella enterica* sub. Typhimurium biofilm formed after exposer to freezing conditions in meat juice models.

	AM			GM			C		
Days	**Beef**	**Mutton**	**Goat**	**Beef**	**Mutton**	**Goat**	**Beef**	**Mutton**	**Goat**
2	24.96±0.00^{d}	22.13±0.07^{e}	17.19±0.9^{c}	18.51±0.008^{ab}	18.27±0.9^{a}	20.76±0.8^{e}	R	R	18.26±0.00^{b}
3	19.05±0.00^{b}	18.97±0.0^{d}	R	19.66±0.9^{bc}	19.67±0.00^{bc}	18.19±0.8^{c}	R	R	20.95±0.05^{c}
4	22.65±0.81^{c}	14.3±0.07^{c}	I	18.81±0.00^{ab}	22.35±0.00^{c}	20.15±0.00^{de}	R	R	26.23±0.05^{f}
7	28.67±0.00^{d}	10.68±0.00^{b}	R	20.68±0.00^{cd}	20.51±0.00^{b}	13.84±0.03^{a}	R	R	26.69±0.00^{f}
14	26.98±0.8^{de}	20.01±0.9^{d}	R	21.83±0.00^{d}	19.38±0.00^{ab}	18.37±0.00^{c}	R	R	25.7±0.2e^{f}
21	27.91±0.00^{e}	27.31±0.00^{f}	R	19.62±0.01^{bc}	21.92±0.00^{c}	18.88±0.00^{cd}	R	R	25.18±0.8^{e}
30	17.87±0.00^{b}	19.93±0.8^{d}	R	17.73±0.00^{a}	18.05±0.00^{a}	16.21±0.00^{b}	R	R	R^{a}
Control	R	R	R	20.38±1.07^{cd}	19.71±0.16^{ab}	23.2±0.9^{f}	16±0.1	28.51±0.81	23.7±0.9^{d}

Different lowercase letters indicate significance ($p<0.05$) in each column. AM: Ampicillin, GM: Gentamicin, C: Chloramphenicol. R: resistant (C: <12; AM: <13; GM: <12), I: intermediate resistant (C: 13-17; AM: 14-16; GM: 13-14).

Evaluation of susceptibility to antibiotics

After 48 h of biofilm formation, bacteria in the biofilm phase (attached to the surface) were isolated using sonication at 40 kHz for 2 min (Sonica, England), and then their susceptibility to three broad-spectrum antibiotics (chloramphenicol (C), gentamycin (GM), and ampicillin (AM); Padtan-Teb, Tehran, Iran) was examined using the disk diffusion method (Kaboudari et al., 2024b). The results were analyzed according to the CLSI manual (CLSI, 2020).

Statistical analysis

Statistical analysis was performed with one-way analysis of variance (ANOVA) followed by post hoc Tukey test using SPSS software (IBM, SPSS Inc., USA, version 27). The significance limit was considered to be 0.05 ($p < 0.05$). All tests were performed in three replications.

Results and Discussion

The results of changes in antibiotic susceptibility and the development of resistance in *S.* Typhimurium and *L. monocytogenes* are shown in **Tables 1** and **2**, respectively. Based on the results, the antibiotic resistance in the three models of meat juice types and different freezing time conditions showed significant decreasing and increasing changes that were significant differences between the two bacteria as well as freezing times and most importantly, between the three types of juice.

The control groups of *S.* Typhimurium and *L. monocytogenes* were sensitive to chloramphenicol, which caused bacterial resistance when freezing meat juice model (at all times). Gentamicin showed the least changes (increasing/decreasing) against the freezing conditions of the meat juice model. As the duration of freezing stress increased, the antibiotic susceptibility of the bacteria decreased. Also, among the three antibiotics, the highest resistance was found in the case of chloramphenicol, which could be very important in the spread of the antibiotic resistance.

Table 2. Changes in antibiotic susceptibility (diameter of the inhibition zone ± standard deviation) of *Listeria monocytogenes* biofilm formed after exposure to freezing conditions in meat juice models.

	AM			GM			C		
Days	**Beef**	**Mutton**	**Goat**	**Beef**	**Mutton**	**Goat**	**Beef**	**Mutton**	**Goat**
2	23.82±0.00^{cd}	24.97±0.00^{f}	I	20.53±0.008^{bc}	20.97±0.81^{b}	21.01±0.00^{bc}	R	R	19.51±0.8^{b}
3	21.91±0.00^{c}	20.61±0.01^{c}	I	23.05±0.00^{d}	23.73±0.00^{c}	21.75±0.00^{c}	R	R	18.86±0.00^{b}
4	20.63±0.00^{c}	18.7±0.08^{a}	R	23.13±0.00^{d}	21.97±0.00^{b}	18.53±0.8^{a}	R	R	24.57±0.00^{c}
7	24.78±0.00^{d}	27.59±0.00^{g}	R	21.98±0.00^{c}	25.93±0.00^{d}	23.89±0.00^{d}	R	R	26.74±0.00^{d}
14	20.32±0.00^{c}	23.15±0.09^{e}	R	21.71±0.00^{c}	21.66±0.00^{b}	19.72±0.6^{ab}	R	R	26.4±0.09^{d}
21	22.9±0.00^{c}	28.39±0.08^{h}	R	21.49±0.00^{c}	21.82±0.00^{b}	18.9±0.8^{a}	R	R	18.33±0.00^{b}
30	16.42±0.00^{b}	22.41±0.00^{d}	R	17.15±0.00^{a}	20.68±0.00^{b}	18.42±0.00^{a}	R	R	R
Control	R	20.45±0.09^{b}	R	19.42±0.00^{b}	20.11±0.00^{a}	19.18±0.00^{ab}	R	28.51±0.81	25.48±0.00^{cd}

Different lowercase letters indicate significance ($p<0.05$) in each column. AM: Ampicillin, GM: Gentamicin, C: Chloramphenicol. R: resistant (C: <12; AM: <13; GM: <12), I: intermediate resistant (C: 13-17; AM: 14-16; GM: 13-14).

In the case of *Salmonella* spp., livestock and poultry are the most common reservoirs of disease outbreaks. During meat processing, *Salmonella* spp. can be transmitted to the environment and final meat products through cross-contamination. Humans may be infected through the consumption of undercooked meat and poor kitchen hygiene practices (Kaboudari et al., 2022; Manafi et al., 2020). The high prevalence of *Salmonella* infections is likely attributed to their high prevalence in meat processing environments (Pouillot et al., 2012). It is believed that in its natural state, this microbe exists mainly as biofilms, which can increase their survival rate. Bacterial cells residing in biofilms are more resistant to various stresses than their planktonic counterparts (Ferreira & Domingues, 2016). *Salmonella* spp. can form biofilms under well-defined *in vitro* conditions that have been studied extensively (Kaboudari et al., 2024a; Manafi et al., 2020). However, these *in vitro* conditions are very different from those encountered in the food processing environment. Hence, biofilms in the real food processing environment may exhibit different growth and/or survival behavior compared to those evaluated *in vitro*. Currently, due to technical challenges, there is a limited possibility to perform biofilm studies in the real meat processing environment. Therefore, meat extract and juices residues have been used to create a culture medium in the laboratory that simulates the real situation. Frozen raw meat exudates, also known as juice, have been identified as an important source of bacterial contamination on food processing surfaces (Kaboudari and Aliakbarlu, 2025). Meat juice (sterilized by filtration) has been used as a food-based model to simulate nutrient availability in meat processing studies (Li et al., 2017; Ferreira & Domingues, 2016). Most of these studies have been conducted on planktonic cultures, and the understanding of the interaction between juice and microbial biofilms is limited. Wang et al. (2007) found that *Salmonella* growth in a biofilm was slower when formed in chicken broth compared to *in vitro* culture medium of TSB. Thus, juice may be a complex nutrient matrix that can play different roles in biofilm formation and bacterial cell survival. Therefore, more comprehensive studies are needed to clarify the effects of meat juice and its storage conditions on *Salmonella* biofilm development and their survival in the biofilm.

Several food-related stresses, including storage temperature (refrigeration and freezing), acidity, osmotic pressure, and gentle heating of food, may affect the characteristics of bacteria in foods. These stressors often affect bacteria simultaneously. Studies on the impact of food-related stresses on the antibiotic resistance changes in foodborne pathogens are increasing (Al-Nabulsi et al., 2015; Wu et al., 2021; Uddin et al., 2019). Bacteria exhibit different responses and behaviors under stressful conditions such as temperature, osmotic stresses, and acidity. Changes in antibiotic susceptibility are one of these bacterial responses (Dawan & Ahn, 2022). Environmental stresses can induce antibiotic resistance in bacteria (Fang et al., 2016). McMahon et al. (2007) investigated the effect of different concentrations of salt (NaCl) on the antibiotic resistance of *Salmonella* Typhimurium, *Escherichia coli*, and *Staphylococcus aureus*. Their results showed that salt concentrations higher than 4.5% increased the antibiotic resistance of all bacteria tested.

Conclusion

The present study was a preliminary study to measure changes in antibiotic susceptibility as well as the development of antibiotic resistance. This study contributes to the development of resistance reduction strategies against *S.* Typhimurium and *L.* monocytogenes from the perspective of the relationship between biofilm-forming and antibiotic resistance. Further researches are needed in terms of the composition of meat juices and extracts, especially the residues of meat juices on the abiotic surface. Additional studies could focus on the interaction between specific components of meat juices (e.g., protein types and quorum sensing molecules) and bacterial biofilm formation. In this case, we may be in a position to develop a strategy targeting the precise components that contribute to biofilm growth and thus achieve efficient biofilm reduction. Furthermore, modification of surface materials applied in meat processing and preservation could be a potential research direction, given that changes in surface properties play a key role in cell attachment. Proper food storage and processing strategies can ultimately reduce the problem of antibiotic resistance in human and livestock communities, which can reduce economical losses and also increase the public health values.

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Conflicts of interest

The author declares that has no conflict of interest.

Disclaimer

The author declares that doesn't use AI based websites

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